The role of hydrology in determining the distribution patterns of invasive willows (*Salix*) and dominant native trees in the Lower River Murray (South Australia)

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( )

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*Name:*___________________ Susan L. Gehrig_____________________________

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To the Willow-tree

1. Thou art to all love lost the best,
The onely true plant found,
Wherewith young men and maids distrest,
And left of love, are crown'd.

2. When once the Lover's Rose is dead,
Or laid aside forlorne;
Then Willow-garlands 'bout the head,
Bedew'd with teares are worne.

3. When the Neglect, (the Lover's bane)
Poor Maids rewarded be
For their love lost; their onely gaine
Is but a Wreathe from thee.

4. And underneath thy cooling shade,
(When weary of the light)
The love-spent Youth, and love-sick Maid,
Come to weep out the night.

Robert Herrick

(1648)

Salix babylonica (Weeping Willow)

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Abstract

This thesis explores the hydrological factors that may contribute to the observed distribution patterns of invasive willows (*Salix*) and native trees (*Eucalyptus camaldulensis, E. largiflorens* and *Acacia stenophylla*) along the Lower River Murray (LRM) in southern Australia. An initial survey, establishing the diversity and flowering biology of *Salix* taxa was carried out to ascertain the extent of invasion, and the likelihood of hybridisation, which may accelerate invasion. *S. babylonica*, *S. fragilis*, *S.* × *chrysochoma* and *S.* × *rubens* occur in the study region, each represented by a single gender. None were present on floodplains, but the most dominant taxon, *S. babylonica*, occurred along the entire length of the main channel. No seed or seedlings were observed; hence reproduction is likely to be asexual.

More detailed survey work was then carried out to characterise the distribution patterns of the dominant *S. babylonica* and co-occurring natives (*Eucalyptus camaldulensis, E. largiflorens* and *Acacia stenophylla*) along a hydrologic gradient produced by the extensive weir system in the LRM. In weir pools, variation in daily water levels of weir pools is low (± 0.1 m) immediately upstream of the weir, but higher immediately downstream (0.2-1.0 m daily). The distribution of natives was uniform across weir pools, while *S. babylonica* was more abundant above weir structures, suggesting low tolerance to variable water regimes.

Hypotheses relating to the observed distribution patterns were then tested experimentally on juveniles of the *S. babylonica*, *E. camaldulensis* and *A. stenophylla*. The experiment was carried out in outdoor ponds using an orthogonal design, with four elevations in relation to water level (-25 cm, 0 cm +25 cm, + 50 cm) under each of three water regimes. Experimental water regimes manipulated the magnitude of daily water level changes (static, 0 m day^{-1}; moderate, ± 0.05 - 0.15 m day^{-1}; high, ± 0.2 -0.5 m day^{-1}) to mimic typical hydrological conditions across weir pools in the LRM. Final biomass and mean relative growth rates (*S. babylonica*, 0.0403 ± 0.002 g m^{-2} day^{-1}; *A. stenophylla*, 0.0249 ± 0.0017 g m^{-2} day^{-1}; *E. camaldulensis*, 0.0204 ± 0.0016g m^{-2} day^{-1}) of all 3 species were unaffected by water regimes (i.e. water fluctuations), but were affected by elevation. Survival of both *S. babylonica* and *A. stenophylla* was lowest at low elevations where inundation was high. At higher elevations (+25 cm, +50 cm) the RGR of *S. babylonica* juveniles was much higher than the native juveniles.

To test if the persistence of adults of each species along hydrologic gradients were associated with differing tolerances to water deficits and water use characteristics, *S. babylonica* and native species were examined under typical hydrological conditions in the field and during an unusual drawdown. *S. babylonica* occurring at the lowest elevations on riverbanks, had the least negative predawn

shoot water potential ($\psi_{predawn}$), followed by the natives, which were at higher elevations. *A. stenophylla* had the lowest stable carbon isotope ratio ($\delta^{13}C$) values (by 1.7 ‰) on the riverbank; suggesting more profligate water use than *S. babylonica* and *E. camaldulensis*. However, all riverbank trees had significantly less negative $\psi_{predawn}$ and lower $\delta^{13}C$ than native trees on floodplains, consistent with higher water availability on riverbanks. The position and stable oxygen isotope ratio ($\delta^{18}O$) values were consistent with riverbank *S. babylonica* sourcing their water directly from the river or from shallow soil-water sources (<0.25 m). In floodplain habitats, depth to water was > 2.5 m, and groundwater was 5 times more saline (4.97 ± 0.88 dS m^{-1}) than river-water. Native trees with deep roots, the ability to lower water potentials and alter water use efficiencies may be at an advantage in this habitat relative to *S. babylonica*.

Extreme low flows in the LRM, over a 6-month period, provided an opportunity to assess how *S. babylonica* and *E. camaldulensis* responded to a river-water drawdown. During the drawdown, river-water levels fell at a rate of ~2 – 2.5 mm day^{-1} and dropped to a minimum of 0.42 m below the designated pool level. *S. babylonica* and *E. camaldulensis* maintained high $\psi_{predawn}$ across the drawdown period, most likely because riverbank soil water availability was not limited; as depth to water table only decreased marginally (≤0.15 m) and soil water content and soil water potential were high (<1.1 MPa). However, an above average rainfall in February 2003 significantly increased soil water potential in the upper 0.25 m of the riverbank, which correlated with a significant increase in $\psi_{predawn}$ in *E. camaldulensis*, suggesting they were able to use shallow, precipitation derived soil-water sources whereas *S. babylonica* were not. Also under hot, dry conditions, *S. babylonica* had higher transpiration rates and lower instantaneous water use efficiencies than co-occurring *E. camaldulensis*. This suggests that *S. babylonica* may consume larger volumes of water per unit leaf area than natives, if access to water is maintained.

Dedications

For my grandmother, *Elsie 'Carney' Logue*

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I could not begin a study of willows without first consulting the extensive work done by Kurt Cremer. He was renowned for highlighting the magnitude and impact of willow infestation in Australian streams and rivers. We met at the Dunkeld Arboretum, Victoria where I spent days learning firsthand all the intricacies of willow field identification. Kurt's passion originally inspired many aspects of this thesis and his ongoing updates, advice and encouragement was invaluable. Unfortunately Kurt passed away on the 2nd June, 2005, and I hope this work honours him.

Nor could I begin a study on the Lower River Murray without consulting the 'River Legend' - Jack Seekamp. Jack was born and bred on the Murray River, so not only did he remember a time before the weirs were built, but he also had firsthand experience of the system as a soil scientist and hydrologist. Whenever I was up in Renmark he always made time to catch up and until his passing on February 11th, 2007, he never failed to let me know what those 'pesky willows' were up to. I miss my raconteur of the river.

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And Jarrod Stebhens, who was sadly taken from us on August 24th, 2005. "Wherever I travel I think of you and remember your passion for life, for people, for science & learning and most of all – the sea. I understand there is no better way to leave this world than doing what you love, but I still wish you were here to join us when we get together…calling out 'Susie' from across the bar and dashing over to give me one of your big hugs."

Photo by Maya Linnell

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Chapter 1

General Introduction

1.1 Overview

Willows, belonging to the genus *Salix*, are dicotyledonous flowering shrubs/trees with unisex flowers, often borne in catkins (Newsholme 1992). The genus *Salix* includes some 300 species and could almost be considered cosmopolitan, except there are no taxa native to Australasia (see Figure 1.1). Many *Salix* taxa are now invaders in southern hemisphere freshwater environments (Daehler 1998) such as southern Australia, New Zealand and South Africa (Csurhes and Edwards 1998, Henderson 1991, Lester *et al.* 1994, Pidgeon and Cairns 1981). Since the late 19th century over 100 *Salix* taxa were introduced to Australia and over 30 of these are now naturalised (Cremer 1995, Ladson 1997, Willow Strategic Plan 2001). These *Salix* taxa are clearly successful invaders, and this thesis examines aspects of their biology that may contribute to this success.

Invasiveness can be defined as the ability to establish, reproduce and disperse within an ecosystem. Invasive plant species may possess one or a combination of biological attributes that characterise their invasive potential. The most common weeds in Australia are usually generalist and opportunistic; rather than requiring specific niches or special habitat requirements. Major weeds share similar attributes such as: a) high seed production, b) rapid vegetative spread, c) long-lived seeds, d) staggered germination, e) competitive growth, and f) long distance seed dispersal (Weiss and Iaconis 2002). Several hypotheses were postulated to explain the success of exotic plant invaders (see Hierro *et al.* 2005 and Table 1).

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Figure 1.1. Global regions where *Salix* taxa are endemic (shaded), compiled after Newsholme (1992). No taxa are native to Australasia.

Table 1.1 Description of the hypotheses that explain the success of plant invaders as reviewed by Hierro *et al.* (2005).

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Research into each of these hypotheses continues to demonstrate the complexities surrounding the factors involved in determining exotic plant invasion success. For example a disturbance event may modify the abiotic characteristics of the invaded habitat (Hypothesis: #5) in such a way that it is now more compatible with the biotic characteristics of the introduced species, in turn providing an advantage over indigenous species (Hypotheses: # 2, 4, 6, 7) (Richardson 2004). Do many exotics therefore actually cause the decline of natives or simply proliferate as a result of habitat alteration (Gurevitch and Padilla 2004)? Also, anthropogenic activities (e.g. deforestation, agriculture, water diversion, pollution, etc.) often alter the composition of biological communities (Hooper *et al.* 2005) making them more susceptible to invasion. Another frustration is that much of the information on the ecology of invasions in different systems is largely anecdotal. Where studies are conducted they are often biased; failing to integrate invader traits and environmental characteristics or undertake studies that compare native species characteristics with those of the invaders (Cannas *et al.* 2003).

Some *Salix* taxa have become naturalised along the Lower River Murray (LRM) within South Australia (SA). Their presence is correlated with a supposed decline in dominant native trees like *Eucalyptus camaldulensis*, *E. largiflorens* and *Acacia stenophylla*. Yet is it not clear whether *Salix* taxa are actively displacing these natives or merely occupying areas where they have declined. In order to understand the invasive potential of *Salix* taxa this review examines current information about their biotic and abiotic requirements for dispersal, establishment, growth, survival and reproduction and also assesses their environmental impacts in invaded habitats. This information is then synthesised to propose factors and mechanisms that may be influencing the arrival and survival of *Salix* taxa on the LRM.

1.2 Literature Review

1.2.1 Taxonomy

Willows are members of the Salicaceae, a large family that includes poplars, osiers and sallows. *Salix* is the largest genus (> 300 species) in the Salicaceae family (Azuma *et al.* 2000, Brinkman 1974, Newsholme 1992) and fossil leaf fragments and pollen grains (dating from 70 to 135 m.y.a) have exposed an ancient lineage, with two dwarf willows (*S. reticulata* and *S. herbacea*) being some of the earliest known flowering plants ever recorded (Newsholme 1992). When Linneaus first described the family he divided it into 2 genera: *Salix* (willows, osiers and sallows) and *Populus* (poplars), but in the last century the phylogeny of the family had been not been resolved and another two genera, *Chosenia* and *Toisusu* are often included (Azuma *et al.* 2000). *Salix* is divided into three subgenera: the true willows (*Salix*), osiers and sallows (*Caprisalix*) and dwarf, creeping, Arctic or mountain shrub willows (*Chamaetia*), but classification of all the species within each subgenera, has remained uncertain due to their remarkable morphological and genetic diversity (Newsholme 1992). In a horticultural context, the species may then be subdivided into cultivars (e.g. *S. matsudana* 'Tortuosa') and horticultural and wide varieties (e.g. *S. alba* var. *vitellina*) may exist, adding to the taxonomic confusion (Cremer 1995, Newsholme 1992). The term 'taxa' is used here as a collective term to denote any or all-taxonomic divisions below genus (i.e. species, subspecies, cultivars, variety, hybrids). *Salix* therefore embraces more than 500 taxa (Newsholme 1992).

1.2.2 Development and Reproduction

1.2.2.1 Asexual Reproduction

Asexual reproduction is common in *Salix*; occurring via layering and fragmentation (or suckering in the case of *S. exigua*) (Beismann *et al.* 2000, Rood *et al.* 1994, Shafroth *et al.* 1994). Numerous willow species have fragile stem bases (e.g. *S. fragilis*) that fragment under the slightest mechanical stress, such as that imposed by water-currents, wind and floods, providing a significant dispersal mechanism (Beismann *et al.* 2000), although the rate of vegetative spread is slow (~ 3 km per 10 yrs) (Ladson 1997). Investigations into the reproductive phenology of invasive *S.* x *rubens* in Canada has revealed that clonal growth makes a significant contribution to their population structure (Shafroth *et al.* 1994). Many *Salix* taxa are estimated to live for up to 50 – 80 years (Wolf *et al.* 2007); however some taxa are able to form stands by layering (when an intact branch develops roots as the result of contact with soil or other media), and this can make aging difficult.

1.2.2.2 Reproductive Phenology

Willows are chiefly deciduous trees/shrubs and depending on the extent of inter- and/or intra-specific variation, bud break typically occurs in early spring and usually coincides with leaf development. Most willows are single-sexed and produce masses of catkins, dense cylindrical clusters of flowers, usually without petals, in early spring (Newsholme 1992). These flowers are primarily bee and insect-pollinated (e.g. Diptera, Hymenoptera (bees and wasps) and Coleptera), but wind pollination may occur to a limited extent (Fox 1992).

Most *Salix* reach reproductive maturity at ~3 – 8 years (Newsholme 1992); producing vast quantities of small seeds (< 1 mm long) in spring. Seeds bear distinctive tufts of long, cotton-like hairs that facilitate dispersal over great distances (>100 km) by wind or relatively shorter distances by water (Brinkman 1974, Cremer *et al.* 1995, Newsholme 1992). The rate of spread by seed is estimated to be five to ten fold higher (e.g. up to 3.5 km yr^{-1}) than vegetative spread (Cremer, K., *pers. comm.*). Seed dormancy has only been recorded in a few dwarf willow species (Densmore and Zasada 1983) as cited in Newsholme (1992), hence as a general rule, willows create transient seedbanks following seed release in late spring and early summer (Cremer *et al.* 1995, Roelle *et al.* 2001, Thompson and Grime 1979). *Salix* seeds usually germinate within 12 to 48 hours once they have arrived at a site (Brinkman 1974, Cremer *et al.* 1995).

1.2.2.3 Hybridisation

Salix hybrids are produced naturally or artificially through cross-pollination, but hybridisation is often constrained in their native ranges. Hybrids in Europe constitute less than five per cent of the number of native *Salix* populations (Newsholme 1992, Mosseller 1990) because of barriers to interbreeding. Reproductive barriers may be pre-zygotic (e.g. differences in flowering phenology or spatial preferences) or post-zygotic (e.g. seedling inviability, inferior growth performance and reduced fertility in the F_1 hybrid progeny (Mosseller 1990)). Most *Salix* hybrids are fertile and can cross with other hybrids or pure species making field identification very difficult (Cremer 1995, Cremer *et al.* 1995, Newsholme 1992), although some hybrids are consistent in terms of their structure and appearance and are frequently only clones of one sex (Newsholme 1992).

1.2.3 Habitat and responses to abiotic factors

Space, light, nutrients and water are considered fundamental resources for plant growth and performance. Limitation in any of these resources can induce stress and impede productivity (Grime 2001). In freshwater environments, resource availability can by highly dynamic across spatial and temporal scales. Plants may access water from surface water, precipitation, soil-water and/or groundwater, all of which can vary because of seasonality, distance from the river and competition from other plants.

1.2.3.1 Space, light and nutrients

Successful seedling establishment of *Salix* taxa is often correlated with the availability of suitable sites like bare, wet, flat river edges or gravel flats around sandbars, promontories and islands (Cremer *et al.* 1995, Roelle *et al.* 2001, Rood and Mahoney 2000). Substrate texture may be an important factor influencing *Salix* establishment as experimental trials found that the growth and survival of the native European *Salix elaeagnos* was greater in sand than in gravel (Francis *et al.* 2005), although in field trials their establishment was greater in patches containing high amounts of clay and organic matter and low proportions of sand to gravel (Francis and Gurnell 2006). The influence of substrate texture may be influenced by other factors though, as a field study into the growth and survival patterns in native North American *Salix* spp. found that soil texture was not as important a variable as neighbour density (Sher *et al.* 2002).

Perhaps neighbour density is detrimental to *Salix* establishment because it not only limits space availability, but also limits light availability, since *Salix* are generally considered to be light demanding (Newsholme 1992). However an experimental investigation into the effects of shading on *S. matsudana* seedlings found that although establishment was greatly decreased in fully shaded treatments, plants can respond to partial shading by modifying their physiology and canopy architecture (He and Dong 2003).

Salix are also considered to be nutrient demanding (Newsholme 1992). Ericsson (1981) found that high nutrient additions (e.g. N, K, P, Ca and Mg) favoured leaf development in *S. aquatica*, *S. fragilis* and *S. viminalis*, whereas low nutrient additions stimulated root growth. In a field trial, the growth of *S. sericea* increased with nutrient additions, but only in wet soils and there were no significant improvement in growth under dry conditions (Lower and Orians 2004).

1.2.3.2 Water

Water is often one of the main resources affecting the growth of plants (BenDavid-Novak and Schick 1997, Marquez *et al.* 1997, Zavala *et al.* 2000). In riverine environments water may be available from a variety of sources; from surface river-water, precipitation, and soil water to groundwater. Inter and intra-specific biotic differences in rooting patterns may mean some individuals and/or species are more reliant on surface-water and/or precipitation-derived soil-water sources than groundwater. Growth of riparian vegetation will depend upon factors like: water regimes, which vary in time and space (Rea and Ganf 1994, Poff *et al.* 1997), water availability (Loewenstein and Pallardy 1998), the quality of the water source (e.g. salinity and contamination (Kozlowski 1997)) and the specific water requirements of the plant across its ontogeny (i.e. for recruitment, establishment, growth, optimal performance and survival) (ca. Stromberg and Patten 1996, Scott *et al.* 2000)).

1.2.3.2.1 Water regime

Surface water levels in riverine environments are rarely static and exert substantial influence on riparian vegetation growth and distribution (Walker *et al.* 1994a, Poff *et al.* 1997, Blanch *et al.* 2000). Often the term water regime (Brownlow *et al.* 1994, Rea and Ganf 1994, Blanch *et al.* 1999) is used to describe the patterns of water-level variations in time and space. It incorporates variables, such as the frequency, timing and duration of inundation and exposure (i.e. absence of surface water), the depth of inundation and the rate of water level fluctuations (Rea and Ganf 1994, Poff *et al.* 1997). These primary variables also secondarily influence a variety of chemical and physical properties such as soil texture and structure, nutrient availability, pH and salinity (Poff *et al.* 1997). Because water regime influences these and other environmental factors it could be considered a master variable highly correlated with the richness, abundance and diversity of plants in riparian environments (Stromberg 1993). Water regimes within mesic riverine environments are relatively consistent across seasonal, annual and inter-annual time scales in terms of flow frequency and timing, however the timing and duration of floods may still be highly unpredictable (Blom and Voesenek 1996). In contrast xeric riverine environments, like the LRM, are typically erratic in terms of their flooding frequency, duration and magnitude (Harris and Gehrke 1997, Thoms *et al.* 2000).

To maximise reproductive success, the reproductive phenologies of many riparian plants are often attuned to the water regimes of their environments (Grace 1993, Drezner *et al.* 2001, Pettit and Froend 2001). Within the Salicaceae, regeneration is often adapted to regular disturbance by flooding. In many *Populu*s and *Salix* spp., native to Canada and USA, flowering and seed production coincides with spring floods following snow-melts. These floods tend to scour away riverbanks leaving freshly exposed substrate for their wind dispersed seeds to colonise. Since their seeds are only short-lived these bare beds often provide optimal conditions (e.g. ample space, light and moisture) for rapid germination (Busch and Smith 1995, Scott *et al.* 1997, Glenn *et al.* 1998, Mahoney and Rood 1998, Stromberg 1998, Cooper *et al.* 1999, Rood *et al.* 1999, Rood and Mahoney 2000, Kalischuk *et al.* 2001, Karrenberg *et al*. 2002).

However these dynamic, exposed riverine sediments can also be precarious environments for seedling establishment. Because of their shallow, developing root systems, juveniles are often dependent upon surface water and shallow precipitation-derived soil water sources for the first few growing seasons (Shafroth *et al.* 2000) and rapidly receding water-levels following floods may prevent successful establishment. A number of investigations have found that many *Salix* taxa are dependent upon saturated conditions or slow water drawdown rates (1 - 2 cm day^{-1}) following flood recession, so that developing roots can maintain access to sufficient water for growth (Mahoney and Rood 1991, Cooper *et al.* 2001, Horton and Clark 2001). These water requirements in the establishment phase may be why they are often found low on river to floodplain elevation gradients, where soil moisture conditions are high (Mahoney and Rood 1991, Francis and Gurnell 2006). However, rapid drawdown rates in the field may be mediated by the other environmental factors like soil texture and/or structural properties, inter- and/or intra-specific competition for water and the microclimatic characteristics of the site. Seedling mortality may be increased at sites where the soil texture is coarser (e.g. sand, gravel) and does not have the same water holding capacities that are typical of finer grained soils (e.g. clays, silty loams) (Shafroth *et al.* 2000).

The position of seedlings along river-floodplain elevation gradients also influences the extent of their exposure to flooding and inundation within the first few growing seasons. In

Australia, mortality was highest in establishing seedlings of invasive *S. nigra* at lower elevations of a reservoir because they were subjected to greater degrees of inundation in their first few growing seasons (Stokes 2008). Yet studies on other *Salix* taxa suggest they are quite tolerant of flooding. In some instances some flooding may be preferred to no flooding at all. In particular Ohmann *et al.* (1990) found that biomass production of establishing *S. bebbiana*, *S. discolor*, *S. interior*, and *S. rigida* was optimal with a flooding regime of up to 60 days top-flooding in the first few growing seasons.

Floods can drive sediment deposition and erosion so that cohorts of juveniles established at lower elevations may be smothered by sediment or scoured away (Rood *et al.* 1998). It has been reported that *Salix* seedlings growing at low elevations along main channels in the southwestern, USA have strong lateral root development, which possibly protects them from flood scour (Horton *et al.* 2001b). Floods can transform the physical properties of soil causing colloidal swelling, break down of large soil aggregates, decreasing soil temperatures, restricting gas exchange and depleting oxygen concentrations (Ponnamperuma 1984, Kozlowski 1997). Extensive flooding may also decrease nutrient availability and cause soil redox potentials (E_h) to become critically negative (i.e. –75 and –150 mV) leading to increases in phytotoxins (Flessa 1994, Blom and Voesenek 1996). Many *Salix* taxa adapt to flooding and/or inundation by producing adventitious roots (Cardson 1938, Krasny *et al.* 1988) that enhance gas exchange (de Simone *et al.* 2002). Some *Salix* taxa (e.g. *S. viminalis, S. cinerea, S. alba*) (Krasny *et al.* 1998) are apparently capable of oxidising their rhizospheres via convective flow to generate positive soil E_h (Armstrong 1987, Armstrong and Armstrong 1991, Grosse *et al.* 1991, Grosse *et al.* 1996).

During complete submergence photosynthesis might decline or even cease because of decreased light and CO_2 concentration. Some *Rumex* spp. survive deep, prolonged floods by elevating leaves above the water column on elongate petioles (Blom and Voesenek 1996). Other submerged aquatics like *Potomogeton* spp. and *Vallisneria australis* can maximise photosynthetic leaf areas for light capture by adjusting canopy architecture (Blanch *et al.* 1998, Cenzato and Ganf 2001). However there is no published data on whether woody species like *Salix* taxa are able to adjust canopy architecture in response to flooding and/or inundation, although they can do so in response to partial shading (He and Dong 2003). It is more likely that CO_2 concentration is the limiting factor for emergent species, during complete submergence.

Perhaps because of the unpredictability of water regime and its influence on other environmental factors asexual reproduction tends to dominate in aquatic systems (Grace 1993). Although successful establishment following the colonisation by asexual propagules also depends upon the availability and suitability of recruitment sites (Grace 1993, Delgado *et al.* 2001, Drezner *et al.* 2001) asexual reproduction still confers many advantages. Propagules are often dispersed via water therefore they have advantageous properties such as propagule buoyancy, dormancy and longevity to enhance dispersal distances (Delgado *et al.* 2001). In some instances propagules may be continuously produced, and many *Salix* taxa possess fragile stem bases that break under slight mechanical stress (Beismann *et al.* 2000). Propagules can also develop at rapid rates following colonisation because of their greater carbohydrate reserves compared with seeds (Grace 1993).

1.2.3.2.2 Water availability

The availability of surface-water usually declines along river to floodplain gradients, but the extent of this decline is strongly influenced by seasonal and/or climatic factors as well as the water regime of the system. Water stress in riparian environments can be triggered during times of low surface water flow and low precipitation events. Water stress may also occur during prolonged floods where water availability is restricted when soil conditions becoming anoxic, causing stomatal closure in certain species (Pezeshki 2001) . Large inter- and/or intra-annual variations in precipitation and surface water flow in xeric environments mean riparian vegetation in these habitats is exposed to more dry episodes than riparian plants in mesic environments (Horton *et al.* 2001b).

It is believed that many *Salix* taxa are sensitive to water stress induced by low river flow, low precipitation or groundwater decline. In their native range, individual trees of *S. nigra* and *S. gooddingii* - exposed to water deficits - have more negative ψ_{shoot} and lower rates of leaf gas exchange than well watered plants (Busch and Smith 1995, Horton *et al.* 2001, Loewenstein and Pallardy 1998, Shafroth *et al.* 2000). Water stress may also induce morphological adjustments via leaf abscission, declines in leaf area and/or canopy dieback (Busch and Smith 1995, Loewenstein and Pallardy 1998, Horton *et al.* 2001b). Lowenstein and Pallardy (1998) found that leaf abscission can occur in *S. nigra* at reasonably mild water stress levels of predawn shoot water potentials > -0.5 MPa).

1.2.3.2.3 Water source and quality

As the availability of surface-water declines along river to floodplain gradients the availability of other water sources such as precipitation derived soil-water and groundwater may become increasingly important for riparian vegetation (Busch *et al.* 1992, Kolb *et al.* 1997, Snyder and Williams 2000). Yet the use of these water sources will be governed by other factors such as the ability of an individual and/or species to access the water source and the reliability and/or quality of the water source (Stromberg and Patten 1996).

Research into the water relations of *Populus-Salix* riparian forests in North America found that neither species were capable of opportunistically using precipitation derived soil-water. Instead they required uninterrupted access to continually saturated zones like groundwater, surface-water or water drawn into the capillary fringe, restricting them to the stream's edge or where the water-table was shallow (Snyder and Williams 2000, Horton *et al.* 2001b). Similarly, streamside willows (*S. monticola*) in the Rocky Mountains, sourced approximately three quarters of their water directly from streams (Alstad *et al.* 1999) despite the presence of groundwater, however unlike the *Populus-Salix* spp. mentioned above they did not utilise groundwater sources at all, but used summer precipitation derived soil-water instead.

This may be a reflection of the amount of water they need. In a review by Wullschleger *et al.* (1998) quantitative data on water use rates of 67 trees species (across 25 genera) were analysed. They found that 90% of trees had water use rates that ranged from 10 – 200 kg day^{-1}. In their native range *S. fragilis* trees were found to consume up to 103 kg day^{-1} (see Ceremak *et al.* 1984) and *S. matsudana* up to 106 kg day^{-1} (see Edwards 1986) which makes them relatively moderate consumers of water. However it is difficult to compare quantatitve data on tree water use, because generalisations about water consumption measurements are often dependent upon site factors (e.g. climate) or where measurements were taken (e.g. sun-exposed (i.e. higher water consumption) versus shaded branches (i.e. lower water consumption) (Ceremak *et al.* 1984). The quantity of water used will also depend on age. For instance, in the American southwest water use rates were consistently higher in younger *Salix* spp. stands as opposed to the larger, older stands on the outer margins of the forest (Schaeffer *et al.* 2000). In this instance the reliability of water along the primary channel and their age class may well be primary factors influencing their higher water consumption rates (Dawson and Ehleringer 1993, Thorburn and Walker 1994).

Water quality may also significantly influence establishment. Perhaps surprisingly, invasive willows like *S. nigra* and *S. cinerea* in eastern Australia have successfully invaded brackish environments where water-sources are limited and saline (Cremer 1995). Several North American *Salix* taxa (e.g. *S. alba* (and various cultivars), *S. exigua* and *S. nigra*) show a moderate (up to 4 - 6 dS m^{-1}) tolerance to salinity (Swift 1997). Similarly a field survey of invasive *S. babylonica* and *S. fragilis* in Australia showed mature trees were growing in areas where soil water conductivities were up to 11.4 dS m^{-1} (Kennedy *et al.* 2003), however, glasshouse trials found that growth of *S. babylonica* and *S. fragilis* seedlings was severely limited when exposed to soil conductivities between 3 - 7 dS m^{-1}. Thus, while in general *Salix* taxa are regarded as intolerant of salinity, evidence suggests that there is huge variability within the genera and that tolerance to salinity can differ in the field.

1.2.4 Biotic factors influencing Salix

As previously mentioned, many *Salix* taxa are invasive (Cremer *et al.* 1995, Henderson 1992, Lester *et al.* 1994, Walker 2001), having several of the attributes associated with the 'ideal' weed, such as rapid growth, early reproduction, extensive propagule formation, and an adaptable, perennial lifestyle (Grime 1979, Newsome and Noble 1986).

1.2.4.1 Grazing and pathogens

Salix species and associated hybrids are susceptible to pathogens and several grazing enemies in their home ranges such as fungal rusts (e.g. *Melampsora* spp.), leaf chewing beetles (e.g. *Popillia japonica*), spider mites (*Tetranychus* sp.) and leaf mining caterpillars (*Phyllocnistis* spp.) (Orians and Floyd 1997, Pei *et al.* 1999, Sagliocco and Bruzzese 2001). *Salix* in Australia have acquired some diseases since their introduction (Cremer 2003) such as leaf rust (*Melampsora* spp.). Cattle will also graze on *Salix* taxa, indeed *S. babylonica* are recommended as a complementary food supplement for livestock in temperate areas like Bhutan because of the moderate protein content of their leaves (~10 – 25%), as expressed on a dry weight basis (Roder 1992). In recent years, outbreaks of a natural predator of *Salix* taxa, the willow sawfly *Nematus oligospilus* (Hymenoptera: Tenthredinae) have occurred in Australia (http://www.daff.gov.au). Since they were not deliberately introduced into Australia as a means of biological control their method of arrival is unclear, but they are now widespread and cannot be eradicated. Sawfly larvae feed on leaves and large populations can defoliate trees in a single season. Several defoliation events, over a few growing seasons can lead to tree death, although susceptibility will depend on tree age and certain *Salix* taxa are more susceptible to attack than others (Bruzzese & McFadyen 2006, Ede 2006).

1.2.5 Willows as Invaders

Salix taxa are now invaders in many southern hemisphere freshwater environments (Daehler 1998) such as southern Australia, New Zealand and South Africa (Csurhes and Edwards 1998, Henderson 1991, Lester *et al.* 1994, Pidgeon and Cairns 1981). In 1999, all willows (except *S. babylonica*, *S.* x *calodendron* and *S.* x *reichardtii*) were listed as one of Australia's Twenty Weeds of National Significance (WoNS; http://www.weeds.org.au). The exclusion of *S. babylonica*, *S.* x *calodendron* and *S* x *reichardtii* has been a matter of contention as there were naturalised populations in Australia at the time the list was drafted, but the aesthetic value of *S. babylonica* is often held in high regard by the Australian community (Holland-Clift and Steel 2008).

Alterations to the composition and structure of riparian vegetation can modify aquatic processes because riparian vegetation provides habitat, shelter and food resources for native fauna, influences the quantity and composition of organic inputs and the nutrient, sedimentation, temperature and light regimes of watercourses (Bunn *et al.* 1993, Bunn *et al.* 1999). Invasive *Salix* taxa now form a significant component of the riparian vegetation along watercourses within Australia (Cremer *et al.* 1995) and have transformed the landscape (Table 1.2).

Table 1.2 Generalised traits of native Australian sclerophyllous trees and deciduous trees that can influence aquatic processes in riparian environments

Evergreen	**Deciduous**
Long-lasting wood that produces snags and many hollows	Rapidly decomposing wood that does not produce snags and hollows
Often several long flowering events per year	One seasonal, short flowering event per year
Sparse canopy	Dense canopy (in most instances)
Shed many branches and bark across year	Shed a small number of branches and bark across a year

Salix taxa were often deliberately planted in Australia along streams and rivers to stabilise banks and prevent erosion (Perkins 1903), because it was wrongly believed that native trees (e.g. *Eucalyptus* spp. and *Acacia* spp.) destabilised banks due to their overhanging weight (Abernethy and Rutherford 2000). This practice is now discouraged as *Salix* tend to produce mono-specific stands with large masses of fine, lateral root mats that trap silt, preventing the formation of undercut banks and reducing habitat for platypus, tortoises and many species of native fish (Ladson 1997, Serena and Williams 1997). In addition, river reaches lined with native trees (e.g. *Eucalyptus* spp. and *Casuarina* spp.) support a greater abundance and diversity of woodland birds than *Salix*- lined streams (*S.* × *rubens*) (Clift *et al.* 2004). Native trees often offer multiple and longer flowering events providing continuous food sources for nectar feeding insects, birds and marsupials (Ladson 1997). Mature *Salix* have relatively softwood compared with natives so they do not form the hollows that many native marsupials and birds need for shelter. Nesting sites (Ladson 1997) and habitats, food and spawning sites for in-stream fauna are also reduced (Ladson 1997) because snags produced by *Salix* decompose at a faster rate than those produced by hardwood natives (Jensen 1996).

Most Australian trees offer valuable habitat for native invertebrates such as spiders and insects underneath their bark, whereas *Salix* do not (Ladson 1997). Greenwood *et al.* (2004) found that sections of the Tarago River in southeastern Australia that were invaded by *S.* × *rubens* had significantly lower diversity and abundance of canopy arthropods than native lined sections. In New Zealand *Salix*-lined reaches along streams and rivers were found to have significantly lower macroinvertebrate abundance and biomass compared with native lined reaches, especially in summer and autumn (Lester *et al.* 1994).

The deciduous nature of *Salix* taxa means that leaf drop occurs in one large peak in autumn unlike Australian natives where leaf abscission occurs intermittently across the year with a slight peak in the summer months (Read and Barmuta 1999). *Salix* leaves breakdown in half the time that many native leaves do (Schulze and Walker 1997) and do not support the same assemblages of biofilms (i.e. microorganism assemblages of bacteria, fungi and algae) (Schulze and Walker 1997). Compounds such as phenolics and tannins in *Salix* leaves (Binns *et al.* 1968) are also reported to be toxic to certain native fish species (Gehrke *et al.* 1993). Research highlights that *S. borealis* and *S. phylicifolia* are capable of accumulating toxic elements (e.g. Cd and Zn) in their shoots and leaves (Stoltz and Greger 2002). The reduced temporal availability of *Salix* leaves, reduced biofilm abundance and composition and presence of harmful compounds leads to poorer macroinvertebrate abundance and biodiversity across the year (Pidgeon and Cairns 1981).

Many *Salix* taxa produce dense canopies when mature, which significantly reduce the availability of light (≤ 80%) to banks and watercourses (Lester *et al.* 1994). It is believed that heavy shading created by willow canopies is not conducive to the germination and establishment requirements of native vegetation (Cremer *et al.* 1995). Large *Salix* canopies can also decrease water temperatures, especially during the summer months (Lester *et al.* 1994).

Large amounts of *Salix* litter mass enter watercourses following autumn senescence and *Salix* leaves contain about half the amount of structural tissue (e.g. lignin and cellulose) as leaves from Australian native trees and macrophytes, so they have very rapid decomposition rates (Janssen and Walker 1999). This rapid breakdown may elevate nutrient levels and possibly accelerate primary production processes and lead to eutrophication or nuisance plant growth (Bunn *et al.* 1999). In Tasmania, *Salix* taxa lined streams had significantly lower dissolved oxygen levels (i.e. 7.3 mg L^{-1} DO) than streams lined with *Eucalyptus* and *Acacia* spp. (8.3 mg L^{-1} DO), although values did not fall into the critical range (i.e. below 60% saturation) (Read and Barmuta 1999).

Salix trees may also form dense root mats that alter channel morphology. Along the Snowy River in New South Wales willow-lined river reaches are often shallower and wider than native-lined reaches (Erksine *et al.* 1999). At times of high flow the river is forced to move around the dense stands of willows, exacerbating the effects of flood scour (Ladson 1997).

1.2.6 Brief description of the Lower River Murray

The Murray-Darling Basin (MDB) is Australia's largest river catchment in the interior of southeastern Australia. The name of the Basin is derived from its two major rivers, namely: Murray and Darling Rivers. Since colonisation, the MDB bears the weight of regulation practices and water resource development since it embodies one of the most important agriculatural areas within Australia (Norris *et al.* 2001). The Lower River Murray, where this study was conducted, refers to the 830-km stretch of the River Murray below the Darling Junction (Fig. 1.2). In ecological terms, the LRM is considered a distinct 'environmental unit' when compared with its parent rivers (i.e. upper-middle Murray and Darling River). It has no significant tributaries and hydrologic behaviour is governed by flows from the upper to middle Murray (note that inflows from the Darling are highly variable, but usually low). The LRM is regulated by a weir system with 10 locks that was constructed between 1922 –1937 to aid year-round riverboat navigation. These locked weirs are primarily operated as impoundment weirs for irrigation purposes and as a result of their construction the LRM now tends to resemble a series of cascading weir pools (Walker 2001).

NOTE:
This figure is included on page 39 of the print copy of
the thesis held in the University of Adelaide Library.

Figure 1.2 Modified map of the River Murray, illustrating the Murray-Darling Junction and lock, weir, dam and barrage system (Image sourced: http://www.murrayriver.com.au/).

Most of the LRM, from Lock 6 (at Renmark) to Lock 1 (at Blanchetown), runs within the state of South Australia (see Fig. 1.3). Climate in this region is defined as semi-arid with an annual mean precipitation ranging from 200-500 mm, while evaporation may be 3 – 6 times higher (i.e. 1200-1500 mm yr^{-1}) (Nicholls 2004). Regulation has meant that although the seasonal frequency of natural flows (winter-spring maximums) has not changed, the flood regime has been altered so that the magnitudes of the seasonal floods have diminished; limiting the frequency and extent of floodplain inundation (Maheshwari *et al.* 1995).

Physically the LRM is typified by low bed slope, sinuosity and power. At a landscape level, the river channel is characterised by four distinct sections: *Valley*, *Gorge*, *Swamplands* and *Lakes* (Walker 2001) (Fig. 1.3). The *Valley* runs from the intersection of the state borders of New South Wales, Victoria and South Australia to the township of Overland Corner (including Locks 10 – 3). It meanders over broad floodplains (5 – 20 km) and includes many riparian wetlands, anabranches and billabongs. In the *Gorge,* from Overland Corner to Mannum (Locks 2 and 1 inclusive) the river flows through a narrow limestone gorge (30 m); where wetland diversity is reduced compared with the *Valley*. Floodplains in *Valley* and *Gorge* zones are affected by poor linkages to the river channel, over-grazing and the removal of woody debris from floodplains and many wetlands upstream of locks are permanently inundated by weir pools (Norris *et al*. 2001). The *Swamplands* section, from Mannum to Wellington, is flanked by old swamp land that has now been reclaimed for crops and pasture. The floodplains within this zone are completely disconnected from the river as a result of the man-made levee banks (Norris *et al.* 2001). From Wellington the LRM enters the *Lake* section encompassing Lakes Alexandrina and Albert). Barrages are installed at the mouth to contain the water before it enters the sea near Goolwa (Walker 2001).

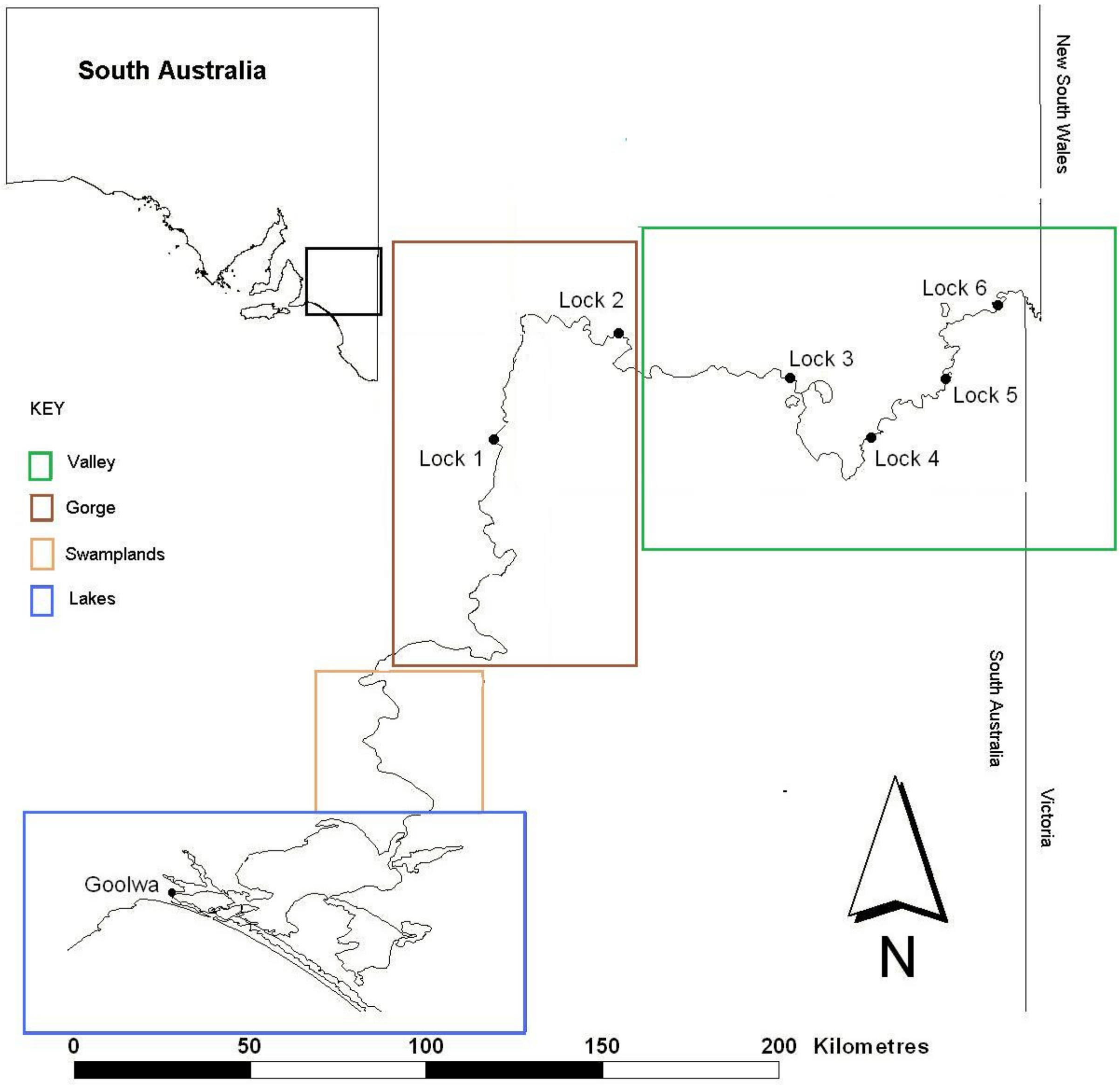

Figure 1.3. Schematic diagram showing the landscape level characteristics of the Lower River Murray within South Australia: *Valley*, *Gorge*, *Swamplands* and *Lakes* (as described in the text).

Prior to regulation, LRM riverbanks were mostly bare, with the exception of a *Eucalyptus camaldulensis* over-storey and an understory of herbaceous annuals/ephemerals (Walker 2001). Historical photographs of the LRM suggest that current day riverbank community structure is most likely an artefact of weir construction (Walker *et al.* 1994, Blanch *et al.* 2000). While *E. camaldulensis* are still an iconic feature along riverbanks there is now a mixed community of emergent (e.g. *Phragmites australis, Typha domingensis, Cyperus gymnocaulos*) and submerged macrophytes (e.g. *Potamogeton crispus, Vallisneria australis*) (Roberts and Ludwig 1991, Walker 1994, Blanch *et al.* 2000). On the floodplains, populations of two dominant native trees, *E. camaldulensis* and *E. largiflorens*, are declining and surviving trees are showing signs of thinning crowns, changes in leaf colour and size, changes in bark colour and atypical leaf abscission which is attributed to both water stress and increasing soil salinity (MDBC 2003). In the *Swamplands*, downstream of the township of Mannum, willows (*S. babylonica* and *S. fragilis*) are a dominant, continuous feature (Margules and Partners 1990, Kennedy 2000). Upstream of Mannum, in the *Gorge* and *Valley* regions, the distribution of *Salix* taxa appears discontinuous (Walker 2001). Hence, the LRM was deemed a suitable site because of these variable distribution patterns in *Salix.*

1.2.7 Threats to the LRM

One of the major concerns in the MDB is believed to be salinity. The MDB is a naturally saline environment as a result of weathering of rocks, groundwater sources and salt deposition over thousands of years by precipitation, but salinity has been exacerbated by human activities such as the installation of drainage flows from irrigation areas, rising groundwater levels due to irrigation practices and inappropriately positioned evaporation basins (MDBMC 1999). In the late 1970's salinity levels within the LRM, in South

Australia, were averaging 0.5 g L^{-1} (or 0.78 EC), with a mean annual salt-increment of 0.007 g L^{-1} yr^{-1} (Mackay *et al.* 1988). In-stream salinity in the *Valley* and *Gorge* zones are now considered to be improving (see MDBMC 1999 and MDBMC 2001), as a result of salt interception schemes and water diversion practices, but rising floodplain groundwater and continued upstream activities are again raising concern that salinity will begin to rise to unacceptable levels (> 800 EC by World Health Organisation standards) in the next 50 years (Jolly *et al*. 2001). Similarly, in 2001, 20000 ha of land in the LRM were affected by dryland salinity, but another 20000 ha could become affected within the next 40 years (MDBMC 2001).

A snapshot assessment of MDB condition by Norris *et al.* (2001) concluded that the degradation of biological and environmental condition is a consequence of multiple impacts, not just salinity. Within the catchment, the extent of degradation increases towards the Murray River mouth and major threats impacting upon vegetation in the LRM within South Australia are primarily related to dam and weir operations and associated factors such as un-seasonal inundation of floodplains or a reduction in flooding which all contribute to increased water stress.

1.3 Summary

A list of the possible factors influencing willow establishment has been provided in Table 1.2. Research suggests that *Salix* taxa are capable of a high reproductive output via sexual and asexual means. In their native range the dispersal of seeds and/or propagules is often cued to late spring floods. Flood scour often provides optimal recruitment sites that provide available space, low competition, high light and high moisture. However establishment of recruits may be limited if water-level drawdown rates are too fast as establishing root systems are dependent on surface-water or precipitation derived water sources for the first few growing seasons. Similarly the frequency, magnitude and duration of floods in the first few growing seasons following recruitment may also affect establishment. Overall research suggests that *Salix* are intolerant of water stress conditions (i.e. induced by low river/stream flows, drought conditions or groundwater decline) and a need for reliable, high quality water sources.

On the LRM, *Salix* taxa proliferate above the Locks, but are absent for some distance immediately below each Lock. As a result of weir operations the water levels above each Lock are highly stable and it may be that this particular water regime encourages *Salix* growth and survival. On the other hand, the water regime below each Lock can be highly variable with increased episodes of overbank flooding and subsequent exposure. Since many *Salix* taxa appear sensitive to highly variable flooding and/or exposure episodes this environment may possibly inhibit their recruitment and establishment. From casual observations it has also been observed that *Salix* are not present on the floodplains of the LRM, but are instead confined to riverbank edges. The apparent confinement of *Salix* taxa to the riverbanks of the LRM suggests they may be sensitive to water stress, have higher water use requirements and a need for reliable, fresh water sources when compared with dominant native trees. In this thesis I examine the patterns of willow (*Salix* taxa) distribution on the Lower River Murray (SA) and the mechanisms that may be driving this distribution.

Table 1.3: Model of biotic and abiotic factors proposed to influence *Salix* taxa introduction and establishment along the Lower River Murray, South Australia.

Invasion Stages of an Introduced Individual or Population of *Salix*			
Introduction	**Establishment**	**Reproductive Output**	**Dispersal**
INTRODUCTION May be deliberate or accidental via seedlings, propagules and/or seeds	**SUCCESSFUL** Available space High light availability High nutrient availability Low herbivore and/or pathogen pressures Low neighbour density (competition) *WATER:* Stable water regime High water availability Reliable water source High water quality	**Vegetative** ⟹	**SLOW-EXPANDING POPULATION**
		Seeding ⟹	**FAST-EXPANDING POPULATION**
	UNSUCCESSFUL No available space Low light availability ⟹ Low nutrient availability High herbivores and/or pathogen pressures High neighbour density (competition) *WATER:* Fluctuating water regime Low water availability Unreliable water source Low water quality		**NO POPULATION**

1.4 Thesis Outline

To characterise the geographic and small-scale composition of the regional *Salix* taxa within the LRM, the location of each taxon was recorded to clarify their current distribution patterns (Chapter 2). The flowering biology for regional taxa was also determined.

Salix taxa distribution appears discontinuous along the upstream-downstream gradients of the LRM, suggesting their distribution may be influenced by weir operations. In Chapter 3, the presence and/or absence of *S. babylonica* and the co-occurring natives (*E. camaldulensis, E. largiflorens* and *A. stenophylla*) were recorded along weir pools. Their abundance along each weir pool was also scored to determine if their distribution and abundance correlated with the water regimes created by weir pools.

The inference from the above survey that highly variable, fluctuating water regimes may inhibit growth and survival patterns of establishing *Salix* propagules was further examined in Chapter 4. Survivorship, relative growth rates and meristem production of propagules of *S. babylonica* subject to different water regimes and elevation was compared with seedlings of *E. camaldulensis* and *A. stenophylla* in experimental ponds.

The apparent confinement of *Salix* taxa to the riverbanks of the LRM suggests they may be sensitive to water stress, have higher water use requirements and a need for reliable, fresh water sources when compared with dominant native trees. In Chapter 5 a comparative assessment of seasonal differences in plant water status (i.e. shoot water potential (ψ_{shoot})) and gas exchange parameters for *S. babylonica, E. camaldulensis* and *A. stenophylla* in riparian and floodplain habitats was made. Long-term water-use-efficiency (i.e. the ratio of carbon gained to water lost) was also assessed by determining the $\delta^{13}C$ of the above species. The source of water used by *S. babylonica* within riparian habitats across a growing season was also determined using $\delta^{18}O$ isotope analysis.

Drought conditions prevailed across much of the LRM region in 2002 to 2003 and provided a unique opportunity to assess the drought tolerances of *Salix* taxa. In Chapter 6, the comparative physiological responses (i.e. ψ_{shoot} and leaf gas exchange parameters) of *S. babylonica* and *E. camaldulensis* to a 6-month period of extreme low river flows and below average annual precipitation was investigated.

Chapter 7 summarises the key findings of this study. The implications of the improved understanding of the hydraulic requirements of long-lived riparian trees are discussed in reference to river management. Future research ideas are proposed and possible applications of these findings for willow management and control are discussed.

Chapter 2

Taxonomic survey of the genus *Salix* (Salicaceae) along the Lower River Murray, South Australia.

2.1 Introduction

Many *Salix* taxa (Salicaceae) are now considered key freshwater invaders in countries such as Canada, South Africa, New Zealand and Australia (Cremer 2003, Daehler 1998, Henderson 1991, Henderson 1992, Ladson 1997, Lester *et al.* 1994, Shafroth *et al.* 1994). Over 100 *Salix* taxa were imported and deliberately planted in Australia since colonisation and over 30 of these have now become naturalised (Cremer 1995) and classified as 'environmental weeds' (Appendix 2.1). On the LRM invasive *Salix* tend to produce monospecific stands (Walker 2001), and their introduction is often linked with reductions in habitat and food resources for native fauna as well as changes to channel morphology (Cremer *et al.* 1995, Erksine *et al.* 1999, Ladson 1997).

When *Salix* were first introduced to Australia it was considered unlikely that cross-pollination would occur because in most cases only cuttings of one gender per taxon were imported (Cremer *et al.* 1995). Although hybridisation, either naturally or artificially, between *Salix* taxa is well documented, it is not a common occurrence in their native ranges (Newsholme 1992, Mosseller 1990). In Europe, hybrids constitute less than five per cent of the total native *Salix* populations. Individual *Salix* taxa are preserved in their native ranges because of natural barriers to interbreeding, such as asynchronous flowering times and non-overlapping geographical and ecological distributions (Neumann (1981) cited in Cremer 2003).Yet many of the introduced *Salix* in Australia have proven to be highly fertile and to readily interbreed with either pure species or even other hybrids (Cremer

1995, Cremer 2003, Cremer *et al.* 1995) suggesting that many of the natural barriers to interbreeding were overcome. As a result, willows have proliferated in the eastern states (Cremer 1995).

Climatic differences between regions where *Salix* have originated versus invaded, may explain some why some natural barriers to hybridisaiton have been removed. In *Salix* the sequence of flowering and seed development is largely determined by thermal regimes. The timing of heat pulses in a given year may mean that leaf and/or flower development may be earlier or later in the season, since each taxon respond in a definite and constant way to a certain thermal regime (Mosseller and Papadol 1988). In the LRM, there is a distinct climatic regime (Bureau of Meteorology, SA Govt; see Table 2.1). Temperatures tend to decrease and rainfall increases progressively downstream, while inland, upstream reaches have higher mean maximum temperatures and lower rainfall. In the vicinity of Renmark, mean minimum temperatures in early spring are comparatively low, since the area is prone to severe frosts in early spring (i.e. August and September). In other regions of Australia, the spread of *Salix* appears predominantly the result of asexual (vegetative) reproduction following deliberate plantings (Cremer 2003). In these instances, vegetative spread in *Salix* occurs via layering and/or by fragmentation (Beismann *et al.* 2000), and many *Salix* have stem or twig bases (e.g. *S. fragilis*) that crack easily under the slightest mechanical stress, facilitating their spread (Beismann *et al.* 2000, Rood *et al.* 1994, Shafroth *et al.* 1994).

Table 2.1. Climate data of mean annual rainfall and maximum and minimum temperatures for localities along the Lower River Murray (South Australia). Order of localities represents their position along the upstream to downstream gradient of the river (Bureau of Meteorology, SA Govt). Statistics available from a climate normal period from 1 January 1961 - 31 December 1990.

NOTE:
This table is included on page 50 of the print copy of the thesis held in the University of Adelaide Library.

The discovery of seeding willows in the eastern states has raised some concern since their rate of spread by seed is estimated to be five to ten fold higher (e.g. <3.5 km yr^{-1}) (Cremer, K., *pers. comm.*) than the rate of vegetative spread (~0.35 km yr^{-1}) (Ladson 1997). However the taxonomic diversity and distribution of willows along the LRM, associated floodplains and the surrounding Riverland district remains uncertain (for a physical description of the LRM see Chapter 1).

To recap, prior to regulation, LRM riverbanks vegetation composition and structure consisted primarily of a red gum over-storey (*Eucalyptus camaldulensis*) and understory of herbaceous annuals/ephemerals (Walker 2001). While *E. camaldulensis* are still an iconic feature along riverbanks since regulation, there is now a mixed community of emergent (e.g. *Phragmites australis, Typha domingensis*, *Cyperus gymnocaulos*) and submerged macrophytes (e.g. *Potamogeton crispus, Vallisneria australis*) (Walker 1994a, Blanch *et al.* 2000) and many *Salix* have also become naturalised. Within the *Gorge* and *Valley* regions, their distribution is discontinuous (Walker 2001, further investigated in Chapter 3), however in the *Swampland* region, *Salix* are a dominant, continuous feature (Margules and Partners 1990, Kennedy *et al.* 2003) since they were often deliberately planted to stabilise the earthen levee banks (Perkins 1903). Until recently it was believed that only two *Salix* taxa (*S. babylonica* and *S.* × *rubens*) existed on the LRM, yet Kennedy *et al.* (2003) confirmed that one of the more common willows present had been incorrectly identified and was not *S.* × *rubens,* as originally presumed, but actually *S. fragilis*.

Due to the taxonomic confusion, the primary aims of this investigation was to a) verify the taxonomic diversity of *Salix* within the LRM and Riverland region and b) to characterise the reproductive phenology (i.e. sex, catkin development, flowering times, fruit capsule development and seed release) of the taxa present.

2.2 Methods

2.2.1 Site Description

Most of the Lower River Murray, encompassing ~620 river km, runs within South Australia and includes Lock 6 (at Renmark) to Lock 1 (at Blanchetown) (see Fig. 2.1). The locked weir structures within the LRM primarily operate as an impoundment system to provide water to the surrounding Riverland district (Walker 2001). The Riverland region covers an extensive area (~40000 km^2) and includes a diverse range of agricultural/horicultural industries (e.g. vineyards, fruit and/or nut orchards, dairy). The regional climate is semi-arid with annual rainfall 200 – 500 mm and evaporation 1500 –

2400 mm and surface soils within this region are predominantly calcareous being the products of weathered marine sediments (Walker and Thoms 1993).

2.2.2 Taxonomic Survey

The diversity and distribution of *Salix* taxa along the main river channel and surrounding floodplains within the Riverland region was assessed using digital data maps in 'The Murray-Darling Rivers Digital Orthophoto Image Map Series (Version 1, 1993) and distribution reports (Seekamp 1991). Diversity and distribution was verified by vehicle or foot, wherever access was possible. Herbarium specimens and photographs of flowering trees were collected, taken back to the laboratory and identified using the *Salix* field identification key in Cremer (1995) and Fisher (1928) where appropriate. Identification of *Salix* taxa on the LRM was relatively easy due to clear differences in growth form (e.g. erect versus weeping) and crown shape (e.g. narrow versus globular) therefore the *Salix* field identification key was modified and developed for ease of use in the field on the LRM (South Australia) (see Appendix 2.2). Note that the term 'taxa' is used here as a collective term to denote any or all-taxonomic divisions below genus (i.e. species, subspecies, cultivars, variety, hybrids). The exact locations of less common or rare *Salix* taxa were recorded using GPS (GPS 72: Garmin) and mapped.

Flowering biology (i.e. catkin enlargement, flowering times, fruit development and possible seed release) of the dominant *Salix* taxa (n = 20 trees per taxon) at two localities (upstream site of Renmark and downstream site of Murray Bridge) were documented across the flowering seasons (August – October).

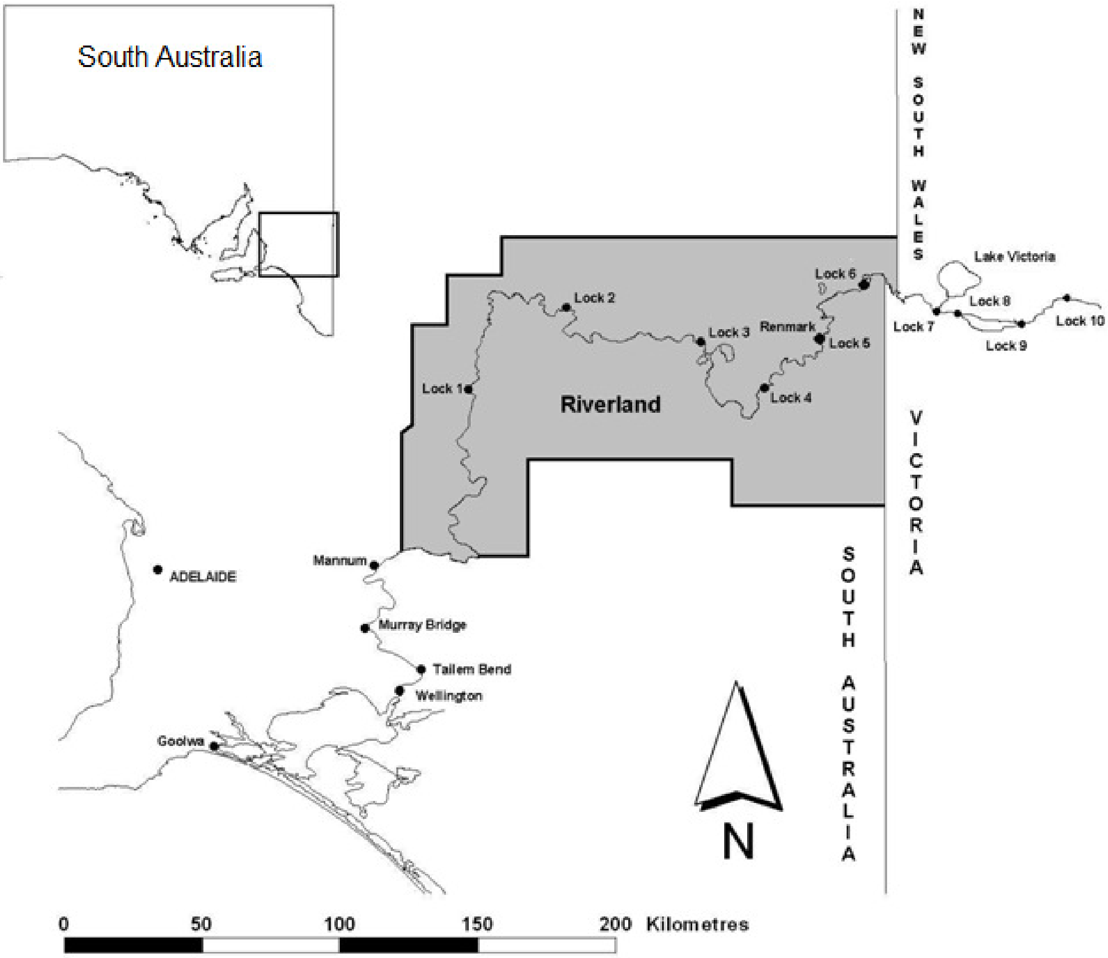

Figure 2.1. Site map of the locked weir system of the Lower Murray River and the surrounding Riverland district (South Australia).

2.3 Results

2.3.1 Taxonomic and Sex Identification

Seven different *Salix* taxa were located and identified growing either along the banks of the LRM or within the Riverland (SA) (Table 2.2). No *Salix* taxa were found growing on the floodplains and we found no evidence of any *Salix* taxa having produced seedlings.

Table 2.2. *Salix* taxa found along Lower River Murray and Riverland region of South Australia. Survey conducted between August – October in 2001 and 2002.

Scientific Name	**Common Name**	**Male/Female**
Salix babylonica	Weeping Willow	Female
Salix fragilis	Crack Willow	Male
Salix × *rubens*	Basket Willow	Female
Salix × *chrysocoma*	Golden Weeping Willow	Male*
Salix humboldtiana	Pencil Willow	Male
Salix matsudana × *alba*	Matsudana Hybrid Willow	Male/Female**
Salix matsudana	Tortured Willow	Female

* Predominantly male but may produce some female reproductive structures on same catkin

** Individual female trees found growing on banks of Ral Ral Creek (South Australia) were removed in December 2003.

Naturalised *Salix* taxa (i.e. populations that are able to persist without human intervention and cultivation (Allaby 1992) identified on the LRM were *S. babylonica* (♀), *S. fragilis* (♂), *S.* × *chrysocoma* (♂) and *S.* × *rubens* (♀) and each of these taxa were represented by only one gender (i.e. either wholly male or female populations).

S. babylonica are found along the entire length of the river system (Lock 6 to Wellington) although their distribution is discontinuous (see Chapter 3). This study concurs with Kennedy *et al.* (2003) that mixed stands of *S. babylonica* and *S. fragilis* form a nearly continuous fringe over a 74 km stretch, from Mannum to Wellington (i.e. 150 km to 76 km from Murray Mouth) (Figure 2.2). Evidence of deliberately planted *S. fragilis* trees was seen on the earthen man-made levee banks in the Murray Bridge area (112 river km from the Murray Mouth). Deliberately planted individuals of *S.* × *chrysocoma* were observed in private residences within the Riverland, and naturalised populations of both juveniles and adults of this taxa were found growing on the riverbanks of the LRM and surrounding wetlands in the Murray Bridge locality (Figure 2.2). A small population (< 50 individuals) of adults and juveniles of *S.* × *rubens* were discovered just below Renmark (560 river km from Murray Mouth) (Figure 2.2).

A few individuals of *S. matsudana* (♀) and *S. humboldtiana* (♂) were recorded growing in private riverfront residences of the LRM or private residences of the Riverland district. Male *S. matsudana* × *alba* stands were observed in the surrounding Riverland where they are commonly used as a shelterbelt tree around many orchards and vineyards. In addition, two female *S. matsudana* × *alba* individuals were discovered growing on the banks of Ral Ral Creek (SA) but were removed in December 2003 (Figure 2.3).

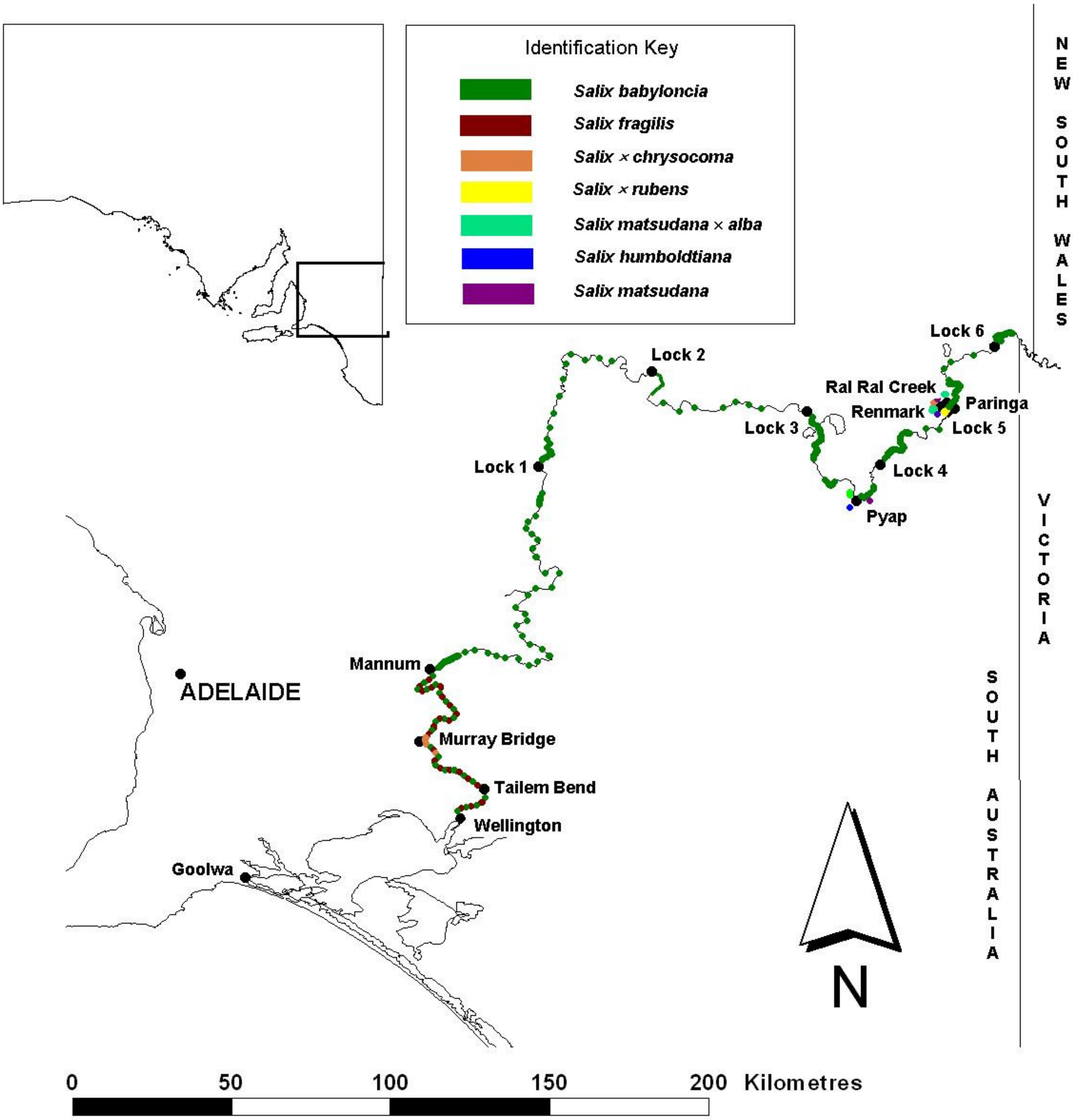

Figure 2.2. Distribution of *Salix* taxa for the Lower River Murray and Riverland region (South Australia)

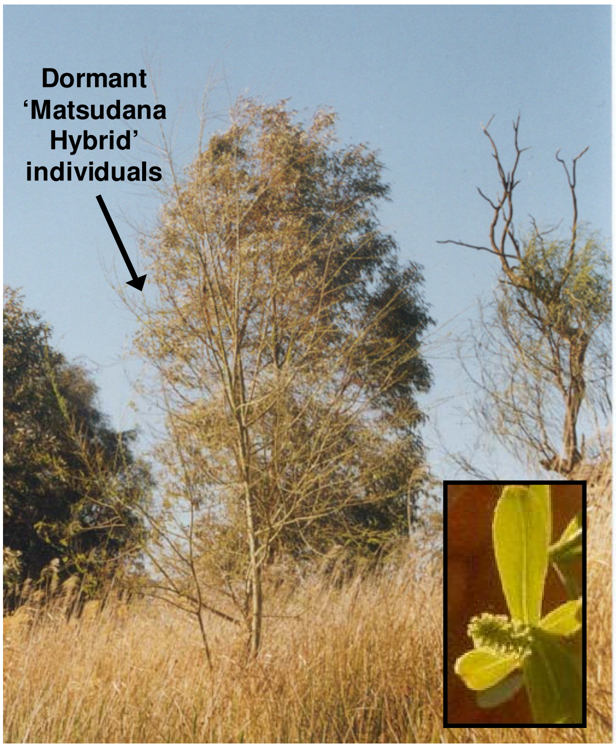

Figure 2.3. Two female 'Matsudana Hybrid' (*Salix matsudana* × *alba*) individuals found at Ral Ral Creek, Renmark (South Australia). Female flowering catkin (Inset). *Note that the 2 individual trees were removed in December 2003.*

2.3.2 Reproductive Phenology

Catkin enlargement and flowering events were the same both within and between the individual trees surveyed for each taxon (n = 20 per taxon). Put another way, developmental stages occurred simultaneously and *en masse* within each taxon. Within the Renmark locality catkin enlargement for *S. babylonica*, *S.* × *chrysocoma* and *S. matsudana* × *alba* began in the last week of August during both 2001 and 2002 as opposed to the first week of October for *S.* × *rubens* (Table 2.3). Similarly the flowering times for *S. babylonica*, *S.* × *chrysocoma* and *S. matsudana* × *alba* began in first week of September as opposed to second week of October in *S.* × *rubens* (Table 2.3). Flowering periods generally lasted for two weeks, with the exception of *S.* × *chrysocoma,* which had a slightly longer flowering time of three weeks (Table 2.3). Male *S. matsudana* × *alba* and female *S. babylonica* were recorded flowering at the same time in the Renmark locality (Figure 2.4). Within the Murray Bridge locality catkin enlargement for *S. babylonica* and *S.* × *chrysocoma* began mid-August, whereas in *S. fragilis*, catkin enlargement began in the last week of September (Table 2.3). Similarly the flowering times for *S. babylonica* and *S.* × *chrysocoma* began in last week of August as opposed to first week of October in *S. fragilis* (Table 2.3). No fruit development, seeds or seed release was observed in any of the *Salix* taxa identified (Table 2.3).

Table 2.3. Reproductive timing of common *Salix* taxa at Renmark (upstream) and Murray Bridge (downstream) sites (South Australia). Dates shown here were for 2001 and 2002 seasons, but note that leaf/flower development may be to 3 weeks earlier or later than dates shown if seasonal temperatures are colder and/or warmer.

Salix **taxa**	**Site**	**Sex**	**August**				**September**				**October**			
S. babylonica	Renmark	Female				C	F	F						
S. babylonica	Murray Bridge	Female			C	F	F							
S. × *chrysocoma*	Renmark	Male*				C	F	F	F					
S. × *chrysocoma*	Murray Bridge	Male*			C	F	F	F						
S. fragilis	Murray Bridge	Male								C	F	F		
S. matsudana × *alba*	Renmark	Male				C	F	F						
S. × *rubens*	Renmark	Female									C	F	F	

* Predominantly male but may produce female flowers on same catkin
C = Catkins enlarging
F = Flowering

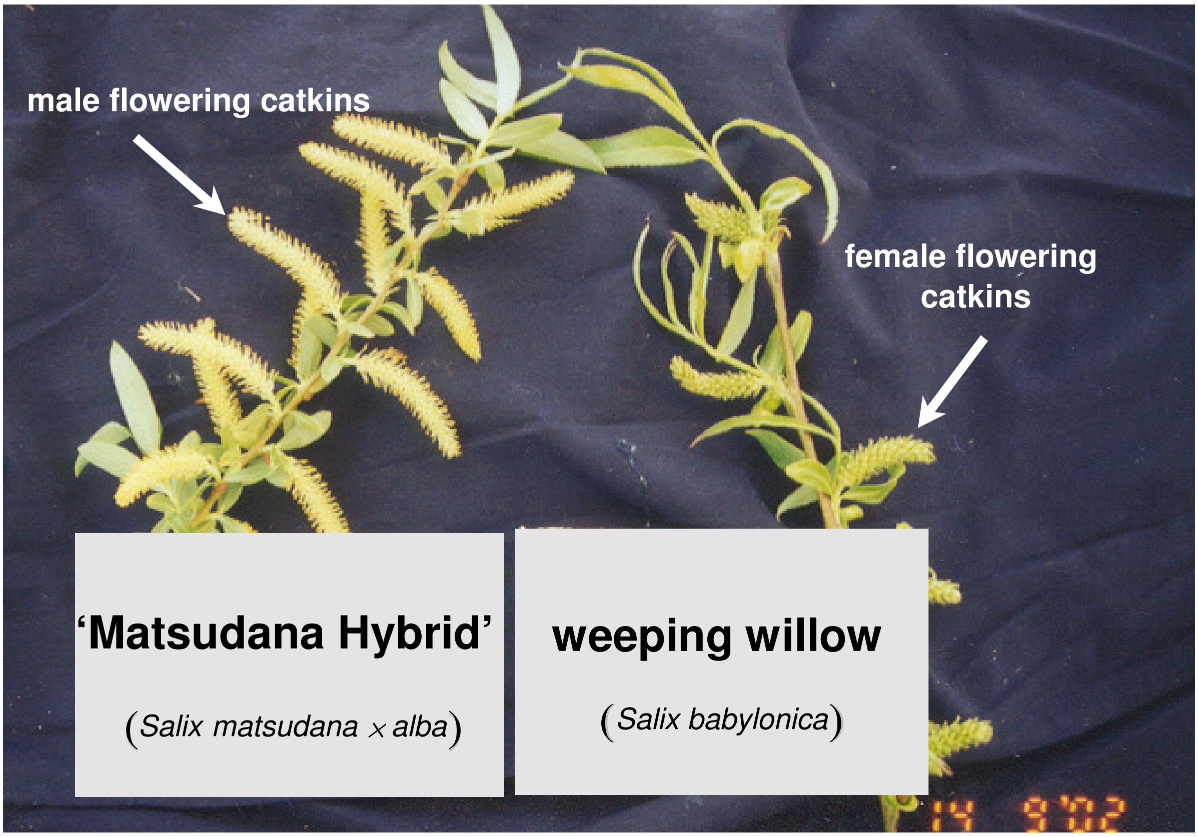

Figure 2.4. Photo capturing synchronised flowering times between male *Salix matsudana* × *alba* ('Matsudana Hybrid') and female *Salix babylonica* (weeping willow) at Renmark, Riverland (South Australia).

2.4 Discussion

Diversity

The under estimation of *Salix* taxonomic diversity on the LRM may simply reflect the fact that until now a complete census had not been undertaken. In the eastern states of Australia, field identification of *Salix* taxa has proved highly complex due to their propensity to hybridise and the fact that key growth characteristics used to identify a particular taxa can differ depending upon seasonal influences and growing conditions (Cremer 1995). In this survey there was no evidence of ripe fruits, seed release or seedlings in the naturalised *Salix* populations suggesting that sexual reproduction has not occurred. The individual trees within each identified taxon also appeared relatively consistent in terms of growth characteristics, such as growth form (upright versus weeping) and crown shape (narrow versus globular) simplifying field identification (see Appendix 2-2). Trees with each taxon were also either wholly male or wholly female suggesting that asexual reproduction mode (via fragmentation and/or layering) dominates. Juveniles of the four naturalised *Salix* taxa (*S. babylonica*, *S. fragilis*, *S.* × *chrysocoma, S.* × *rubens*) were also within a short distance (≤ 5 m) of mature trees and mostly confined to within 1 m – 2 m of the riverbank edge (i.e. no trees were found growing on floodplains, see Chapter 4). Once individual, mature *Salix* trees reach reproductive maturity (as early as 3 yr old) they produce millions of seeds that are potentially dispersed long distances by wind or relatively short distances via water (Brinkman 1974, Cremer *et al.* 1995, Newsholme 1992). If current *Salix* populations were to reproduce sexually then it would be expected that seedlings and/or juveniles would be found in locations beyond established populations, given the long distances that *Salix* seeds can be dispersed.

Reproduction

Based on the evidence that the naturalised *Salix* populations are only dispersing via asexual modes, it is likely that their rate of dispersal along the LRM is relatively slow, at approximately 10 km every 30 years (Ladson 1997). Still the ability of *Salix* taxa to reproduce asexually and maintain population expansion under the regulated conditions of the LRM may allow them some competitive advantages over native vegetation. Many aquatic macrophytes on the LRM are capable of asexual reproduction, however most native riparian trees and shrubs tend to reproduce sexually, although there are exceptions, such as the common floodplain species, *Muehlenbeckia florulenta* (Blanch *et al.* 1999, Chong and Walker 2005). Native eucalypts of the LRM require large, intense floods for successful recruitment, yet current river regulation practices have meant that these flood events are greatly reduced thereby contracting their potential distribution (George *et al.* 2005, Margules and Partners 1990). On the other hand, the ability of *Salix* to layer can lead to slow, yet persistent expansions. By layering, even mature trees suffering considerable crown dieback and thinning, can extend their lifespans beyond the recorded 50 – 80 years (Newsholme 1992).

Flowering

Mass simultaneous catkin and flower development within specific *Salix* taxa is common (Newsholme 1992, Cremer 1995, Argus 2003). In general, it has been noted that in most *Salix* taxa, catkins mature before foliage develops (e.g. *S. fragilis*) (Fisher 1928, Cremer 1995), but this is not always the case; in *S. babylonica, S. matsudana* × *alba* and *S.* × *chrysocoma* catkin and leaf development occur simultaneously. The climatic gradient in the LRM may explain the later *Salix* flowering times and potentially explains why

S. babylonica trees consistently flower two to three weeks earlier than other taxa such as *S. fragilis* and *S.* × *rubens* from year to year.

A similar scenario was also observed between the regionally abundant female *S. babylonica* and the deliberately planted male *S. matsudana* × *alba*. This survey confirmed that flowering times between the two taxa do overlap, but at present *S. matsudana* × *alba* are located a sufficient distance (>10 km) from *S. babylonica* to prevent cross-pollination. Yet the discovery of two *S. matsudana* × *alba* individuals growing on the banks of Ral Ral Creek (SA) alongside female *S. babylonica* highlights the point that many weed introductions are often accidental and that current horticultural legislation for *Salix* management and control within the region may be inadequate. Accidental introductions of either male *S. matsudana* × *alba* or other viable taxa to the LRM may be all that is needed to initiate a bridging link between existing riverbank *S. babylonica* populations.

Hybridisation

Hybridisation may provide a stimulus for increased invasiveness after successful colonisation (Ellstrand and Schierenbeck 2000) since hybridisation between taxa with very different genetic traits can lead to new adaptive traits as a result of heterosis (i.e. hybrid vigour) that are more compatible with colonised habitats (Orians *et al.* 1999). The presence of *Salix* taxa with overlapping flowering does raise some concerns since the potential for hybridisation and seed production in *Salix* populations may provide opportunities for considerable expansion. In the eastern states of Australia *S. babylonica* has hybridised with *S. matsudana* × *alba* and now produces seeds and hybrid seedlings in some rivers systems (Cremer 2003). Cross-pollination between *Salix* taxa on the LRM is prevented due to reproductive barriers such as asynchronous flowering times and spatial separation. Female *S. babylonica* and male *S. fragilis* trees are found growing together, but their flowering times do not overlap. Alternatively, in the case of the female *S.* × *rubens* and male *S. fragilis*, their flowering times do overlap, but at present the two populations are separated by more than 100 km making cross-pollination unlikely. *Salix* taxa do not tend to display pollinator specificity and are primarily insect – pollinated by flies (Diptera), wasps (Hymenoptera), Honeybees (*Apis*), bumblebees (*Bombus*) and beetles (Coleptera). Wind pollination may also occur to a limited extent, therefore trees need to be less than 5 km apart for pollination to occur (Mosseller and Papadol 1988, Fox 1992).

The hybrid *S. matsudana* × *alba* was initially developed in New Zealand (NZ) over 25 years ago for the commercial horticultural industry and subsequently introduced to Australia for the same purposes approximately 15 years ago (Cremer 2003). *S. matsudana* × *alba* were highly recommended to commercial growers as shelterbelt trees because of properties such as rapid growth (up to 3.5 m in the first season), resistance to pests, diseases and fire, as well as high salt and water stress tolerance (Bhojwani 1980). If some of the possible biotic and/or abiotic factors (e.g. water stress and/or salinity sensitivity), that currently constrain distribution were alleviated via interbreeding, as a result of heterosis it is feasible that considerable expansion of *Salix* populations on the LRM and within the Riverland may occur.

Predator and Pathogen Pressures

The success of *Salix* taxa on the LRM may also be attributed to their release from natural predators and pathogens (Ellstrand and Schierenbeck 2000, Stastny *et al.* 2005). Willows in Australia have acquired some diseases since their introduction (Cremer 2003) such as leaf rust (*Melampsora* spp.) which was evident on some mature riparian *Salix* in this investigation. However there were no obvious signs of herbivory on the naturalised riparian *Salix* populations. However, in recent years, outbreaks of a natural predator of *Salix* taxa, the willow sawfly *Nematus oligospilus* (Hymenoptera: Tenthredinae), were identified in Australia (Australian Government Department of Agriculture, Fisheries and Forestry: http://www.daff.gov.au). Since they were not deliberately introduced into Australia as a means of biological control their method of arrival is unclear, but they are now widespread and cannot be eradicated. Sawfly larvae feed on leaves and large populations can defoliate trees in a single season. Several defoliation events, over a few growing seasons can lead to tree death, although susceptibility will depend on tree age and certain *Salix* taxa are more susceptible to attack than others (Charles *et al.* 1998). A report by Ede (2006) found that *N. oligospilus* show clear preferences for certain *Salix* taxa in Australia and have the potential to defoliate and kill the following taxa: *S. fragilis* (and hybrids), *S. nigra*, *S. alba*, *S. alba* var. *vitellina* and *S. matsudana* (and hybrids).

Chapter 3

Distribution of *Salix babylonica* and native *Eucalyptus camaldulensis*, *E. largiflorens* and *Acacia stenophylla* in relation to weir pool gradients of the Lower Murray River, South Australia.

3.1 Introduction

The distribution of riparian vegetation is influenced by environmental factors operating along hydrologic gradients (e.g. upstream-downstream gradients and river-floodplain gradients) (Bendix 1994). In the northern hemisphere, a range of hydrologic, geomorphological and climatic variables predictably change from upstream to downstream. Upstream conditions tend to have lower temperatures, increased precipitation, decreased potential evapotranspiration, greater bed slope and limited floodplains, compared with downstream regions (Patten 1998, Naiman *et al.* 2000). In contrast, the Lower River Murray (LRM) in southern Australia has a distinct climatic gradient; which is opposite to that typically observed, where upstream temperatures are higher and precipitation is less than downstream environments (see Table 2.1, Chapter 2). The river is also highly regulated and now resembles a series of cascading weir pools (Walker 2001), since the construction of a weir system with 10 locks that manipulate river surface-water levels along hydrologic gradients (Walker and Thoms 1993).

Within South Australia, weirs on the LRM operate to maintain upstream 'pool levels' (by removing or replacing stop logs), but do not manipulate river flow (i.e. high, medium and low water levels can all be accompanied by low flow). During seasonal periods when overbank inundation occurs (hereafter referred to as overbank pulse) and weir structures become submerged, there is no control on water levels within the river. But during periods when the river is contained within its banks (hereafter referred to as within-bank pulse), weir operations create a distinct water regimes where water levels above each weir (in the lower pool region) are maintained consistently within the designated pool level, but water levels become increasingly less consistent, especially in the tail-waters (areas immediately below each locked weir), which are subject to considerable daily variations (Blanch *et al.* 1999, Maheshwari *et al.* 1995, Walker 2001, Figure 3.1).

NOTE:
This figure is included on page 67 of the print copy of the thesis held in the University of Adelaide Library.

Figure 3.1. Schematic diagram representing pool regions of the weir pools of the Lower River Murray, South Australia (modified from Walker 2001).

On the LRM, preliminary observations suggest that the distribution of *Salix babylonica* along upstream-downstream gradients is discontinuous. *S. babylonica* appear to flourish above weir structures (Walker 2001), but distribution is sparse immediately below each weir, nor are they present on floodplains, but instead, seem limited to a narrow 2- 3 m margin along the edges of main channels and backwaters. There is very little information on the distribution *S. babylonica* in their native range, but they originated in central to Northern China (CAB International 2000).

The discontinuous distribution of *S. babylonica* along the LRM may reflect their intolerance of variable water regimes and/or their need for reliable surface water sources. It is therefore hypothesised that *S. babylonica* distribution along the LRM will be minimal where water-level amplitudes are greatest (i.e. directly below the weirs) because of the inference that highly variable episodes of inundation and exposure may limit establishment, growth and/or survival of *S. babylonica*. In contrast the distribution of the native trees, *E. camaldulensis*, *E. largiflorens* and *A. stenophylla,* will be uniform across the longitudinal gradients due to their greater tolerance of variable water regimes. To test these hypotheses the water level fluctuations in pool were charcterised and compared with patterns of abundance for *S. babylonica* and dominant native trees.

3.2 Methods

3.2.1 Water regime characterisation

Key components of the water regime gradient across the weir pool bounded by Locks 3 and 4 on the LRM were characterised from stage hydrograph data of daily water-level variations measured in metre Australian Height Datum (mAHD) at four gauge sites along the weir pool that represent weir pool regions (tailwater, upper pool, middle pool and lower pool). At the time of analysis, data for all four gauge sites was only available from the period of 1987–2004. Names and location of the four gauge stations are listed in Table 3.1.

Table 3.1. Site names and location of the four gauges along Pool 3 of the Lower River Murray (Department of Water, Land and Biodiversity Conservation, SA Govt).

Monitoring Gauge Station Name	Weir pool region station represents	River km from the Murray Mouth
Lock 3 (Upstream)	Lower pool	431.4 km
Loveday Pump Station	Middle pool	446.9 km
Loxton Irrigation Pump Station	Upper pool	493.9 km
Lock 4 (Downstream)	Tailwater	516.2 km

If daily river water levels exceeded the designated Pool 3 levels of 9.8 mAHD for more than 50 consecutive days it was classified as an overbank pulse. During the years where annual overbank pulses occurred, components such as: frequency, duration, seasonality, rate of rise and the rate of recession were calculated using the following definitions and equations:

Definition 3.1:

$$\mathit{Overbank\ pulse\ frequency}$$
$$= \text{number of years per data set (total n=17)that overbank pulse occurred}$$

Definition 3.2:

$$\mathit{Overbank\ pulse\ duration} = \text{number of days per year that overbank pulse lasted}$$

Definition 3.3:

$$\mathit{Overbank\ pulse\ seasonality}$$
$$= \text{dates per calendar year that overbank pulse began and finished}$$

Equation 3.1:

$$\mathit{rate\ of\ overbank\ pulse\ rise}$$
$$= \frac{\text{slope of rising hydrograph limb (maximum water level-minimum water level)}}{\text{duration of rising hydrograph limb (number of days of pulse rise)}}\ (\text{cm day}^{-1})$$

Equation 3.2:

$$\mathit{Overbank\ pulse\ recession}$$
$$= \frac{\text{slope of falling hydrograph limb (maximum water level-minimum water level)}}{\text{duration of falling hydrograph limb (number of days of pulse recession)}}\ (\text{cm day}^{-1})$$

A quantitative index of water regime was determined by calculating the percentage of days per available data set for each year that river water levels were either over or under the designated pool level (9.8 mAHD) for Pool 3. Designated pool level was standardised to 0 cm to provide estimations of water-level fluctuations (class intervals in cm) during years of low river flows (i.e. within-bank pulses) (Blanch *et al.* 1999).

3.2.2 Field Survey

A vegetation survey of two weir pools was conducted by boat on 10th – 11th July 2002. The weir pools surveyed were: weir pool 4 (below Lock 5 (34º 11' 16" S, 140º 45' 57"E) to above Lock 4 (34°20' 32" S, 140°34' 38" E)), total pool length 46.2 river km; and weir pool 3 (below Lock 4 (34°20' 32" S, 140°34' 38" E) to above Lock 3 (34°11' 21" S, 140°34' 38" E)), total pool length 84.8 river km (Figure 3.2). In this region the river meanders over broad (5 – 20 km) floodplains, including many riparian wetlands and deflation basins (Walker and Thoms 1993). Periodically the river passes through limestone gorges and several townships.

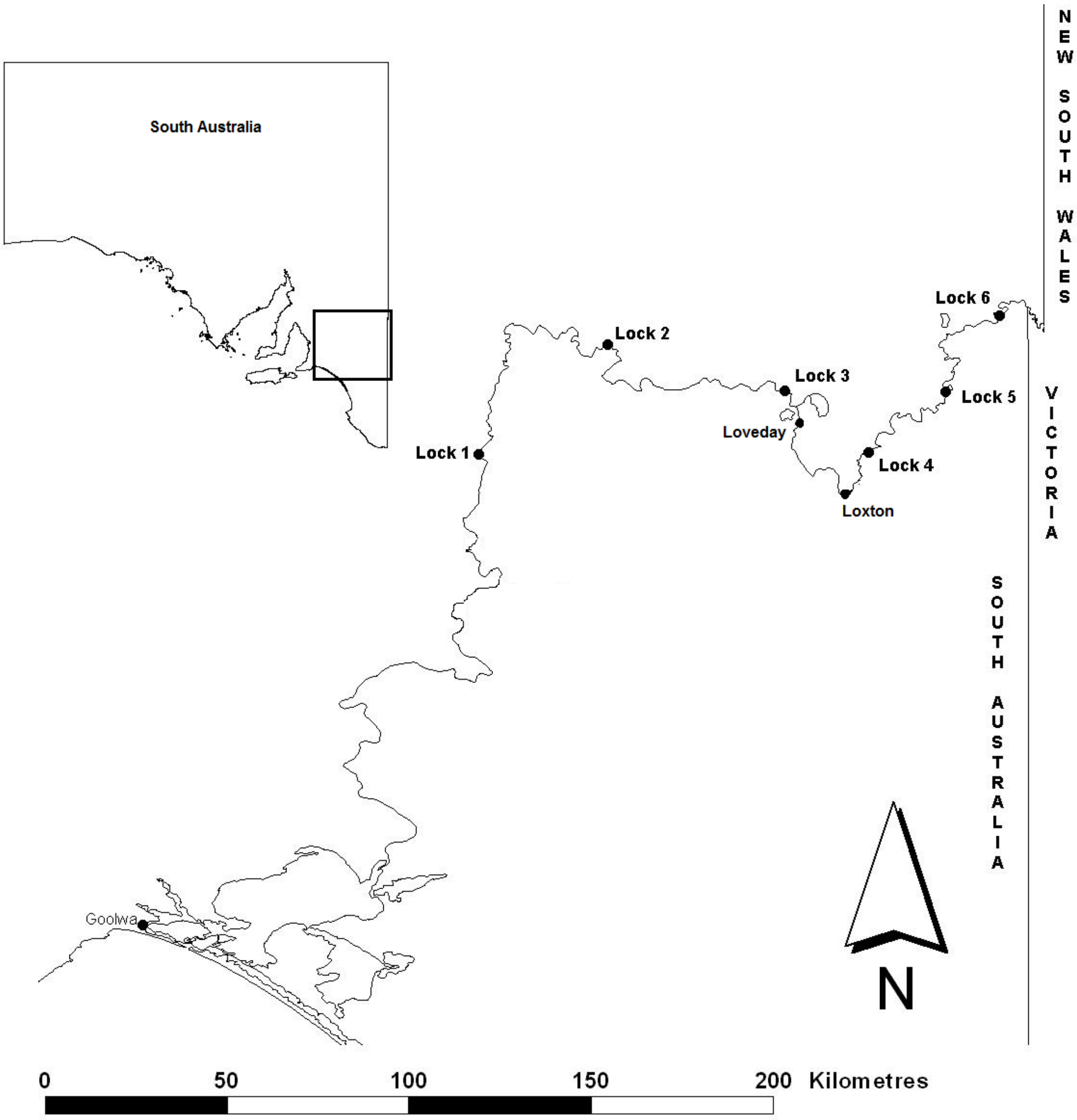

Figure 3.2. Map of the Lower River Murray (South Australia) showing the location of river locks.

Each weir pool was divided into survey cells measuring 500 m (length) × 10 m (width) along the eastern and western banks. The length and width of each survey cell was determined using a GPS (Garmin 72). The multi-stemmed habit of *S. babylonica* precluded a census of individual trees therefore within each survey cell the following were recorded: a) presence or absence scores (presence = 1, absence = 0) and b) relative abundance scores of stand densities for *S. babylonica* and native trees (*E. camaldulensis, E. largiflorens and A. stenophylla*) (Table 3.2). Distribution maps of the ranked abundance scores for each species were made using modified maps (Baker *et al.* 2000) to compare against specific landscape features and/or localities, but are not included.

Table 3.2. Scale of relative abundance used to derive ordinal ranked scores for riparian *Salix babylonica, Eucalyptus camaldulensis, E. largiflorens* and *Acacia stenophylla* across weir pools 3 and 4 of the LRM

Relative Ranked Abundance Score	**Stand density description**
0	Absent
1	Isolated individuals
2	Intermediate: monotypic stands, distinct canopies
3	Continuous: monotypic stands, overlapping canopies

3.2.3 Statistical Analysis

A chi squared 'goodness of fit' test ($\alpha = 0.05$) was used to assess whether there was a difference in the abundance of each tree species along the distance of each weir pool. The *null hypothesis* (H_o) tested whether the distribution of all species was uniform along the entire length of the weir pool (Microsoft ® Office Excel 2003). Logistic regression analysis was used to assess the probability of occurrence of each species in relation to distance along a weir pool (Logistic Regression V. 05.07.20, Pezzullo, J. C. and Sullivan, K. M.: http://statpages.org/logistic.html).

Differences in the mean yearly rates of rise and recession of overbank pulses between weir pool monitoring stations (i.e. distance along a weir pool) were analysed using a one-factor analysis of variance (ANOVA). Differences in the duration of yearly overbank rises and recessions between the weir pool monitoring stations were also analysed using an ANOVA. Means were compared by Tukey-Kramer honestly significant difference test (Tukey's HSD) when appropriate. Analyses were conducted using the program JMPIN (v. 3.2.6: SAS Institute Inc., Cary, NC, USA).

3.3 Results

3.3.1 Water level variations

Stage hydrographs for each monitoring station across the length of weir pool 3, demonstrated that the combination of discharge and weir operations creates a variable water regime gradient along the weir pool (Figure 3.3). Over the period 1987–2004, the amplitude of water level variations decreased with increasing distance downstream of a Lock (Figure 3.4).

During years when within-bank pulses occurred, regions along pool 3 had distinct water regimes as a result of weir operations. In the tailwater region (Lock 4 Station, downstream) daily river water levels fluctuated erratically for 37.2 ± 22.5% of days, with water levels between 0.5 – 1.0 m of pool level (Figure 3.5). In the upper pool (Loxton Pump station), water level fluctuations were moderately variable and for 37.7 ± 17.3% days per annum, water levels were between 0.21 -0.50 m of pool level (Figure 3.5). In the middle pool (Loveday Irrigation Pump station) water levels fluctuated more consistently and for 54.7 ± 9.7% days per annum, water levels were between 0.06 to 0.10 m above pool level (Figure 3.5). In the lower pool, Lock 3 (upstream) water level fluctuations were relatively stable and for 61.0 ± 5.6 % days per annum, water levels were between 0.01 – 0.05 m around pool level (Figure 3.5).

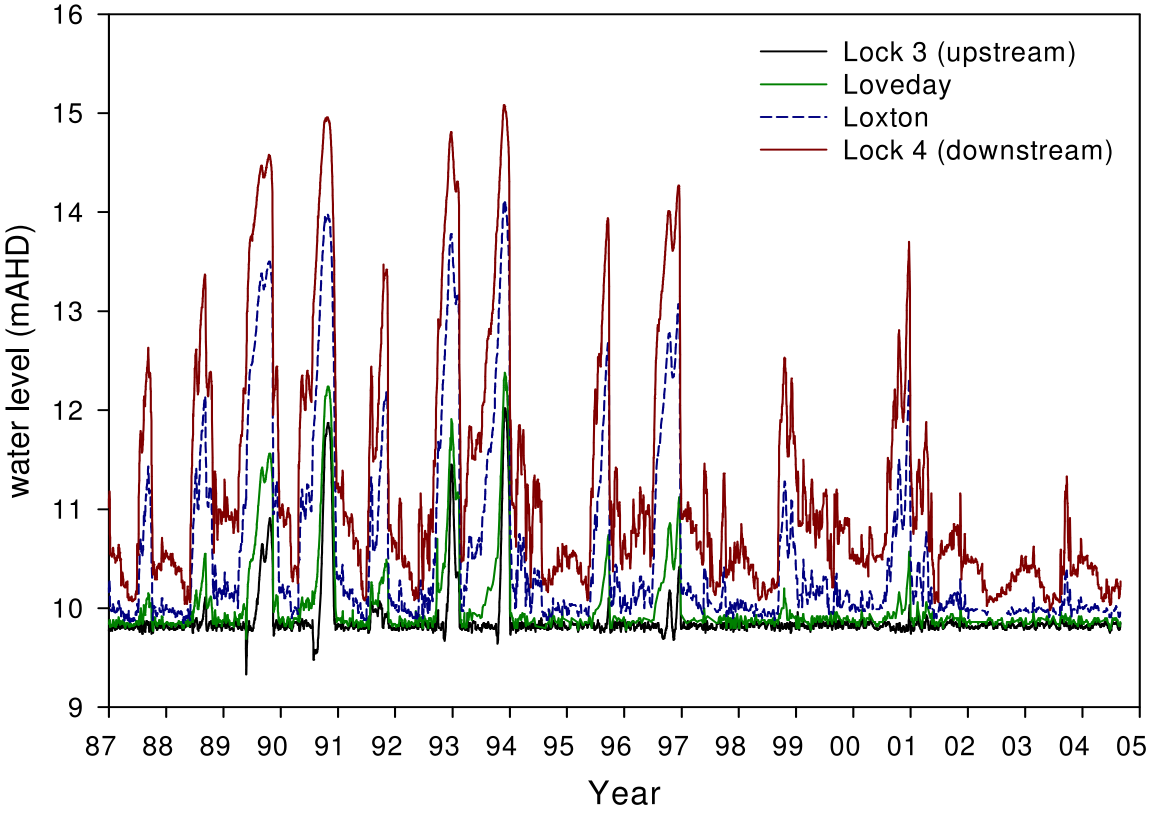

Figure 3.3. Stage hydrographs for 1987 – 2004 (mAHD) at four gauge stations along weir pool 3 of the Lower River Murray, namely: tailwater (Lock 4, downstream); upper pool (Loxton Pumping Station), middle pool (Loveday Pump station) and lower pool (Lock 3, upstream) at 516.2, 493.9, 446.9 and 431.4 river km from Murray Mouth, respectively. Water levels in m Australian Height Datum (AHD). Designated pool level upstream of Lock 3 is 9.8 mAHD

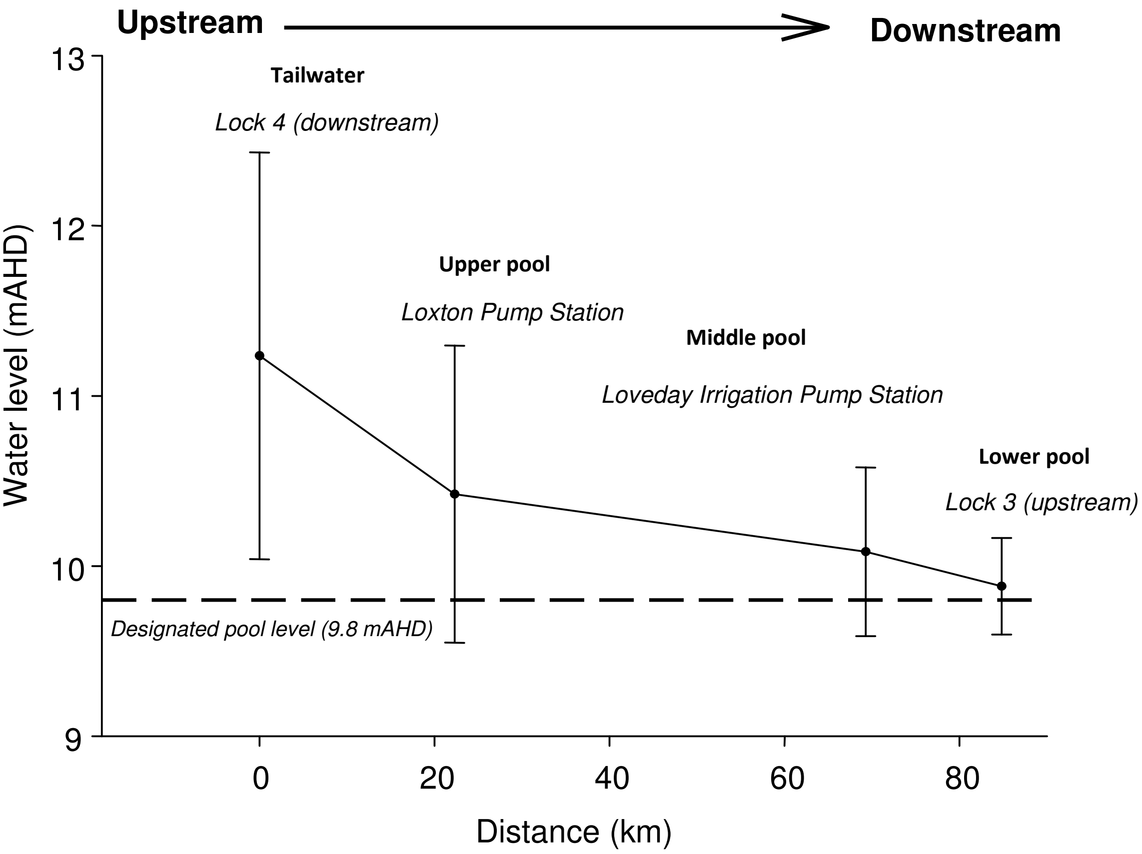

Figure 3.4. Mean water-levels (mAHD) for 1987 to 2004 at each gauge station, namely: tailwater, Lock 4 (downstream);upper pool, Loxton Pumping Station; middle pool, Loveday Pump station; lower pool, Lock 3 (upstream) along weir pool 3 of the Lower River Murray. Total pool length 84.8 km. Zero indicates Lock 4 (downstream) gauge station. Data points show mean daily water variation ± S.D.

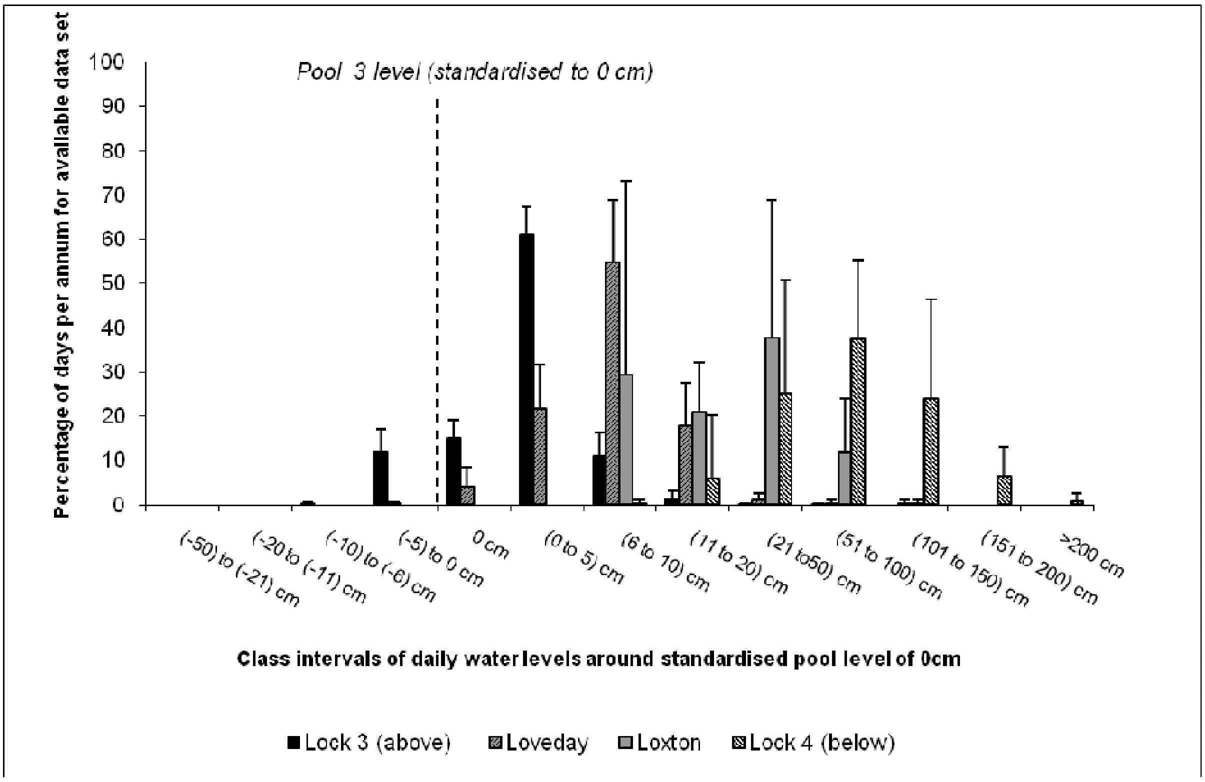

Figure 3.5. Mean percentage of days per annum that daily water level at each gauge location, namely: tailwater, Lock 4, downstream; upper pool, Loxton Irrigation Pump station; middle pool, Loveday Pump Station; and lower pool, Lock 3, upstream, fell into each class interval around the Pool 3 level. Zero indicates the pool 3 level (true elevation 9.8 m Australian Height Datum (AHD)). Data points show mean ± S.D. Data from 1994, 1997, 1999 and 2001 – 2003 (n = 6) records.

3.3.2 Overbank pulses

High river water levels leading to overbank pulses occurred in 11 of the 17 years monitored (overbank pulse = daily river water levels exceeded 9.8 mAHD designated pool level for more than 50 consecutive days) (Fig. 3.2). Overbank pulses with the highest river-water levels occurred in 1989, 1991, 1992-93 and 1994. Between the years 2001 to 2003 there were extremely low flows (Figure 3.2 & Chapter 6). Overbank pulses typically occurred from mid-winter to spring, although there were exceptions such as the late overbank pulses that occurred from November (1992) to early February (1993) (Figure 3.2).

The mean rates of overbank pulse rise did not vary significantly between monitoring stations ($F_{3,\ 38} = 1.18$, $p = 0.33$, Table 3.3). However the duration of overbank pulses did vary between monitoring stations ($F_{3,\ 41} = 11.11$, $p < 0.00$) with the mean number of days that water levels rose as a result of an overbank pulse at Lock 4 (downstream) and Loxton stations being much longer (106.36 and 97.82 days, respectively) than at Loveday and Lock 3 (upstream) stations, 52.36 and 41.56 days, respectively (Table 3.3).

The mean rates of overbank pulse recession varied significantly between monitoring stations ($F_{3,\ 38} = 4.82$, $p = 0.007$, Table 3.3). Mean recession rates at Lock 4 (downstream) and Loxton stations were greater (8.38 and 8.58 cm day^{-1}, respectively) than the mean recession rates at the Loveday and Lock 3 (upstream) stations (3.41 and 3.18 cm day^{-1}, respectively) (Table 3.3). There were no significant differences in the duration of overbank pulse recession between monitoring stations ($F_{3,\ 41} = 2.02$, $p = 0.13$) (Table 3.3).

Table 3.3 Summary of characteristics of the weir pool 3 of the Lower River Murray, South Australia during within-bank or overbank pulses based on data presented in Sections 3.3.1 & 3.3.2. Daily water level data recorded between 1987 - 2003. (Irrigation Office, Department of Water, Land and Biodiversity Conservation, SA Govt). For overbank pulse analysis, data are mean ± S.D and ranges are given in parentheses. The same letters represent values that are not significantly different at α =0.05 level according to Tukey-Kramer honestly significant different test.

	Characteristics	***Tail-water*** *Lock 4, downstream*	***Upper Pool*** *Loveday*	***Middle Pool*** *Loxton*	***Lower Pool*** *Lock 3, upstream*
Within-bank pulse	Range of daily water-level variation	0.06 to > 2 m	0.06 to ≤ 1.5 m	-0.05 to ≤ 1.5 m	-0.1 to ≤ 1 m
	Most frequent interval daily water-levels recorded around pool level	0.5 – 1 m	0.21 - 0.5 m	0.06 – 0.1 m	0.01 – 0.05 m
	Proportion of days per annum daily water-levels recorded in this interval	37.21 ± 22.5%	37.73 ± 17.3%	54.71 ± 9.7%	60.96 ± 5.6 %
Overbank pulse	Overbank pulse seasonality	--------------------Typically mid-winter to spring------------------			
	Rate of overbank pulse rise (cm day^{-1})	2.82 ± 0.87^{A} (1.53– 4.85)	2.47 ± 0.61^{A} (0.95– 3.07)	1.90 ± 0.95^{A} (0.75– 3.59)	2.54 ± 1.2 ^{A} (0.92 – 4.6)
	Duration of overbank pulse rise (days)	106.36 ± 32.18^{B} (46– 141)	97.82 ± 28.59^{B} (46– 154)	52.36 ± 30.79^{A} (7 – 105)	41.56 ± 32.93^{A} (11– 113)
	Rate of overbank pulse recession (cm day^{-1})	8.38 ± 5.24^{B} (3.13 – 22.07)	8.58 ± 5.05^{B} (3.04 – 20.36)	3.41 ± 2.18^{A} (1.3 – 7.97)	3.18 ± 2.29^{A} (0.25 – 7.26)
	Duration of overbank pulse recession	41.27 ± 18.78^{A} (15– 69)	36.20 ± 18.75^{A} (14– 58)	31.60 ± 12.98^{A} (18 – 50)	27.75 ± 14.79^{A} (8– 50)

Downstream of weir → Upstream of weir

Decreasing variability in water level

3.3.4 Tree distribution

The abundance of *E. camaldulensis* along weir pools 3 and 4 was intermediate (Table 3.2) and uniform ($p > 0.05$) (Table 3.7), with distinct monotypic stands of trees with distinct canopies uniformly distributed across both banks of weir pools 3 and 4. *Acacia stenophylla* scored the next highest abundance, with scattered, individual trees uniformly distributed ($p > 0.05$) along both banks of weir pools 3 and 4 (Table 3.8 and Figs. 3.6 & 3.7). Low mean abundance scores indicate that *E. largiflorens* were rarer across both weir pools than the other two native trees, but whereas distribution was uniform along weir pool 4 ($p > 0.05$) (Table 3.8 and Fig 3.6c) it was not along weir pool 3 ($p < 0.05$) (Table 3.8 and Fig. 3.7c). Low mean abundance scores for *S. babylonica* also indicate that they were rare, but abundance was generally not uniformly distributed across most pools (both banks of weir pool 3 ($p < 0.05$) and eastern bank of weir pool 4 ($p < 0.05$)) (Table 3.8; Figs. 3.6d and 3.7d).

A logistic regression test was carried out to determine the likelihood of occurrence of each species in relation to distance along the two weir pools. Although the results are largely inconclusive, some general trends can be determined. Overall the likelihood of occurrence of the native trees tends to be relatively consistent across weir pools (Table 3.9; Fig. 3.8); however likelihood of encountering *E. camaldulensis* is greatest, followed by *A. stenophylla* then *E. largiflorens* (Table 3.9; Fig. 3.8). For *S. babylonica,* the likelihood of occurrence is significantly related to distance along a weir pool (Table 3.8), with, in most instances, presence increasing markedly with ever greater distance downstream of a lock (Figure 3.8).

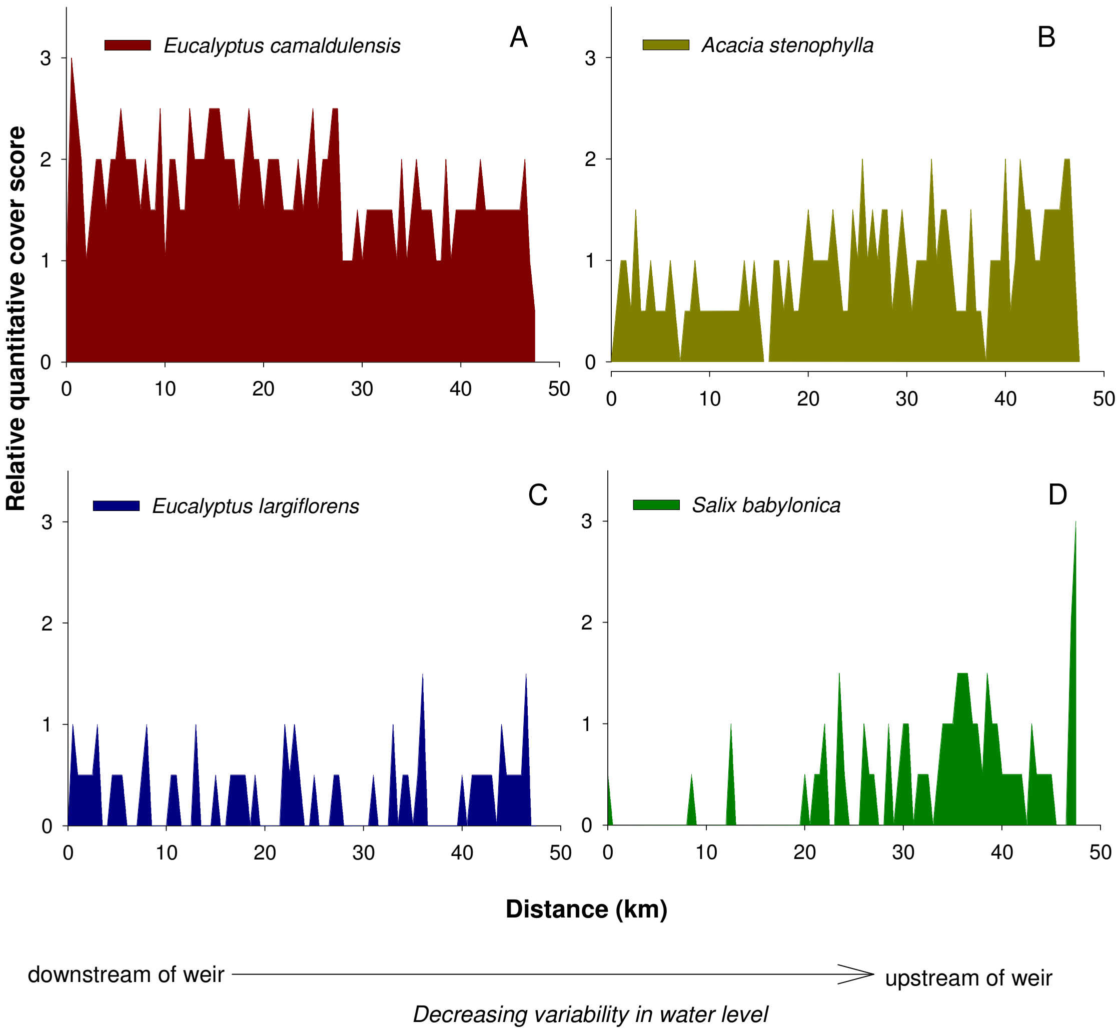

Figure 3.6. Mean quantitative relative cover scores for *E. camaldulensis* (A), *A. stenophylla* (B), *E largiflorens* (C) and *S. babylonica* (D) trees along weir Pool 4 in decreasing order of abundance. Total pool length 84.8 river km (zero denotes downstream of Lock 4).

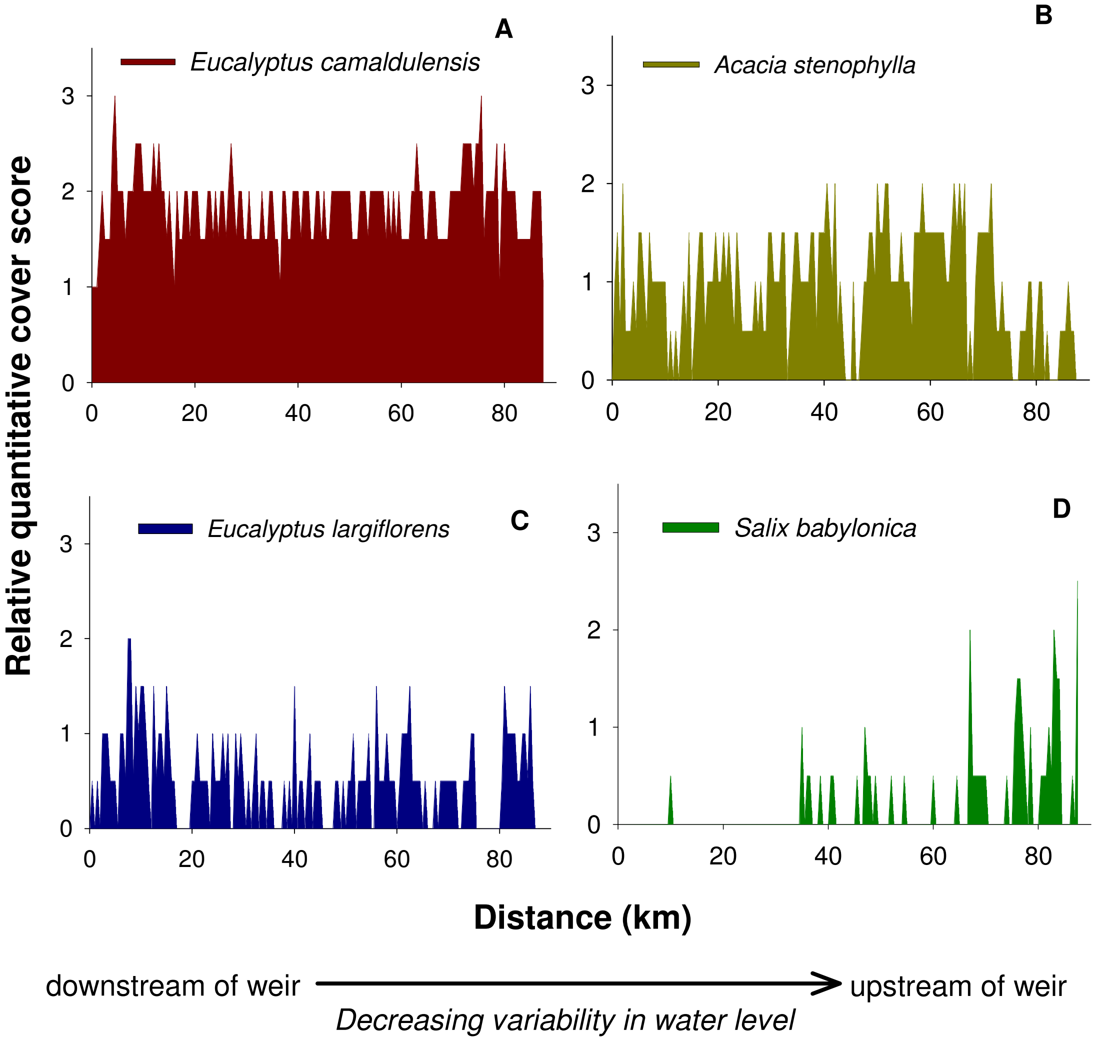

Figure 3.7. Mean quantitative relative cover scores for *E. camaldulensis* (A), *A. stenophylla* (B), *E. largiflorens* (C) and *S babylonica* (D) trees along weir Pool 3 in decreasing order of abundance. Total pool length 84.8 river km (zero denotes downstream of Lock 3).

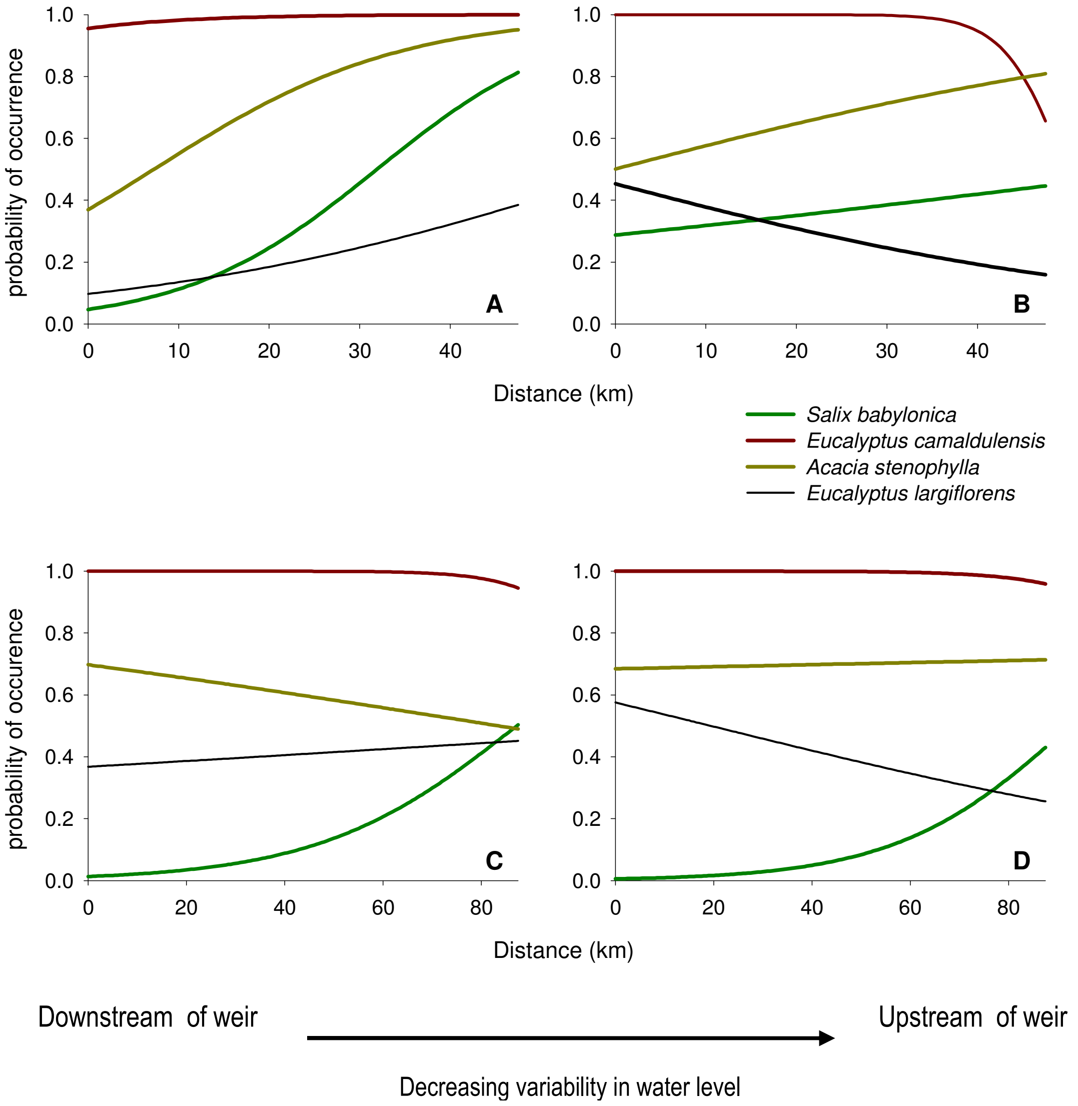

Figure 3.8. Likelihood of occurrence of *S. babylonica, E. camaldulensis, A. stenophylla* and *E. largiflorens* along the right-hand side, eastern (A) and left-hand side, western (B) banks of weir pool 4, and right-hand side, eastern (C) and left-hand side, western (D) banks of weir pool 3, Lower River Murray. Zero (km) denotes downstream of Lock 4 weir.

Table 3.8. Mean relative abundance scores (see Table 2), and chi-squared (x^2) statistics for: *E.camaldulensis*, *A. stenophylla*, *E. largiflorens* and *S. babylonica* on the eastern and western banks of weir pools 3 and 4. (Surveyed 10-11th July 2002 on the Lower River Murray). Significance at $p< 0.05$ represented by * and not significant at $p > 0.05$ represented by n.s.

Species	**Weir pool**	**Bank**	**Abundance (mean ± S.D.)**	**Chi-squared statistic**
Eucalyptus camaldulensis	3	Eastern	1.94 ± 0.04	$x^2_{(1, 175)} = 24.94^{n.s}$
Eucalyptus camaldulensis	3	Western	1.76 ± 0.04	$x^2_{(1, 175)} = 34.46^{n.s}$
Acacia stenophylla	3	Eastern	0.78 ± 0.06	$x^2_{(1, 175)} = 56.95^{n.s}$
Acacia stenophylla	3	Western	0.86 ± 0.07	$x^2_{(1, 175)} = 41.91^{n.s}$
Eucalyptus largiflorens	3	Eastern	0.36 ± 0.06	$x^2_{(1, 175)} = 158.49^*$
Eucalyptus largiflorens	3	Western	0.17 ± 0.04	$x^2_{(1, 175)} = 147.30^*$
Salix babylonica	3	Eastern	0.20 ± 0.04	$x^2_{(1, 175)} = 221.5^*$
Salix babylonica	3	Western	0.17 ± 0.04	$x^2_{(1, 175)} = 221.5^*$
Eucalyptus camaldulensis	4	Eastern	1.66 ± 0.06	$x^2_{(1, 95)} = 17.91^{n.s}$
Eucalyptus camaldulensis	4	Western	1.78 ± 0.07	$x^2_{(1, 95)} = 26.05^{n.s}$
Acacia stenophylla	4	Eastern	0.96 ± 0.07	$x^2_{(1, 95)} = 112.77^{n.s}$
Acacia stenophylla	4	Western	0.86 ± 0.07	$x^2_{(1, 95)} = 121.22^{n.s}$
Eucalyptus largiflorens	4	Eastern	0.23 ± 0.05	$x^2_{(1, 95)} = 82.73^{n.s}$
Eucalyptus largiflorens	4	Western	0.48 ± 0.05	$x^2_{(1, 95)} = 99.4^{n.s}$
Salix babylonica	4	Eastern	0.47 ± 0.07	$x^2_{(1, 95)} = 97.33^*$
Salix babylonica	4	Western	0.32 ± 0.6	$x^2_{(1, 95)} = 114.5^{n.s}$

Table 3.9. Logistic regression chi-squared (x^2) statistics for: *E.camaldulensis*, *A. stenophylla, E. largiflorens* and *S. babylonica* on the eastern and western banks of weir pools 3 and 4. (Surveyed 10-11th July 2002 on the Lower River Murray). Significance at $p < 0.001$, 0.01 and 0.05 represented by ***, ** and * respectively and not significant at $p > 0.05$ represented by n.s.

Species	***Weir pool***	***Bank***	***X^2-statistic***
Eucalyptus camaldulensis	3	Eastern	$x^2_{(1, 175)} = 1.13^{n.s.}$
Eucalyptus camaldulensis	3	Western	$x^2_{(1, 175)} = 9.85^{**}$
Acacia stenophylla	3	Eastern	$x^2_{(1, 175)} = 2.69^{n.s.}$
Acacia stenophylla	3	Western	$x^2_{(1, 175)} = 0.06^{n.s.}$
Eucalyptus largiflorens	3	Eastern	$x^2_{(1, 175)} = 0.43^{n.s}$
Eucalyptus largiflorens	3	Western	$x^2_{(1, 175)} = 6.51^{**}$
Salix babylonica	3	Eastern	$x^2_{(1, 175)} = 27.30^{***}$
Salix babylonica	3	Western	$x^2_{(1, 175)} = 0.89^{n.s.}$
Eucalyptus camaldulensis	4	Eastern	$x^2_{(1, 95)} =2.64^{n.s.}$
Eucalyptus camaldulensis	4	Western	$x^2_{(1, 95)} =2.04^{n.s.}$
Acacia stenophylla	4	Eastern	$x^2_{(1, 95)} = 15.9^{***}$
Acacia stenophylla	4	Western	$x^2_{(1, 95)} = 3.59^{n.s.}$
Eucalyptus largiflorens	4	Eastern	$x^2_{(1, 95)} = 3.52^{n.s}$
Eucalyptus largiflorens	4	Western	$x^2_{(1, 95)} = 4.05^{*}$
Salix babylonica	4	Eastern	$x^2_{(1, 95)} = 26.60^{***}$
Salix babylonica	4	Western	$x^2_{(1, 95)} = 23.63^{***}$

3.4 Discussion

Distribution of S. babylonica *and natives*

The uniform distribution patterns and high abundance of *E. camaldulensis* and *A. stenophylla* along the entire length of the weir pools suggests a broad tolerance to both variable and stable water regimes. *E. largiflorens* was largely absent to rare along the weir pools (i.e. low abundance scores). Distribution was uniform along one pool, but not the other. *E. largiflorens* woodlands tend to occupy the higher elevations and outer parts of the floodplain (MDBC 2003, Mensforth *et al.* 1994) whereas *E. camaldulensis* woodlands are more common in low lying regions along the fringes of riverbanks and in areas that are more frequently flooded (George *et al.* 2005). In the analysis, the measured abundance scores per distance for all four species were compared with a nominated intermediate abundance score of 1.5 per distance measurement, in order to assess whether abundance was uniform (or not) across a weir pool. In hindsight this nominated abundance score of 1.5 was possibly too high for *E. largiflorens* and did not reflect their rarity along riverbanks (i.e. mean abundance ranged between 0.17 – 0.48). If a ranked abundance score of 0.5 is used as a comparison in the chi-squared test instead - then no significant differences in *E. largiflorens* abundance are found across weir Pool 4 $x^2_{(1,\ 95)} = 33.5$ p >0.01 or weir Pool 3 $x^2_{(1,\ 175)} = 73.5$, p >0.01 suggesting that this species is rare, but may be found along the entire length of the weir pool.

In contrast the distribution patterns for *S. babylonica* were non-uniform; *S. babylonica* was almost completely absent immediately downstream of weirs, and increased steadily in abundance along the length of the weir pools. An investigation of common littoral and floodplain understory plants of the LRM, by Blanch *et al.* (1999), found that ~50% of the reeds and sedges surveyed were uniformly distributed along the entire length of the weir pools suggesting broad tolerances to variable water regime, but a few species (e.g. *Typha domingensis, Juncus aridicola, Vallisneria australis, Schoenoplectus validus*) were only found in permanently flooded river reaches, suggesting a requirement for stable water regimes. Similarly, my data suggest that *S. babylonica* also requires relatively stable water regimes characterised by daily water variations of <0.1 m day^{-1}.

Water level variability

Variability in daily water levels when the river-water is within banks may have significant effects on species within woody riparian vegetation during their regeneration phase (Roberts *et al.* 2000). Although periods of exposure, potentially alleviate the effects of constant inundation, this may also increase water stress in recruits and juveniles since they are usually dependent upon surface water and/or shallow precipitation derived sources for the first few growing seasons (Shafroth *et al.* 2000). Seedlings of many North American *Populus* and *Salix* taxa are dependent upon continually saturated conditions or slow water drawdown rates (<2 cm day^{-1}) so developing roots can maintain access to water (Amlin and Rood 2001, Amlin and Rood 2002, Horton and Clark 2001b, Kranjcec *et al.* 1998, Mahoney and Rood 1991). On the other hand, in North America, invasive *Tamarix ramosissima* seedlings can tolerate rapid drawdown rates (up to 4 cm day^{-1}), possibly as result of their greater root elongation rates. *T. ramosissima* seedlings therefore tend to persist at higher positions along river to floodplain elevation gradients (Casanova 1994, Cooper *et al.* 1999, Shafroth *et al.* 2000, Roelle *et al.* 2001). Similarly, *Acacia* and *Eucalyptus* spp. tend to produce bimodal root systems (Awe *et al.* 1976) with extensive lateral growth and deep tap roots that penetrate to depths > 20 m (Stone and Kalisz 1991).

When water is limited, *E. camaldulensis* seedlings can allocate more biomass to root systems (Gibson *et al.* 1994, Gibson *et al.* 1995, Li 1998). Deep, responsive root systems, would allow trees like *T. ramosissima* and *E. camaldulensis* to switch to deeper, stable groundwater sources when surface water sources are unreliable (Jolly and Walker 1996, Mensforth *et al.* 1994). In contrast, there is no evidence that established *S. babylonica* trees possess deep root systems capable of accessing alternative water sources during periods of low flow, and therefore their distribution is inhibited. Observations of established *S. babylonica* trees (during the survey period) that had been removed mechanically from riverbanks during removal operations indicated that a large proportion of root growth was constrained to the upper 0.5 m of the soil profile (*personal observations*).

The strong lateral root development in *Salix* is suggested to be a protective adaptation against the erosive effects of flood scour (Horton *et al.* 2001b, Schutten *et al.* 2005). However my results show that, along the LRM, *S. babylonica* are unlikely to experience flood scour as it is the regions below weirs that experience the greatest potential for high current and increased wave action. In the tail-waters immediately below locks, bank complexity is often reduced while sediment erosion is increased and deposition decreased, especially during episodes of overbank pulses (Thoms *et al*. 2000). It is possible that *S. babylonica* propagules may be particularly vulnerable to the erosion below weirs during their recruitment and establishment phases (Walker 1985, Levine and Stromberg 2001, Walker 2001). Yet the recruitment of asexual, invasive *S. nigra* in south east Australia is correlated with the level of river disturbance index (RDI) (associated with flooding frequency), with the likelihood of finding asexual recruits increasing with increasing RDI (Stokes and Cunningham 2006). In contrast, my field observations, where *S. babylonica* were only present in regions characterised by stable water regimes with minimal disturbance, suggest that *S. babylonica* establishment is less likely in areas of greater disturbance.

Inundation

The effects of inundation will also influence the regeneration and maintenance phases of riparian vegetation (Bendix and Hupp 2000, Roberts *et al.* 2000). For example, the time and duration of periods of inundation could prevent the establishment of woody vegetation occupying sites close to the water (Keddy and Reznicek 1986). There were significant differences along weir pools in terms of the timing and duration of overbank pulses and lead to inundation. In the regions immediately below a weir, episodes of overbank pulse typically started in mid-winter and persisted for up to 100 days before receding. Trees native to the LRM such as *E. camaldulensis* and *E. largiflorens* rely upon winter-spring flooding for seedling recruitment (Dexter 1978, George *et al.* 2005, Roberts and Marston 2000, Jensen *et al.* 2008). But *S. babylonica* trees are dormant during winter, hence even if propagules are broken off, dispersed and deposited, the timing of inundation may mean they are unlikely to grow and establish for several weeks. On the other hand, in the regions above a weir, episodes of overbank pulse start later in spring (possibly reflecting the travel time between weirs), when *S. babylonica* are active.

The differences in the duration of overbank pulses along a weir pool may also be important. Native *E. camaldulensis* seedlings can produce adventitious roots in response to flooding and tolerate up to ~110 days of inundation and submergence (van der Moezel *et al.* 1988). Similarly most *Salix* taxa are supposedly tolerant of waterlogged conditions because they too can produce long-lived adventitious roots (Grosse *et al.* 1996, Krasny *et al.* 1998). Ohmann *et al.* (1990) even found that some *Salix* taxa can accumulate biomass and grow faster under submergence regime of up to 60 days per growing season. This suggests that for some *Salix* taxa, some flooding is preferential to no flooding at all, although de Oliveiria and Piedade (2000) found that for established *Salix martiana* trees on the whitewater floodplains of Central Amazonia (Brazil) prolonged submergence of >120 days decreased survivorship. At the time of this survey, there was no available information about the flooding tolerance of *S. babylonica*, but this was further investigated in Chapter 4 since it is possible that propagules are only likely to establish where flooding duration is relatively short, such as in the regions immediately above weirs, where typical overbank pulse duration times found in this study were ~ 35 days.

Exposure

The differences in the rates of water recession following an overbank pulse could also be a factor influencing the observed distribution patterns in *S. babylonica*. In the regions above a weir, recession rates were typically slower (ranging from 0.25 to 7.5 cm day^{-1}) as opposed to the rapid recession rates experienced in the regions below a weir (ranging 3 to > 20 cm day^{-1}). As mentioned previously rapid drawdown (>2 cm day^{-1}) of surface water following inundation has been shown to inhibit seedling establishment in other *Salix* taxa (Mahoney and Rood 1991). Even if *S. babylonica* were to establish in the regions below weirs following an inundation episode, the daily water level variations of more than ±20 cm day^{-1} during periods when the river is within its banks, may inhibit *S. babylonica* growth in the first few seasons, especially if they are reliant on surface-water.

Elevation

It is possible that the characteristics of a water regime that most influence distribution of riparian vegetation are the depth of inundation and the extent of dry periods (Grace and Wetzel 1982, Smith and Brock 2007). Thus, elevation above river level is an important consideration as it influences the extent of inundation and exposure that plants will experience (Denneler *et al.* 1999). A lower position on an elevation gradient may increase access to a greater variety of water sources (e.g. river-water, ground water) in the long-term (Chapter 5). However, there is also likely to be an increase in the potential for prolonged episodes of water-logging or submergence, especially in recruits (Chapter 4). Most *Salix* were introduced to Australia after many of the weirs were constructed in the 1920- 1930's (Perkins 1903, Smith 1998), however, it is possible that their distribution not only reflects the regulated regime, but also, to a degree, historical plantings (e.g. around townships). This could explain the persistence of a few individuals in river reaches that seem to be outside of the apparent tolerance threshold (i.e. >-0.2 to 0.5 m day^{-1} variation in daily water levels). On the other hand, many of the established native trees on the LRM are likely to be more than 100 years old (Margules and Partners 1990), and it is possible that their ubiquitous and uniform distribution along the upstream to downstream gradients reflects their tolerance to the history of flow regimes prior to regulation. Indeed, Roberts and Ludwig (1991) found that *E. camaldulensis* were growing in the extreme ends of gradients related to exposure to wave action and current flow, which suggests they are tolerant to greater levels of disturbance. In my study, age class scores relative to distances were not recorded since it is only recently that a method for determining the age of trees native to the LRM has been developed (George *et al.* 2005), although in hindsight it would have been possible to score height classes to provide some data on age structure. The use of historical and current aerial photographs would assist riparian vegetation analysis

(Oetter *et al.* 2004), but these are generally unavailable for large sections of the LRM. If available, aerial photographs and satellite data would enable analysis of vegetation dynamics, especially vegetation changes following flood disturbances (Muller 1997), also correlating riparian vegetation associations with landscape attributes such as soils, elevation gradients and water sources (Peterson *et al*. 2005).

Chapter 4

Effect of different hydrological water regimes on the establishment of *Salix babylonica* propagules and native tree seedlings (*Eucalyptus camaldulensis* and *Acacia stenophylla*).

4.1 Introduction

The previous chapter reported that *S. babylonica* is more likely to be present above weir structures where water regimes are relatively stable, but absent for some distance below the locks where water levels are comparatively unpredictable and highly fluctuating (i.e. > 0.2 m day^{-1}). It is possible that highly fluctuating water levels experienced in the tail-water environments of weir pools inhibit the establishment and growth of *S. babylonica* propagules. On the other hand, the likelihood of occurrence of native trees, such as *E. camaldulensis* and *A. stenophylla*, across the weir pools was not related to variable water levels, suggesting that distribution, growth and survival is independent of water regimes created by weir operations.

Environmental gradients reflect patterns of environmental variation across four dimensions (i.e. longitudinal, lateral, elevation and temporal scales) (Ehrenfeld *et al.* 1997). Variation in vertical dimensions related to elevation, or temporal scales, may be just as important as the horizontal longitudinal and lateral dimensions that account for spatial variation because it influences the extent of inundation and exposure that vegetation experiences (Keddy and Reznicek 1986, Denneler *et al.* 1999). A lower position on an elevation gradient may increase access to a greater variety of water sources (e.g. river-water, precipitation-derived soil-water and/or ground water) in the long-term (Shafroth *et al.* 2000, Synder and Williams 2000), however, on daily to seasonal scales, episodes of inundation and oxygen deprivation (as a result of substrate saturation) or sudden re-exposure to a fully aerated environment, would increase (ca. Ponnamperuma 1984, Kozlowski 1997, Braendle and Crawford 1999, Sand-Jensen and Frost-Christensen 1999).

Plants use a variety of allometric (e.g. leaf area per total mass of plant, plant height, biomass partitioning), developmental (e.g. leaf and meristem canopy structure), metabolic (e.g. leaf photosynthetic capacity and respiration losses) and phenological (e.g. leaf and plant lifespan and seasonal activity) variables to maximise growth (Korner 1991). The importance of any one of these growth variables is often species-specific and influenced by environmental pressures. In environments with low productivity (e.g. low nutrient and water availability and/or high herbivory), increased root mass allocation and improved leaf longevity may aid survival whereas in highly productive environments increased leaf expansion may help to increase competitiveness (Poorter 1989).

Many species are sensitive to episodes of water-logging and top-flooding, especially juveniles (Bowman and McDonough 1991, Tardif and Bergeron 1999, Roberts *et al.* 2000) and hence allometric, developmental, metabolic and phenological factors may be affected. Increasing water levels can restrict access to atmospheric CO_2 (Čížková-Končalová *et al.* 1992) and oxygen (Yamasaki 1984, Sorrell and Tanner 2000), so plants may respond by elongating leaves and/or or stems to maintain an emergent canopy (Waters and Shay 1990, Sorrell *et al.* 2002) or increasing biomass allocation to adventitious roots (Pezeshki *et al.* 1998) and/or producing aerenchymous tissue (Bacon *et al.* 1993, Blom and Voesenek 1996) to enhance gas exchange (Flessa 1994, Kozlowski 1997, Lorbiecke and Sauter 1999). However, some are incapable of adjusting growth in response to flooding. Such as when *Betula papyrifera* seedlings experienced top-flooding for ≤60 days, shoot growth and root growth was reduced and the growth of leaves that had formed prior to flooding were shed, and the formation of new leaves prevented (Tang and Kozlowski 1982). Similarly, when waterlogged for a period of 80 days *Eucalyptus robusta* seedlings exhibited signs of leaf chlorosis, premature leaf abscission, reduced stem elongation and formation of adventitious roots (Clemens and Pearson 1977). As discussed in Chapter 3, *Salix* taxa that occur on frequently inundated sites produce numerous adventitious roots; usually within a few days of flooding (Carlson 1938, Krasny *et al.* 1988). Some *Salix* taxa found growing in continuously saturated soils often form pink aerial root tips that are believed to enhance root aeration (Gill 1970) and adventitious roots in response to water-logging (Jackson and Attwood 1996) in some taxa flooding is preferential to no flooding at all (Ohmann *et al.* 1990), although if the duration of flooding is prolonged then growth may be impaired (de Oliveiria and Piedade 2000). Similarly, for *E. camaldulensis* they too are able to produce adventitious roots in response to flooding but survivorship may be seriously reduced if periods of inundation exceeded ~110 days (van der Moezel *et al.*1988).

The position of recruits along hydrologic and elevation gradients will also determine the magnitude and duration of drying episodes they are exposed to in the first few growing seasons. Increased episodes of exposure, although alleviating the effects of inundation, may lead to water stress in establishing trees since most riparian seedlings and propagules are dependent upon surface water and shallow soil-water precipitation sources for the first few growing seasons because of their shallow, developing roots systems (Shafroth *et al.* 2000). Establishing tree seedlings that are capable of rapid root extension to reach relatively permanent soil-water and alluvial groundwater sources, may improve their ability to persist during prolonged periods of exposure (Jonsson *et al.* 1988, Stone and Kalisz 1991, Stromberg 1998, Tedala 2004, Nasra *et al.* 2005).

On the LRM, *A. stenophylla* are found not only on the riverbank edges, but also extend out into the floodplains in association with native *Eucalyptus largiflorens* trees and *Muehlenbeckia florulenta* shrubs. *E. camaldulensis* tend to be more dominant along the riverbank and lower lying floodplain regions (Walker 2001) and as previously mentioned, *S. babylonica* are confined to the riverbank edge only. At present, there is only limited information about the optimal environmental conditions that promote germination and subsequent establishment requirements in many of these riparian species (Chong and Walker 2005, George *et al.* 2005, Jensen *et al.* 2008).

This study was conducted to determine if water regime and/or elevation are the key factors influencing the establishment of *S. babylonica* propagules and native seedlings. The relative tolerances of *S. babylonica* and native trees, *E. camaldulensis* and *A. stenophylla*, to a range of fluctuating water regimes along an elevation gradient were investigated. It was hypothesised that *S. babylonica* propagules would have a greater tolerance for static and moderate fluctuating water regimes (± 0 – 15 cm day^{-1}) compared to highly fluctuating water regimes (>15 cm day^{-1}), as expressed by a greater biomass accumulation, relative growth rates and leaf area ratio, due to their preference for slow drawdown rates when establishing and sensitivity to water-limiting conditions. Higher growth rates in *S. babylonica* are also predicted to confer a higher specific leaf area (SLA) and a greater allocation to leaf area and lateral canopy structure (i.e. greater allocation to second-order (2°) branches, etc.) compared to the natives, especially under static and moderately fluctuating water regimes, because of their distinctive "weeping" growth habit with decumbent branching (on ground). It was also expected that the survival and growth of establishing native tree seedlings *E. camaldulensis* and *A. stenophylla* would be independent of water regimes.

It was also predicted that the inundation tolerances would reflect the natural distribution of the species across riverbank elevation gradients in the field, with greater survivorship and growth of *S. babylonica* at lower elevations due to their ability to produce numerous lateral roots and adventitious roots which are advantageous in water-logged conditions. Greater survivorship and growth of the native species at higher elevations (non-water-logged) was expected due to their ability to rapidly produce extensive, deep root systems that can access deeper groundwater sources and their limited ability to tolerate saturated soil conditions for extended periods of time.

4.2 Methods

4.2.1 Plant Material

Cuttings of *S. babylonica* (~ 10-16 primary nodes per cutting with a diameter of 0.5 – 1 cm) were harvested from second year growth of mature trees (locality: Kingston-On-Murray, LRM: 34° 13' 18.37"S, 140° 20' 46.17"E) in late September 2002. Cuttings were then kept in cold storage and within 1 – 2 days of harvesting were potted into 0.5 L seedling bags, filled with coarse sand. Cuttings were left to strike and establish for a further 10 weeks with daily watering. Two months later, tube stock seedlings of *E. camaldulensis* and *A. stenophylla* (12-16 weeks old) were purchased from a private nursery (Berri Native Plants: seeds sourced from Kingston-On-Murray, LRM).

4.2.2 Establishment Phase

On 27th January (2003) the established seedlings/cuttings of each species were potted up into 25 L potting bags and allowed to harden off for a further 2 weeks with daily watering. The bags were filled with 60:40 mix of sandy loam mix which was selected for its consistent texture, composition and low nutrient availability (Morris 1998). So that the plants were not nutrient-limited during the experiment, a slow release fertiliser (Osmocote®: Osmocote Plus®: Scotts Australia) was incorporated into the top 15 cm of the soil at 10 g per bag in a 70: 30 ratio to ensure an adequate supply of macro and micronutrients (Morris 1998) at an equivalent loading of 100 g N m^{-2} $yr^{-1.}$ All filled bags were then topped with a 3 cm layer of cricket pitch clay as a means of preventing nutrient leaching once the bags were in the ponds.

The day before the pond experiment was implemented (8th February 2003), juvenile plants (n = 20 per species) were randomly selected and harvested to determine initial parameters for growth analysis. Leaf areas (m^2) of fresh leaves were measured using a Delta-T leaf area meter (Delta-T Devices Ltd. Cambridge, England). Harvested plants were divided into leaves, stems (non-leaf) and roots, oven dried for 72 hours at 80°C and the dry weights measured. Canopy architecture was assessed by measuring nodal distribution and branching order (see Fig. 4.1).

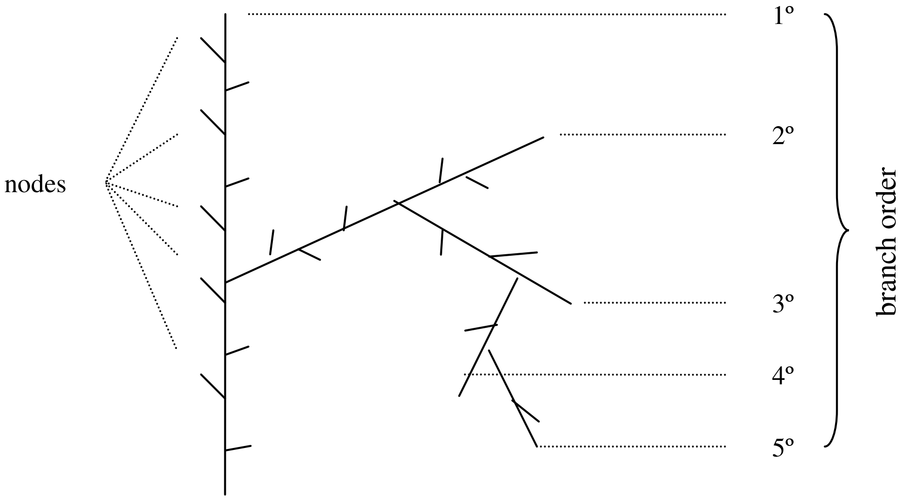

Figure 4.1. Diagram illustrating classification of branching order (1° = first-order, 2° = second-order, 3° = third-order, 4° = fourth-order, 5° = fifth-order) and nodes of propagules and seedling trees.

From the remaining juvenile trees, 96 replicates per species were selected and randomly allocated amongst three outdoor ponds (4.5 m × 3.5 m × 1.2 m deep). The seedlings and propagules were then transplanted into Ribloc® columns with a height of either: 100, 75, 50 or 25 cm (× 30 cm diameter). The columns ensured pots were at elevations of either: -25, 0, + 25 and +50 cm; relative to the baseline surface water within the pond. Each column was filled with 60:40 mix of sandy loam to be used as a base to allow a 25 L potting bag, containing the seedling and propagules, to be inserted at the top. The bags were perforated at the bottom so that sufficient contact between the potting soil and Ribloc column soil would allow capillary uptake (see Fig. 4.2).

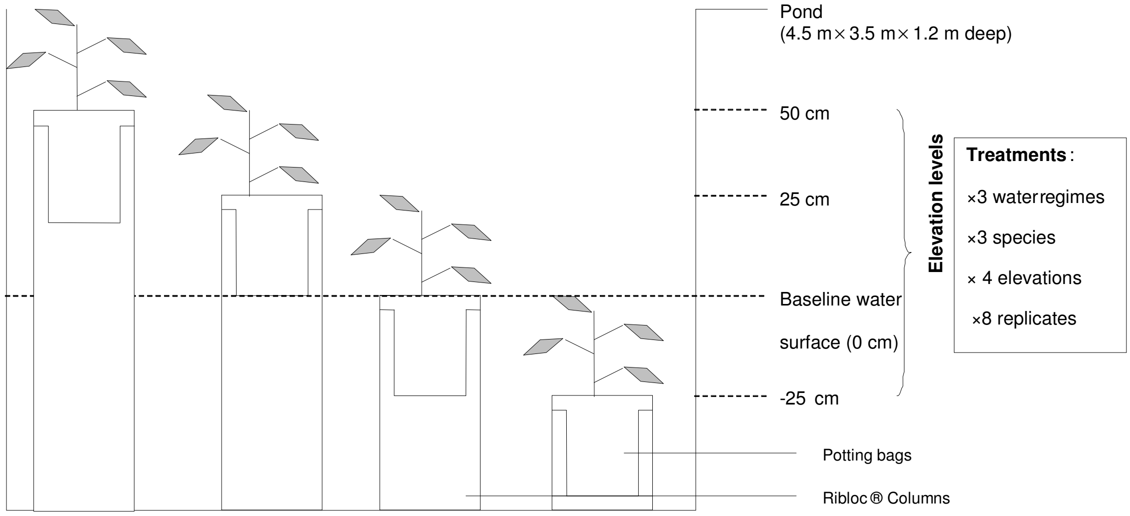

Figure 4.2. Schematic of experimental design to test effects of static, moderate and high fluctuating water regimes.

4.2.3 Water Regimes

Characteristic weir pool water regimes were determined from stage hydrograph data of water-level variations at four gauge sites along weir pool 3 during the period of 1987-2004 (see Chapter 3). Initially, the water level in each pond was raised 3 cm day^{-1} until it reached the baseline water surface level. Three water regimes were then employed for a period of 72 days around this baseline level (0 cm): static (0 cm day^{-1}), moderate (± 5 – 15 cm day^{-1}) and high (± 20 – 50 cm day^{-1}) (Fig. 4.3). The static water regime simulated the water regime commonly experienced in the lower pool regions of weir pools. The moderate water regime simulated a water regime that is frequently experienced in the middle pool of weir pools and likewise the high water regime simulated that commonly experienced in the upper pools and tailwaters of weir pools (see Chapter 3). The experiment ran for 72 days (9th February until 22nd April, 2003).

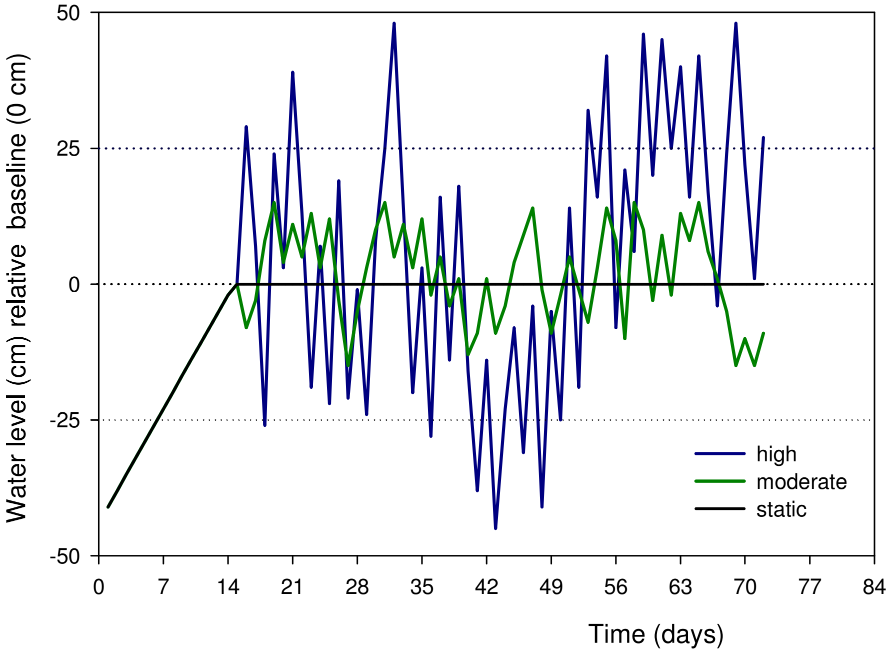

Figure 4.3. Simulated experimental water regimes. Static regime (0 cm day-1), moderate regime (± 0.05 – 0.15 m day-1) and high regime (± 0.2 – 0.5 m day-1).

4.2.4 Data Collection and Analysis

At the end of the experiment, survivorship for each species and treatment level was determined. As plants were harvested, a sub-sample of five replicate trees of each species was randomly selected from each treatment and each pond for measurements of node distribution and branch order to determine canopy architecture (Fig 4.1). From this same sub-sample, a further sub-sample of leaves from *S. babylonica* and *E. camaldulensis* and phyllodes from *A. stenophylla* (herein referred to as leaves) were harvested and leaf area (cm^2) determined (L_A) and the leaves were dried for 72 hours at 80ºC and leaf dry weight (g DW) measured. These measurements were used to determine the relationship between L_A and leaf dry weight (g DW) for each species from each elevation treatment level. Final total leaf area (cm^2) for each replicate was then determined using these relationships (Table 4.1) from the values of total leaf weight (g DW).

Table 4.1. Linear relationships for leaf area (cm^2) to leaf weight (g DW). L_A = leaf area, L_W = leaf weight.

Species	**Elevation**	**r^2**	**p-value**	**Equation**
Salix babylonica	+50	0.86	<0.0001	$L_A = 4.75 + 11.82\ L_W$
	+25	0.92	<0.0001	$L_A = -0.29 + 16.44\ L_W$
	0	0.94	<0.0001	$L_A = 1.45 + 14.90\ L_W$
	-25	0.26	0.65*	$L_A = 1.94 + 2.89\ L_W$
Eucalyptus camaldulensis	+50	0.87	<0.0001	$L_A = 1.67 + 9.65\ L_W$
	+25	0.82	<0.0001	$L_A = 4.44 + 9.88\ L_W$
	0	0.84	<0.0001	$L_A = 3.83 + 6.70\ L_W$
	-25	0.76	<0.0001	$L_A = 3.42 + 5.14\ L_W$
Acacia stenophylla	+50	0.81	<0.0001	$L_A = -1.19 + 3.10\ L_W$
	+25	0.59	0.0014	$L_A = 1.50 + 1.66\ L_W$
	0	0.53	0.0062	$L_A = 0.60 + 2.05\ L_W$
	-25	0.96	<0.0001	$L_A = -0.02 + 2.84\ L_W$

*relationship not significant and therefore data not included in analysis.

All trees were then harvested washed and divided into leaf, stem (non-leaf), root and adventitious roots (if present) components and dried for 72 hours at 80ºC and the dry weight measured. Measurements of leaf weight ratio (LWR), stem weight ratio (SWR) and root weight ratio (RWR) provided a dimensionless index of biomass partitioning of plants to leaf, stems and roots on a weight basis and were calculated following Evans (1972) where:

Equation 4.1

$$\mathrm{LWR}=\frac{\text{total leaf weight}}{\text{total biomass}}\ (\mathrm{gDW})$$

Equation 4.2

$$\mathrm{SWR}=\frac{\text{total stem weight}}{\text{total biomass}}\ (\mathrm{gDW})$$

Equation 4.3

$$\mathrm{RWR}=\frac{\text{total root weight}}{\text{total biomass}}\ (\mathrm{gDW})$$

The following growth parameters: relative growth rate (RGR), net assimilation rate (NAR), leaf area ratio (LAR), specific leaf area (SLA) were calculated according to Evans (1972) and Hunt *et al*. (2002).

Equation 4.4

$$\mathrm{RGR}=\frac{ln\,W_2 - ln\,W_2}{t_2 - t_1}\ (\mathrm{gm^{-2}day^{-1}})$$

Where W_1 and W_2 are plant dry weights (g DW) at times t_1 and t_2 (days).

RGR can be further divided into two components, the net assimilation rate (NAR) and the leaf area ratio (LAR).

Where RGR = NAR ×LAR

NAR is defined as the rate of increase in plant biomass per unit leaf area per unit time and is closely connected with the photosynthetic activity of the leaves whereas LAR is the leaf area per gram total biomass and can be viewed as a morphological index of plant form(Evans 1972, Harper 1977, Hunt *et al.* 2002).

Photosynthetic leaf areas are L_1 and L_2 (cm^2).

Equation 4.5

$$\mathrm{NAR} = \frac{W_2 - W_1}{t_2 - t_1} \times \frac{\ln L_2 - \ln L_1}{L_2 - L_2} \ (\mathrm{gm^{-2}\ day^{-1}})$$

Equation 4.6

$$LAR = \frac{L_2 - L_1}{W_2 - W_1} \times \frac{\ln W_2 - \ln W_1}{\ln L_2 - \ln L_1} \ (\mathrm{m^{-2} kg^{-1}})$$

LAR can be further sub-divided into two other components LWR (Equation 4.1) and specific leaf area (SLA),

Equation 4.7

$$\mathrm{SLA} = \frac{\text{leaf surface area}}{\text{total leaf weight}} \ (\mathrm{m^{-2}\ kg^{-1}})$$

Where: LAR = SLA × LWR

4.2.5 Statistical Analysis

Separate analyses were done to compare differences in total biomass and the growth analysis variables (i.e. RGR, NAR, LAR, SLA, LWR, SWR and RWR) between species and the treatment factors of water regime and elevation, using a three-factor analysis of variance (3- way ANOVA). Differences in node distribution relative to branch order between water regime and elevation were analysed separately for each species, using a two-factor analysis of variance (2-way ANOVA). Means were compared by Tukey-Kramer honestly significant difference test (Tukey's HSD) when appropriate. Data were log transformed (total biomass and node distribution) or log (x + 1) transformed to meet assumptions of normality and homoscedasticity and for all statistical tests $\alpha = 0.05$. Data were analysed using JMP-IN (vers. 3.2.6 or 4.0.3).

4.4 Results

4.4.1 Exposure/Inundation

In all water regimes, plants were slowly inundated for a period of 14 days as water levels were raised to the baseline water surface level (0 cm) (Fig. 4.3). Following this period substrate and root mass, and some proportion, if not all of the aerial portion of the plants at the -25 cm elevation were permanently top-flooded in the static water regime. Likewise the substrate and root mass of plants at the 0 cm elevation were also permanently water-logged, but aerial portions remained fully exposed. Seedlings/propagules at +25 and +50 cm elevations experienced no water-logging or top-flooding.

In the moderately variable water regime, where water levels fluctuated ± 5 – 15 cm day^{-1}, surface water levels dropped below the baseline (0 cm) for a total of 24 days and aerial portions of the plants at the -25 cm elevation experienced some relief from top-flooding, but the substrate and root mass remained permanently water-logged. At the 0 cm elevation, substrate and root mass were constantly water-logged, but aerial portions of the plants only experienced periodic episodes of top-flooding. Soil remained unsaturated at the higher elevations (+25 and +50 cm) and aerial portions of the seedlings/propagules were always fully exposed.

In the highly variable water regime where water levels fluctuated by ± 20 – 50 cm day^{-1} plants at the -25 cm elevation experienced episodes of exposure (23 days) and occasionally (7 days) even the substrate and root mass were exposed. Substrate and root mass of plants at the 0 cm elevation and +25 cm encountered degrees of inundation (24 and 11 days, respectively) and within that time aerial portions would have experienced episodes of top-flooding. Substrate and root mass of plants at the +50 cm elevation also experienced periods of inundation, but aerial portions always remained fully exposed.

4.4.2 Survivorship

Overall, mortality was highest for *S. babylonica* across the experimental period with 75% loss at -25 cm elevation in the moderate and high water regimes. *A. stenophylla* seedlings also suffered a moderate loss (37.5%) of seedlings within the static water regimes at -25 cm elevation. In contrast there was full survivorship of *E. camaldulensis* seedlings at all elevations across all water regimes by the end of the experimental period (Table 4.2).

able 4.2. Percentage of alive *Salix babylonica* and *Eucalyptus camaldulensis* and *Acacia stenophylla* seedlings (n = 8) at the completion of pond experiment in relation to elevation and water regime (i.e. static, moderately variable and highly variable)

				Elevation								
	-25 cm			**0 cm**			**25 cm**			**50 cm**		
	Water regime			**Water regime**			**Water regime**			**Water regime**		
Species	static	mod	high	static	mod	high	static	mod	high	static	mod	high
S. babylonica	62.5	25	25	75	87.5	75	100	75	87.5	87.5	100	100
E. camaldulensis	100	100	100	100	100	100	100	100	100	100	100	100
A. stenophylla	62.5	100	100	100	87.5	100	100	100	100	100	100	100

4.4.3 Total biomass and biomass partitioning

Growth factors across species were influenced by elevation and water regime, but significant interactive effects suggest that individual species' responses can only be explained in reference to both primary factors of elevation and water regime (Table 4.3).

There was a general trend across species for total biomass to increase significantly with increasing elevation ($p< 0.0001$). Total biomass for all species was significantly lower at -25 cm elevation, followed by 0 cm elevation compared with the markedly greater biomass for all species at the higher elevations (+25 and +50 cm) irrespective of water regime (Fig. 4.4a-c) suggesting that water-logging as a result of top-flooding was a crucial variable. Highly significant interactions between species × elevation ($p<0.0001$) indicate that these trends were not consistent in that *E. camaldulensis* had significantly greater biomass than *S. babylonica* and *A. stenophylla* at the lower elevations, suggesting a slightly greater tolerance to water-logged and top-flooded conditions. However, responses may have been biased by the different initial biomass of plants prior to the experiment, namely: *E. camaldulensis* = 12.07 ± 0.95 (g DW), *S. babylonica* = 3.19 ± 0.47 (g DW), *A. stenophylla* = 1.96 ± 0.21g (DW*)* and not the treatment (see later in RGR).

A significant water regime × elevation × species interaction ($p = 0.03$) highlights that no one water regime or elevation position influenced either species. Total biomass for

E. camaldulensis was greater at the +50 cm elevation in the highly variable water regime (Fig 4.4a), but for *S. babylonica* total biomass was highest and similar at +25 and +50 cm elevations across all water regimes (Fig. 4.4a-c). For *S. babylonica* and *E. camaldulensis*, final total biomass was lower at 0 cm elevation and even lower again at the -25 cm elevation. For *A. stenophylla* total biomass was consistently less than the other two species across all treatments. Again, these responses may have been biased by the different initial biomass of plants prior to the experiment,

Significant interactive effects in terms of LWR, SWR and RWR as a function of total biomass reflected diverse responses of biomass partitioning to the treatments of water regime and elevation (Fig. 4.5a-i). LWR was relatively consistent across all elevations within the moderately and highly variable water regimes (Fig. 4.5d-i) but tended to increase with increasing elevation within the static water regime (Fig. 4.5a-c) indicating that the effects of permanent water-logging may have detrimentally influenced leaf development for all species at the lower elevations (i.e. -25 and 0 cm). This trend was most pronounced in *S. babylonica* and not in the other two species (Fig. 4.5a-i). *S. babylonica* recorded the highest SWR for all species at the -25 cm elevation in the static water regime suggesting under this treatment there was a possible investment of growth to stems or more likely leaf abscission at this elevation (Fig. 4.5 a-c).

Significant interactive effects in RWR for elevation × species (p =0.0015) and elevation × water regime × species (p= 0.02) were found, although there is a trend that RWR was greatest in all species in the static water regime at the 0 cm and +25 cm elevations. *S. babylonica,* in particular had the greatest RWR allocation at the 0 and +25 cm elevations within the static water regime (Fig. 4.5a). The high RWR for *S. babylonica* may in part be explained by a high ratio of adventitious root formation (g DW): total root mass (g DW) at the 0 cm elevation in the moderately variable water regime (see Table 4.4). *S. babylonica* tended to form adventitious roots at the lowest elevations across all three water regimes. Some adventitious root formation was also recorded in *E. camaldulensis* at the -25 cm elevation in the static and moderately variable water regimes as well as the 0 cm elevation in the static water regime (Table 4.4). In conclusion, there were no differences in LWR, SWR and RWR between *E. camaldulensis* and *S. babylonica*, but *A. stenophylla* tended to have greater LWR and lower RWR than the other two species (Tukey's HSD) (Fig 4.5c, f, i) which may be a function of the thicker phyllodes that they produce in comparison with the other two species and/or poorer root development (Fig 4.5 a-i).

Table 4.3. *F* statistics and p-values ($\alpha = 0.05$) for total biomass (g DW), leaf weight ratio, shoot weight ratio and root weight ratio between species, water regime and elevation (3- way ANOVA) in *S. babylonica*, *E. camaldulensis* and *A. stenophylla*.

Factor	Total Biomass (g DW)	Leaf weight ratio (LWR)	Shoot weight ratio (SWR)	Root weight ratio (RWR)
Water regime	$F_{2, 262}$ =172.76, p <0.0001	$F_{2, 262}$ =5.37, p = 0.005	$F_{2, 262}$ =5.07, p = 0.007	$F_{2, 262}$ =6.62, p = 0.002
Elevation	$F_{3, 262}$ = 41.32, p <0.0001	$F_{3, 262}$ = 10.85, p <0.0001	$F_{3, 262}$ = 0.051, p = 0.68	$F_{3, 262}$ = 9.42, p <0.0001
Species	$F_{2, 262}$ = 0.14 p = 0.87	$F_{2, 262}$ =4.75, p = 0.0096	$F_{2, 262}$ = 1.85 p = 0.15	$F_{2, 262}$ = 1.58 p = 0.21
Water regime × elevation	$F_{6, 262}$ =11.21, p = 0.002	$F_{6, 262}$ = 2.51 p = 0.023	$F_{6, 262}$ =0.64, p = 0.70	$F_{6, 262}$ =0.46, p = 0.87
Species × elevation	$F_{6, 262}$ =86.7, p <0.0001	$F_{6, 262}$ =3.11, p = 0.017	$F_{6, 262}$ = 5.51, p <0.0001	$F_{6, 262}$ = 3.73, p =0.0015
Water regime × species	$F_{5, 262}$ =0.94, p = 0.44	$F_{5, 262}$ = 1.12, p = 0.35	$F_{5, 262}$ = 0.95, p = 0.43	$F_{5, 262}$ = 0.07, p = 0.99
Water regime × elevation × species	$F_{12, 262}$ =3.16, p = 0.003	$F_{12, 262}$ =0.75, p = 0.70	$F_{12, 262}$ =3.85, p <0.0001	$F_{12, 262}$ =2.07, p =0.02

Table 4.4. Ratio of adventitious roots: total root biomass for *S. babylonica* propagules and *E. camaldulensis* and *A stenophylla* seedlings (n = 3 - 6). Values represent mean ± SE. There were no adventitious roots formed above the 0 cm elevation.

Elevation	**-25 cm**			**0 cm**		
Water regime	static	moderate	high	static	moderate	high
S. babylonica	0.075 ±0.032	*	*	0.13 ±0.045	0.054 ±0.037	0.034± 0.02
E. camaldulensis	0.069 ± .063	0.018 ± .013	0	0.012 ± 0.01	0	*
A. stenophylla	0	0	0	*	0	0

* Data excluded due to low replicate numbers

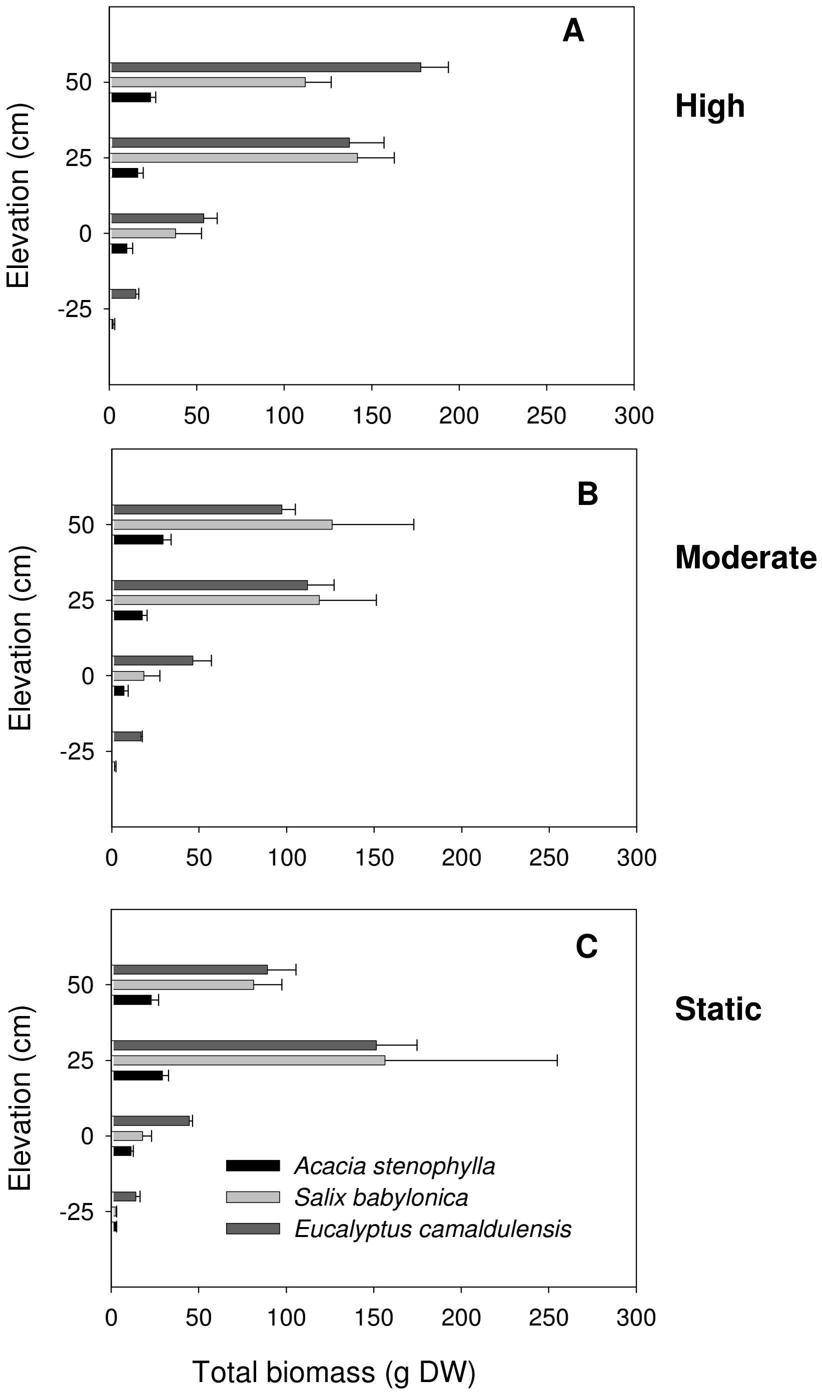

Figure 4.4. Total biomass (g DW) of *E. camaldulensis*, *S. babylonica* and *A. stenophylla* across four elevations (-25, 0, 25 and 50 cm) subjected to three fluctuating water regimes (A) high (B) moderate and (C) static. Initial mean biomass for each species was: *E. camaldulensis* =12.07 ± 0.95 g DW, *S. babylonica* = 3.19 ± 0.47 g DW, *A. stenophylla* = 1.96 ± 0.21g DW). Data points represent mean ± SE (n = 6 – 8).

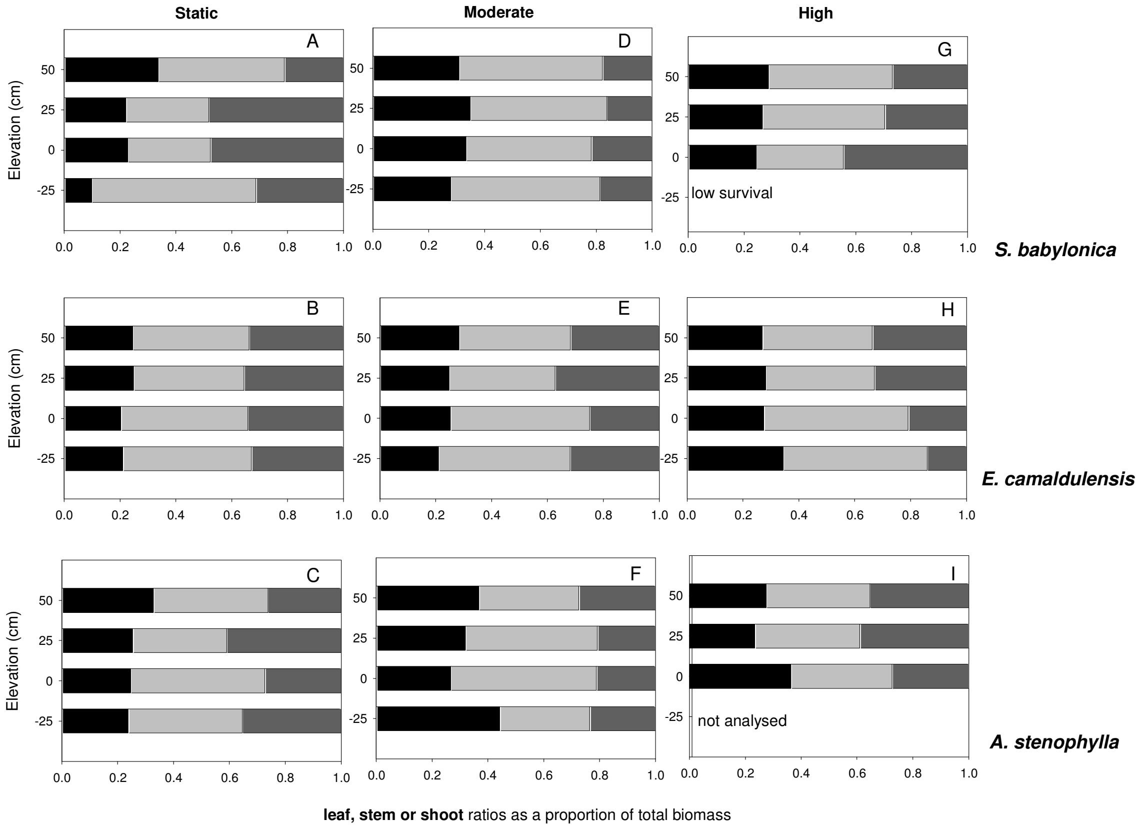

Figure 4.5. Leaf weight ratio (LWR) (black), stem weight ratio (SWR) (light grey) and root weight ratio (RWR) (dark grey) for *Salix babylonica* (A, D, G) *Eucalyptus camaldulensis* (B, E, H) and *Acacia stenophylla* (C, F, I) across four elevations (-25, 0, +25 and +50 cm). Subjected to three fluctuating water regimes: static (A, B, C), moderate (D, E, F) and high (G, H, I). *Data not included due to poor survival.

4.4.4 Growth analysis

RGR increased for all species with increasing elevation from -25 to +25 cm but did not change between +25 and +50 cm elevations (Table 4.5, Fig. 4.6.a-c). The differences in the RGR between species were altered by elevation ($p<0.0001$), but not by water regime (Table 4.5, Fig. 4.6 a-c). The RGR of *S. babylonica* appears to be greater than either of the natives when grown at higher elevations (+25 and +50 cm). In contrast, at the lowest elevation (-25 cm), only *E. camaldulensis* is able to achieve positive RGRs. At 0 cm elevation the RGR of all species appears comparable (Fig 4.6 a, b, c).

There were significant differences between NAR across species, with data showing that high RGR was maintained in *A. stenophylla* by significantly higher NAR ($p<0.0001$) but lower LAR ($p<0.0001$) than for the other two species (Fig. 4.6a-c and Fig 4.6 d-f). Hence the data show that the other two species were similar and had a leafier growth habit, whereas *A. stenophylla* was photosynthetically more efficient despite reduced leaf expansion. NAR for *E. camaldulensis* and *A. stenophylla* was low at the -25 cm elevation, but increased and did not change between 0 and +50 cm elevations. NAR for *S. babylonica* could not be determined at the -25 cm elevation due to minimal leaf mass present, but data for the remaining elevations show that NAR was similar across the 0, +25 and +50 cm elevations (Fig. 4.6d-f). All species recorded negative NAR at the lower elevations (-25 and 0 cm) (Fig 4.6d-f), suggesting that although the leaves were retained on the plants, there was no photosynthetic activity.

Although there was a significant species × elevation interaction ($p<0.0001$) LAR of species appears to be altered somewhater by elevation. For *E. camaldulensis*, LAR was similar at the -25 and 0 cm elevations, but increased and did not change between the +25 and +50 cm elevations. For *A. stenophylla* LAR was low between -25 and +25 cm elevations, but increased significantly at +50 cm elevations (Fig. 4.6g-i). These also appear to be differences between species, which may reflect the differences in SLA between species (since LAR = SLA × LWR). *S. babylonica* had the highest mean SLA (14.95 ± 0.46 m^2 kg^{-1}) and therefore the thinnest leaves, followed by *E. camaldulensis* (8.36 ± 0.18 m^2 kg^{-1}) then *A. stenophylla* (2.51 ± 0.04 m^2 kg^{-1}).

Table 4.5. F statistics and p-values ($\alpha = 0.05$) for relative growth rate (mg g day^{-1}) net assimilation rate (g m^{-2} day^{-1}), leaf area ratio (m^2 kg^{-1}) between species, water regime and elevation (3- way ANOVA).

Factor	**RGR (mg g day^{-1})**	**Net assimilation rate (g m^{-2} day^{-1})**	**Leaf area ratio (m^2 kg^{-1})**

Water regime	$F_{2,263}$ = 2.38, p= 0.098	$F_{2, 228}$ =1.15, p = 0.31	$F_{2, 260}$ =2.84, p =0.06
Elevation	$F_{3,263}$ = 181.47, p<0.0001	$F_{3, 228}$ = 57.72, p <0.0001	$F_{3, 260}$ = 55.51, p <0.0001
Species	$F_{2,263}$ = 10.67, p<0.0001	$F_{2, 228}$ =50.13, p <0.0001	$F_{2, 260}$ = 271.83 p <0.0001
Water regime × elevation	$F_{6,263}$ = 1.48, p = 0.19	$F_{6, 228}$ = 1.12, p = 0.35	$F_{6, 260}$ =0.41 p = 0.87
Species × elevation	$F_{6,263}$ = 6.87, p<0.001	$F_{5, 228}$ = 3.04, p = 0.007	$F_{5, 260}$ = 10.99, p <0.0001
Water regime × species	$F_{5,263}$ = 2.12, p= 0.079	$F_{6, 228}$ = 0.28, p = 0.89	$F_{6, 260}$ = 1.27, p = 0.28
Water regime × elevation × species	$F_{12,263}$ = 0.34, p= 0.98	$F_{12, 228}$ =1.24, p = 0.26	$F_{12, 260}$ =0.84, p = 0.60

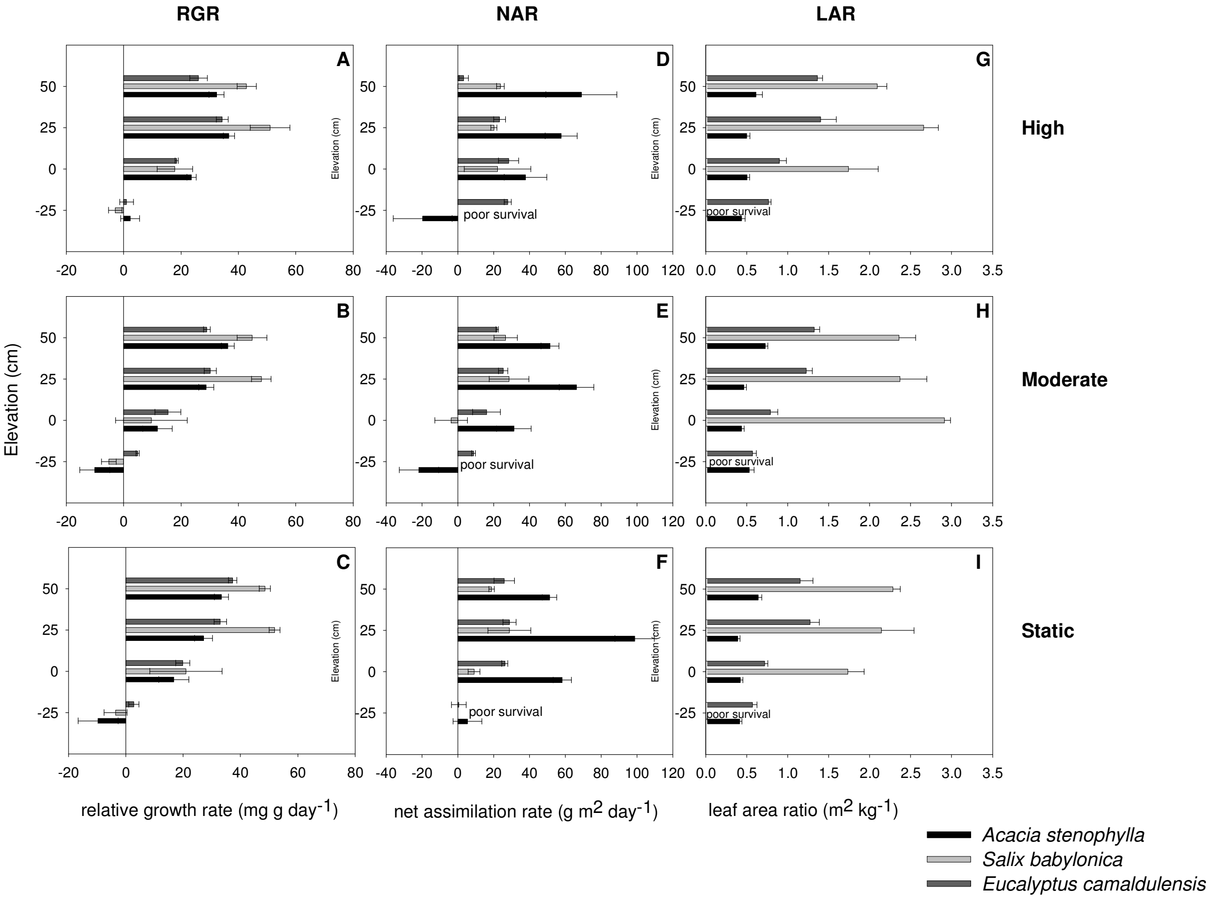

Figure 4.6(a-i). Relative growth rates (mg g day^{-1}), net assimilation rates (g m^2 day^{-1}) and leaf area ratios (m^2 kg^{-1}) for *E. camaldulensis*, *S. babylonica* and *A. stenophylla* across four elevations (-25, 0, +25 and +50 cm) subjected to three fluctuating water regimes: static, moderate and high. Data points represent mean ± SE (n = 3 – 8). *Data for *S. babylonica* at -25 cm elevation not included for NAR and LAR due to minimal leaf mass present.

4.4.5 Branching structure

<u>*4.4.5.1* Salix babylonica</u>

S. babylonica had a high degree of lateral branching, with more 2° and 3° node allocation, than 1° node allocation (Fig. 4.7a-c). Allocation to 1° nodes was significantly influenced by water regime ($p = 0.005$, see Table 4.6) with a higher allocation of primary growth in the static and highly variable water regimes (Fig. 4.7 a-c). However, primary growth was unaffected by elevation ($p = 0.18$, Table 4.6). In terms of allocation to 2° and 3° nodes, a significant interaction ($p = 0.04$ and $p = 0.018$, see Table 4.6) indicates that node allocation trends were not consistently explained by water regime or elevation. General trends indicate the allocation to 2° nodes increased from -25 to +25 cm elevation, but then dropped slightly at the 50 cm elevation, especially within the static and moderately variable water regimes (Fig. 4.7a-c). There was a greater allocation to 3° nodes at the 0 cm elevation within the moderately variable water regime (Fig. 4.7 b), compared with the greater allocation of 3° growth, at the higher elevations (+25 and +50 cm) under the static and highly variable water regimes (Fig. 4.7 a, b). Allocation to 4° nodes was not influenced by elevation, but was significantly different between water regimes ($p= 0.035$, seet Table 4.6) with fewer 4° nodes in the highly variable water regime (Fig. 4.7c). There was no allocation to 5° nodes as a result of treatment, with the exception of one juvenile in the static water regime (Fig. 4.7 a).

4.4.5.2 Eucalyptus camaldulensis

E. camaldulensis had an intermediate degree of lateral branching with a greater proportion of 1° and 2° nodes compared with the other two species (Figs. 4.7a-i). Allocation of 1° and 2° nodes in *E. camaldulensis* did not differ significantly across water regime, but did differ significantly as a result of elevation ($p=0.035$ and $p<0.0001$ respectively, see Table 4.6) with allocation to 1° and 2° nodes increasing from -25 to +25 cm elevation then dropping slightly at the +50 cm elevation (Figs. 4.7d-f). However the significant elevation × species interaction for 3° allocation ($p=0.03$) shows tertiary growth was not as clearly influenced by elevation (Table 4.6). In general, allocation to 3° nodes appeared to increase from -25 to +25 cm elevations, but then there was little difference between 3° allocation at the +50 cm elevation within the static and highly variable water regimes (Fig. 4.7d,f). However, allocation to 3° nodes at the +50 cm elevation in the moderate water regime declined (Fig. 4.7e). There was a slight significant difference ($p = 0.049$, see Table 4.6) a result of elevation in the allocation to 4° nodes, with 4° growth only occurring in the higher, +25 and +50 cm elevations (Fig. 4.7 d, e, f). There was no allocation to 5° nodes as a result of treatment, with the exception of one juvenile in the highly variable water regime (Fig. 4.7 f).

4.4.5.3 Acacia stenophylla

Overall, there was a greater allocation to 1° node in *A. stenophylla* (see Figs. 4.7g-i). Again the significant significant interaction ($p=0.007$) shows that node allocation was not consistent across elevations and water regimes (Table 4.8). General trends suggest 1° node allocation increased with increasing elevation, (note the -25 cm elevation not included due to insufficient data), ($F_{2,\,37} = 28.84$, $p<0.0001$); although allocation to 1° node did not differ across elevations in the highly variable water regime. Allocation to 2° was minimal at 0 cm elevation, but increased significantly at the higher, +25 and +50 cm elevations ($F_{2, 37} = 15.07$, $p<0.0001$). Overall, *A. stenophylla* seedlings did not tend to produce many 3°, 4° and 5° nodes, but those individuals that did, mostly did so within moderate water regime (Fig. 4.7h).

Table 4.6. F statistics and p-values ($\alpha = 0.05$) for primary (1°) secondary (2°), tertiary (3°) and quarternary (4°) and for *Acacia stenophylla, Salix babylonica* and *Eucalyptus camaldulensis* (2-way ANOVA). N/A = not applicable.

Species	**Factor**	**Primary (1°) node allocation**	**Secondary (2°) node allocation**	**Tertiary (3°) node allocation**	**Quaternary, (4°) node allocation**
Salix babylonica	Water regime	$F_{2,60} = 5.84$, p=0.005	$F2_{,60} = 0.75$ p = 0.48	$F_{2,60} = 4.16$ p= 0.02	$F_{2,60}$ =, 3.63 P = 0.035
	Elevation	$F_{3,60} = 1.68$ p= 0.18	$F_{3, 60} = 2.7$ p<0.0001	$F_{3,60} = 32.99$ P<0.001	$F_{3,60} = 2.52$ p= 0.07
	Water regime × elevation ×	$F_{6,60} = 0.62$, p = 0.71	$F_{6,60} = 2.43$ p= 0.04	$F_{6, 60} = 4.19$, p = 0.018	$F_{6,60} = 1.25$ p=0.29
Eucalyptus camaldulensis	Water regime	$F_{2,61} = 0.18$, p= 0.83	$F_{2,61} = 1.93$ p= 0.16	$F_{2,61} = 1.73$ p= 0.1882	$F_{2,61} = 0.035$ p= 0.96
	Elevation	$F_{3,61} = 3.12$, p= 0.035	$F_{3,61} = 42.51$ p<0.0001	$F_{3,61} = 38.52$, P<0.0001	$F_{3,61} = 2.8$ p= 0.049
	Water regime × elevation ×	$F_{6,61} = 0.81$, p= 0.57	$F_{6,61} = 1.62$ p= 0.16	$F_{6,61} = 4.02$, p= 0.03	$F_{6,61} = 1.66$ p= 0.15
Acacia stenophylla	Water regime	$F_{2,37} = 0.22$ p= 0.63	$F_{2,37} = 2.10$ p= 0.16	$F_{2,37} = 4.14$ p= 0.049	N/A
	Elevation	$F_{3,37} = 30.68$ P< 0.0001	$F_{3,37} = 17.82$ P< 0.0001	$F_{3,37} = 2.79$ p= 0.072	N/A
	Water regime × elevation ×	$F_{6,37} = 9.51$ P< 0.0001	$F_{6,37} = 1.1$ p=0.38	$F_{6,37} = 2.2$ p= 0.07	N/A

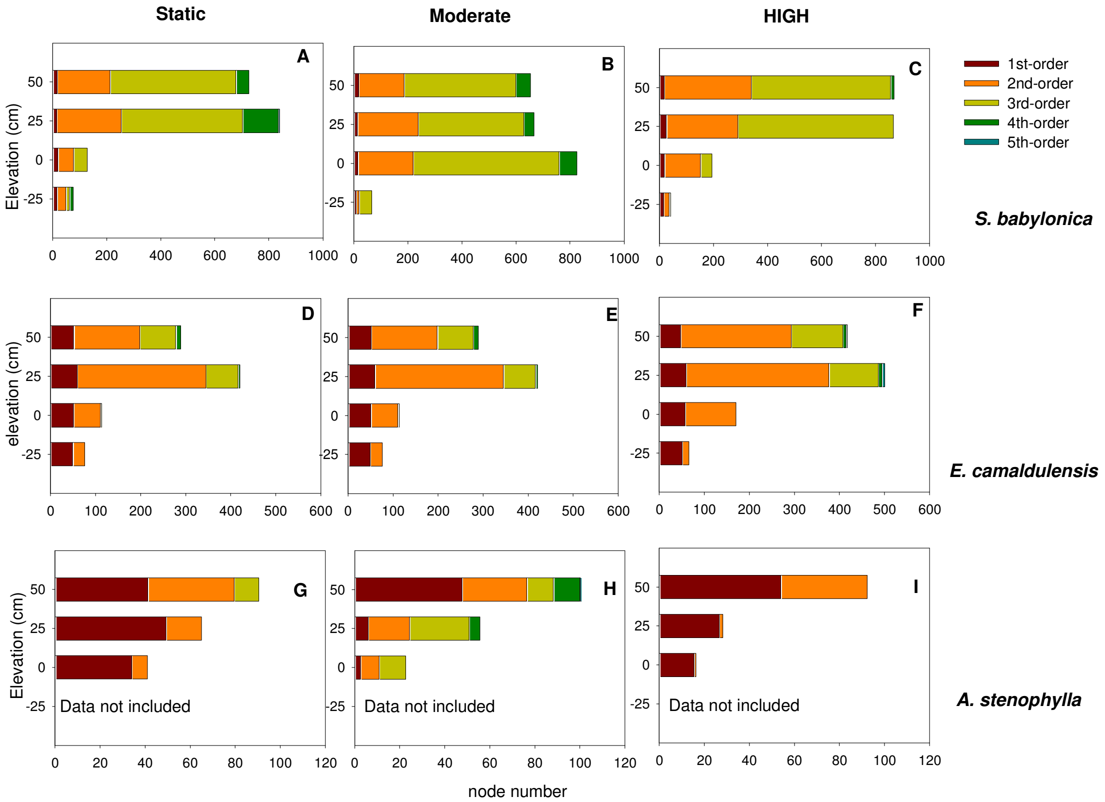

Figure 4.7. Node number and distribution along branch order for *Salix babylonica* (A-C), *Eucalyptus camaldulensis* (D- F) and *Acacia stenophylla* (G-H) exposed to static (A, D and G), moderate (B, E and H) and high (C, F and I) fluctuating water regimes. Data points represent mean values only (n = 3-8). * data not included due to lack of sufficient data.

4.5 Discussion

General trends from this study suggest that water regimes were not a primary factor inhibiting the establishment and growth of *S. babylonica*, hence other processes such as dispersal may also explain some of the observed distribution patterns in the field. Overall, elevation was the major influence on most of the growth factors measured for all three species, and growth was less at low elevations suggesting that none of the species are particularly tolerant of continual soil-saturation and top-flooding.

Top-flooding

Tree seedlings growing at the -25 cm elevation predominantly experienced the combined environmental conditions of water-logging and top-flooding where aerial portions of seedlings and propagules were regularly inundated with surface water, hence submerging photosynthetic tissue. Although many submerged and emergent macrophytes and some terrestrial species are capable of morphologically adjusting stem and/or petiole length, and leaf and canopy architecture to maximise photosynthetic areas (Blom and Voesenek 1996, Blanch *et al.* 1998, Cenzato and Ganf 2001, Mommer and Visser 2005) a combination of negative NAR, low LWR and LAR at this elevation suggest that leaf development and photosynthetic activity in all species were impaired as a result of top-flooding.

Low allocation to first order branching at -25 cm elevation for all species also suggests that species were incapable of adjusting canopy architecture to ensure that aerial portions of plants were projected above the water-line as a result of top-flooding. Growth and survivorship of *S. babylonica* was particularly affected at this elevation, which did not support the expectation that they would be tolerant of water-logging and top-flooding that had a duration period of <100 days (Ohmann *et al.* 1990, de Oliveiria and Piedade 2000) or capable of canopy adjustment to intercept light (He and Dong 2003). In the field, *S. babylonica* trees growing at lower elevations may use layering so that a proportion of their roos are out of the saturated zone and hence able to escape the detrimental effects of water-logging. Also trees in the field have shoots visibly arising out of the water and with pink roots growing under the waterline.

Water-logging

Most growth variables improved at the 0 cm elevation where tree seedlings predominantly experienced water-logged conditions and only partial or no top-flooding suggesting a limited tolerance to soil-saturation. Smith *et al.* (2001) found considerable variation in a range of tree seedlings' (i.e. *Corymbia maculata*, *Lophostemum confertus*, *Platanus orientalis* and *P. acerifolia*) tolerance to water-logging. In general, waterlogging suppressed both root and shoot growth in all experimental species, however both *C. maculata* and *P. orientalis* were able to initiate new root growth in response to flooding. *E. camaldulensis* were capable of adventitious root formation at this elevation (particularly within the low water regime where water-logging was continual), which may partially explain the general increase in RWR at this elevation to facilitate root aeration (de Simone *et al*. 2002). Although these three species continued to grow across the 10 weeks of water-logging at this elevation, it would be interesting to know the length of time they could endure water-logging before growth is seriously impeded. For example, survivorship of riparian *Acer negundo* saplings in North America is considerably reduced if inundation exceeds more than 85 days in the growing season (Friedman and Auble 1999).

Exposure

There was very little difference in most of the growth variables measured between the higher elevations (+ 25 cm, +50 cm) for all species indicating that the factors that inhibited growth at the lower elevations were alleviated. In most instances total biomass was more than two-fold the total biomass measured at the lower elevations. Contrary to initial predictions *S. babylonica* did not have the greatest final total biomass at these higher elevations compared to native species, but they did have the higher RGR. This is unsurprising since the initial starting biomass for *S. babylonica* was approximately 25% of the initial biomass for *E. camaldulensis*. The ability to opportunistically capture resources is a common feature in most successful plant invasions (Davis *et al.* 2000, Shea and Chesson 2002) and high seedling relative growth rates are positively correlated to woody plant invasiveness (Groktopp and Rejmanek 2007) which suggests they had the potential to have the greatest biomass, had the experiment continued.

Growth strategies

Despite growing under similar environmental conditions and being free from competitive interactions, significant inter-specific differences in RGR between species existed. In *S babylonica* and *E. camaldulensis*, high RGR was achieved by greater LAR and SLA. Leaves with a high LAR and SLA may have a competitive advantage because they maximise light interception with a minimum investment of biomass since they have a low tissue density (Poorter 1989, Wright and Westoby 1999, Wright and Westoby 2000). Allometric factors such as leaf area are related to aspects of canopy architecture since highly branched shoots and wide canopies help to maximise leaf area and light assimilation (Korner 1991, Bonser and Aarssen 2001, Archibald and Bond 2003).

Greater lateral branching in these two species under optimal conditions also suggests an emphasis on light interception to maintain high RGR. An even greater degree of third-order branching in *S. babylonica* propagules than *E. camaldulensis* may provide even greater competitive advantage by reducing light availability and possibly suppressing the establishment of nearby flora (Tremmel and Bazazz 1995). A higher investment of lateral canopy growth may also aid structural stability, defence against herbivores and reproduction (Kohyama and Hotta 1990) and help to alleviate potential evapotranspiration deficits by modifying micro-climatic conditions (Kelly and Ogle 1990).

A. stenophylla had significantly lower RGR than the other two species, but tended to have a greater NAR suggesting a growth strategy where the emphasis is less on maximising light interception via increased leaf area and more on nutrient and water acquisition and conservation. An investment in thicker, denser (i.e. highly lignified) and heavily cutinised leaves can lead to improved leaf longevity, resistance to herbivory, frost and drought resistance and diminished nutrient loss via leaching. All of these variables provide advantages for persisting in adverse environments (Poorter 1989).

Water requirements

Growth of all species was not necessarily any greater in the experimental water regimes that simulated the stable water regimes (i.e. low) that occur in regions above weirs on the LRM. However, greater growth at the higher elevations compared to lower elevations was consistent for all species. The higher elevations (+25 cm, +50 cm) experienced less water-logging and top-flooding, irrespective of the water regime. Perhaps *S. babylonica* have water use requirements, such as a need for reliable surface-water source or an inability to tap into deeper groundwater sources as they establish (Busch and Smith 1995, Horton *et al.* 2001, Loewenstein and Pallardy 1998, Shafroth *et al.* 2000), which restricts them to regions of the river where water regimes are stable, as long as their position on the elevation gradient is greater than +25 cm to alleviate the negative effects of water-logging and top-flooding.

Dispersal

This experimental design only took into account establishment, but other factors such as dispersal mechanisms and subsequent propagule and seedling development could also influence the distribution of these species. Absence of a particular species from an expected region may reflect dispersal failure rather than unsuitable habitat conditions. Seed recruitment may be limited in some riparian species during flooding and/or inundation events because increases in the depth and duration of inundation limits available seedbed sites (Blom *et al.* 1990). As discussed in Chapter 3, to maximise reproductive success, the reproductive phenologies of many riparian plants are often attuned to the water regimes of their environments (Pettit and Froend 2001).

E. camaldulensis population demographics on the LRM floodplains suggest episodic recruitment and subsequent survival reflect their need for inundation to increase reproductive success (Margules and Partners 1990, George *et al.* 2005) *A. stenophylla* appeared to perform best at the higher elevations across all water regimes, yet the previous survey (see Chapter 3) suggests that, although present along weirs, they are not abundant. It is possible that weir water regime gradients imposed by river regulation introduced environmental sieves (i.e. filters) that exclude *A. stenophylla* germination (Mahoney and Rood 1998), but as yet very little is known about the reproductive phenology and growth strategies of *A. stenophylla*. Markedly slower growth rates that the other two species may also mean they are less able to compete for available space and resources thereby restricting their distribution.

Perhaps *S. babylonica* may not be present in the regions below weirs because they are simply still slowly expanding their range. One factor influencing the arrival of asexual propagules at a site is the sensitivity of the parent plant to fragmentation as a result of water-currents, flood events and/or wind (Delgado *et al.* 2001). Assuming that *S. babylonica* stem bases fragment easily (see Beismann *et al.* 2000) the dispersal of propagules is not likely to be a factor limiting the establishment of *S. babylonica* in upper pool and tail-water environments. In fact, weir operators have reported that they often see

S. babylonica propagules pass through the weir systems (Drogemuller, G. *pers. comm.*). Even if dispersal of fragments were limited, *S. babylonica* are able to layer hence maintaining population expansion, but at a considerably slower rate.

Erosion

In the field, establishment of recruits may be influenced by site availability. Flooding and highly fluctuating surface water levels can lead to increased bank substrate instability (Naiman and Decamps 1997, Rood *et al.* 1998). It is possible that erosion is an important factor influencing the establishment of *S. babylonica* propagules. *Salix* spp. are commonly found growing at low elevations along main channels in southwestern USA because they have strong lateral root development, which is believed to provide protection against the effects of flood scour (Horton *et al.* 2001b). Root weight ratios as a proportion of total biomass were quite high in *S. babylonica* propagules especially at the 0 cm elevation, which were subjected to a greater frequency and duration of water-logging in all water regimes. The high RWR suggests *S. babylonica* have the potential for substantial root development, yet at this elevation a considerable proportion of the roots produced were adventitious which may not provide any anchorage for establishing seedlings.

Chapter 5

Seasonal water use patterns in *Salix babylonica*, *Eucalyptus camaldulensis* and *Acacia stenophylla* along a river to floodplain gradient.

5.1 Introduction

In riverine environments, water can be sourced by plants from surface river-water, precipitation, soil water and/or groundwater. During periods of low river flow, however, tree growth and survival will be influenced by their ability to tolerate reduced water availability through the soil profile (Stromberg *et al.* 1991) and/or their capacity to use other water sources, such as groundwater and precipitation (Taylor *et al.* 1996). This could also influence the relative success of native and invasive riparian species in riverine environments. Predicting the success of invasiven species will depend on understanding their responses to environmental factors like water-table fluctuations and soil moisture levels across the river-floodplain gradient (Tickner *et al*. 2001).

Riparian corridors are prone to both natural and anthropogenic disturbances like flooding, water regulation, fire, vegetation clearance and the introduction of pest plant and animal species (Askey-Dorin *et al*. 1999). Increased on-farm storage in dams and impoundments along the Murray River have considerably reduced the amount of surface flow reaching the river and have thus modified hydraulic characteristics (Beavis and Lewis 2001). Regulation of the LRM now means that the river is dominated by low flows and occasional high flows; reducing the frequency of mid-range flows. The seasonal timing of natural flows of summer-autumn minimums and winter-spring maximums have shifted slightly, and in particular the magnitude of the seasonal flood peaks has been reduced, limiting the frequency and extent of floodplain inundation (Walker *et al.* 2001, Ward *et al.* 1999).

In most cases, the availability of surface-water declines with increasing distance from the river to the floodplain (Mensforth *et al*. 1994, O'Grady *et al*. 2002). The extent of this decline is influenced by seasonal and climatic factors as well as the water regime of the system (i.e. frequency, timing, duration and extent of inundation and /or exposure) (Poff *et al.* 1997, Rea and Ganf 1994, Brownlow *et al.* 1994, Budelsky and Galatowitsch 2000, Roelle *et al.* 2001, Stromberg 1993). Flooding promotes high species richness since regular floods can shape the channel dynamics of the system. The variety of microhabitats created by flooding can result in fluctuating productivity, decreased intra- and inter-specific competitive interactions, or complete disturbance leading to a periodic return of early successional stages (Richards *et al*. 2002).

The response of vegetation to the shifting availability of water on spatial and temporal scales shapes distribution patterns. Vegetation distribution along environmental gradients is influenced by two primary factors: differences in a species tolerance to resource levels and their competitive ability (Dawson 1990). Water-requirements are strong determinants shaping the distribution of long-lived riparian vegetation, such as trees (Taylor *et al.* 1996). Adaptations, especially rooting strategies, to different soil moisture regimes may determine success as depth of water extraction varies between species (Ehleringer and Dawson 1992) and within species (Flanagan *et al*. 1992). Physiological adaptations that lead to higher water use efficiency (Busch and Smith 1995) are often indicative of a successful species capable of growing in periodically stressful environments (i.e. where productivity is reduced) (Cleverly *et al.* 1997). Maximum negative shoot water potentials (ψ_{shoot}) can vary between co-existing species, and can provide an index of the water extraction capacity of root systems, and an indication of their relative tolerance to reduced water availability (Aranda *et al*. 2000). It is likely that a species that can tolerate reduced water availability may have the competitive edge over co-occurring species that are not as resistant to drought conditions. The occurrence of *S. babylonica* along riverbank edges, but their absence from floodplain regions may reflect specific components of their water relations, such as an intolerance to reduced water availability, a dependence on fresh, continual water sources and/or inefficient water use (ca. Cleverly *et al.* 1997, Loewenstein and Pallardy 1998, Pezeshki *et al.* 1998).

Measurements of the diurnal and seasonal fluctuations in ψ_{shoot} and leaf-gas exchange provide a relative assessment of how individual plants and populations are responding to reduced water availability within their habitat (Busch and Smith 1995, Horton *et al.* 2001, Loewenstein and Pallardy 1998). Plant water availability is determined by the ability of the plant to lower the root water potential below that of the soil, causing water to move down the hydraulic gradient from the soil into the plant (Scholander *et al.* 1965). Investigations into *S. nigra* and *S. gooddingii* have found that these species are sensitive to reduced water availability. Individual trees experiencing water stress exhibit signs of low plant water status (i.e. more negative ψ_{shoot}) and lower gas exchange rates (Busch and Smith 1995, Horton *et al.* 2001, Loewenstein and Pallardy 1998). On the other hand, the dominance of *E. camaldulensis* on the Central Murray River floodplains is linked to its ability to survive periodic inundation and drought; being dependent on short-term floods in order to withstand subsequent drought episodes (Bacon *et al.* 1993a).

The ability of plants to use a variety of water sources may also influence their position within a riverine landscape. For example, *E. camaldulensis* and *E. largiflorens* on the LRM are distributed from the riverine zones into the floodplains (Margules and Partners 1990) and are considered opportunistic in their water use (Mensforth *et al.* 1994, Thorburn and Walker 1994, Thorburn *et al.* 1993). On the Murray floodplains, these two species will access saline groundwater, yet switch to fresh soil water and/or surface water sources following high rainfall, flooding and/or bank recharge (Jolly and Walker 1996, Mensforth *et al.* 1994, Holland *et al.* 2006). Similarly, *E. camaldulensis* that line tributary creek edges only sourced 50% of their water from the creek itself and the remainder was sourced from the soil surface water and/or groundwater (Mensforth *et al.* 1994, Thorburn and Walker 1994, Thorburn *et al.* 1993). In riparian ecosystems in the western United States, mature *Acer* spp. growing in close proximity to a perennial mountain stream only obtained a small fraction of their water from the stream itself. Even during the peak of the growing season the trees were not accessing stream water, but were using groundwater sources instead (Dawson and Ehleringer 1991). This implies that surface water may be of limited importance for mature riparian trees in semi-arid and arid regions because it represents an unreliable water source whereas groundwater is more stable (Ehleringer and Dawson 1992). In semi-arid areas where the water regime is often erratic, the ability of riparian trees to use combinations of groundwater and other water sources is an important adaptation for surviving periods of low river flow and/or drought (Thorburn and Walker 1994).

In contrast, north American *Populus*-*Salix* riparian forests were not capable of opportunistically using water from precipitation and/or floods. Instead they required uninterrupted access to water from continually saturated zones like groundwater, surface water or water drawn into the capillary fringe. As result they were restricted the stream's edge or areas where the water-table was shallow (Horton *et al.* 2001, Snyder and Williams 2000). Similarly streamside *Salix monticola* in the Rocky Mountains, directly sourced ~75% of their water from streams (Alstad *et al.* 1999).

The close proximity of willows to the main river channel along the LRM may reflect their need to access reliable water sources (Horton and Clark 2001). Based on their distribution, and data on other *Salix* species, it is predicted that *S. babylonica* are physiologically suited to riverbank, but not floodplain environments along the LRM. Specifically *S. babylonica* should have high (i.e. less negative) ψ_{shoot} and leaf gas exchange rates and lower WUE (i.e. fewer units of carbon fixed per units of water transpired) than co-occurring native species on riverbanks. In contrast native trees like *E. camaldulensis* and *A. stenophylla* should show a greater range in their water status and gas exchange measurements, reflecting the greater range in their distribution across the lateral river to floodplain gradient. It is also predicted that *S. babylonica* should source their water directly from the river itself or from river water drawn into the capillary fringe of the soil while the natives would use a range of water sources including ground water and precipitation.

5.2 Methods

5.2.1. Field sites

A pilot study, in which diurnal water relations of the three species were measured, was conducted on a riverbank site within Loch Luna Reserve (Cobdogla, South Australia: 34°13’734”S, 140º22’590”E). Loch Luna Reserve (2059 ha) was established in 1985 around a range of water bodies including narrow creeks and shallow swamps. Subsequently, a seasonal study of water relations and gas-exchange characteristics was conducted in Katarapko National Park (34°20' 32" S, 140°34' 38" E) (Fig 5.1), where a riverbank and associated floodplain site were selected for the study. In Katarapko National

Park the river meanders over broad (5 – 20 km) floodplains. These floodplain areas contain many wetlands both permanent and semi permanent.

Within Katarapko, the riverbank site (34º 20’ 31.4’’S and 140º 34’31.2” E) was situated close to Lock 4 on the LRM. Riparian vegetation at all sites is composed of a wooded overstorey dominated by *E. camaldulensis*, *S. babylonica*, *A. stenophylla* and *E. largiflorens*, plus sedges (e.g. *Cyperus gymnocaulos*), and reeds (e.g. *Phragmites australis, Typha domingensis*). The floodplain site (34º20’ 35.3 S, 140º34’15.5” E) was situated approximately 1 km NW from the riverbank site. Here the floodplain is dominated by *E. camaldulensis*, *E. largiflorens* and *A. stenophylla* with an understorey of grasses and shrubs (Mensforth *et al.* 1994). Soils are predominantly clay (close to main river channel and existing or prior creek beds) overlying alluvial sands, which consists of fine to coarse sand with varying amounts of silt and clay (Jolly and Walker 1996). Climate is semi-arid with warm, dry summers (mean temperature ~29ºC) and cold, wet winters (mean temperature ~7°C), with average rainfall of 265.1 mm yr^{-1} (Bureau of Meteorology, South Australia.).

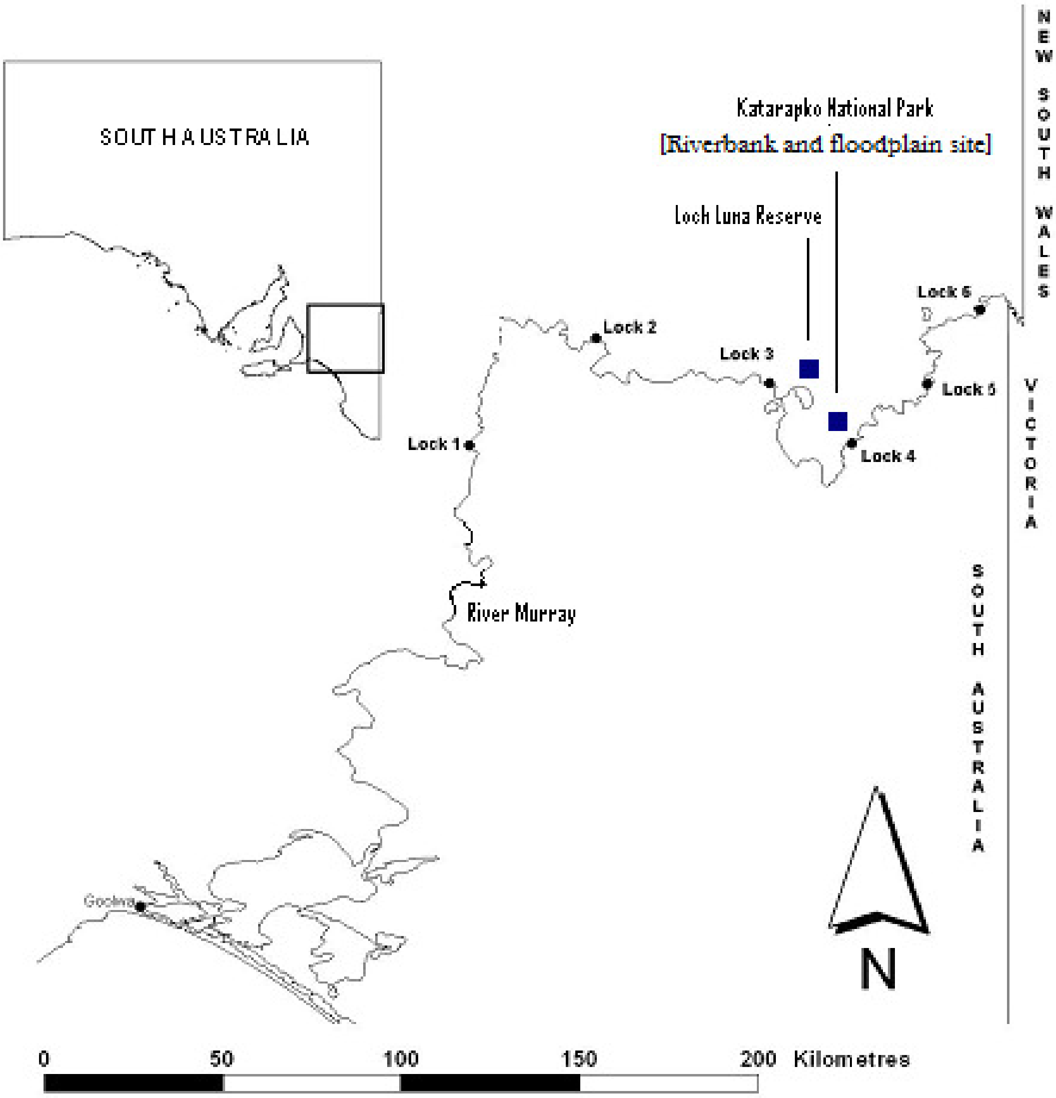

Figure 5.1. Location of the two study sites: Loch Luna Reserve (Cobdogla) and Katarapko Conservation Park, Lower River Murray (South Australia).

5.2.2 Pilot Diurnal Water Potential Study

Prior to the main investigation into seasonal differences in water relations of willows and native trees on riverbank and floodplain sites, some preliminary investigations were conducted at Loch Luna Reserve. Diurnal ψ_{shoot} was measured on 18th January 2002, on four randomly selected replicates of riverbank *S. babylonica*, *E. camaldulensis* and *A. stenophylla.* Shoot water potential (ψ_{shoot}) was measured every two hours, for each replicate tree, across the day to ensure that the minimum diurnal value would be captured in the subsequent seasonal study. A Scholander pressure chamber measured predawn and midday ψ_{shoot} (MPa) (Scholander *et al.* 1965). Three shoot samples (~ 3-5 leaves per shoot) were collected from each replicate tree (n = 12 per species) from a height of ~1.5 m and transported back to the pressure chamber in a sealed plastic bag. Measurements were made ≤10 min following harvesting. Additionally, the height (m) of trees relative to the water level along the riverbank edge was also measured using a theodolite and 5 m staff. Height measurements were made on 10 replicates per species (*S. babylonica*, *E. camaldulensis* and *A. stenophylla*) including trees used for diurnal ψ_{shoot} measurements.

5.2.3 Seasonal responses of riverbank and floodplain trees

Following the pilot study, seasonal measurements were made of predawn and midday ψ_{shoot}, leaf-gas exchange and leaf δ^{13}C were made on riverine and floodplain trees. Seasonal soil water potential measurements were collected from the riverbank site. Seasonal δ^{18}O signatures were obtained for *S. babylonica* tissue, soilwater, and river-water and floodplain groundwater (Table 5.1). Measurements were conducted across the growing season for the deciduous invasive, *S. babylonica,* and native trees (2nd September 2002 to 1st May 2003).

Table 5.1. Field sampling protocol for riverbank and floodplain trees. Study period: 2nd September 2002 to 1st May 2003 represents active growing season for the deciduous invasive, *Salix babylonica,* and also for the native trees, *Eucalyptus camaldulensis* and *Acacia stenophylla*.

SPECIES	***RIVERBANK SITE***			***FLOODPLAIN SITE***		
	S. babylonica	*E. camaldulensis*	*A. stenophylla*	*S. babylonica**	*E. camaldulensis*	*A. stenophylla*
$\psi_{predawn}$ and ψ_{midday}	Every 6 weeks [§]	Every 6 weeks [§]	Every 6 weeks [§]	***N/A***	Every 6 weeks [§]	Every 6 weeks [§]
Gas exchange parameters (*A*, *E* and g_s)	Every 6 weeks [§]	Every 6 weeks [§]	Every 6 weeks [§]	***N/A***	Every 6 weeks [§]	Every 6 weeks [§]
Soil gravimetric water potential and $\psi_{soil\ matric}$)	Every 6 weeks [§]	Every 6 weeks [§]	Every 6 weeks [§]	***N/A***	***N/A***[¥]	***N/A***[¥]
Long term Water Use Efficiency ($\delta^{13}C$)	Week30[π]	Week30[π]	Week30[π]	***N/A***	Week30[π]	Week30[π]
Water source ($\delta^{18}O$)	Weeks 1, 6 & 18[b]	***N/A***	***N/A***	***N/A***	***N/A***	***N/A***

**Salix babylonica* not present on floodplains of Lower River Murray

§ Measurements were made every 6 weeks (weeks 1 to 30 inclusive) across the growing season.

¥ Measurements for floodplain soils unattainable

π Measurements made at end of growing season (i.e. Week 30)

þ Measurements made Week 1, 6 and 18 only across the growing season

5.2.3.1 Seasonal water potential and leaf gas exchange

Seasonal monitoring of predawn (0430 -0600 hr) and midday (1130 – 1300 hr) ψ_{shoot} was conducted for 4 replicate trees of each species (3 shoots per tree, n = 12 per species) on the riverbank and floodplain sites per sampling trip (6 sampling trips). Assimilation (A) rates (μmol CO_2 m^{-2} s^{-1}), transpiration (E) rates (mmol H_2O m^{-2} s^{-1}) and stomatal conductance (g_s mmol m^{-2} s^{-1}), were measured *in situ* on 3 replicate leaves of each species at the riverbank and floodplain sites. Measurements were made at midday (1330 – 1400 hrs) when photon flux density (PFD) reached a diurnal maximum >1000 μ mol m^{-2} s^{-1} using an open-system Infra Red Gas Analyser (LCA-4: ADC Bioscientific Ltd, UK) on one fully, expanded mature leaf for each replicate. As a result of instrument failure during the December 2002 and February 2003 sampling trips, gas exchange variables were unable to be measured; instead a Chlorophyll fluorometer (Mini-PAM: Heinz-Walz GmbH, Effeltrich Germany) was used on leaves that were dark adapted for 1 hour, to measure F_v/F_m (ratio of variable to maximum chlorophyll fluorescence which provides a measure of optimum quantum efficiency of Photosystem II in dark adapted leaves). Non-stressed leaves commonly have F_v/F_m values between 0.8 – 0.83 (Ball *et al.* 1995).

5.2.3.2 Seasonal soil sampling (gravimetric water potential and $\psi_{soil\ matric}$)

The upper clay surfaces of the soil profile of the floodplain site were so dry and crumbly, that insufficient soil samples were unable to be collected at depths >0.01 m. Thus, soil moisture measurements were made from the riverbank site only across the sampling period (with the exclusion of sampling done on 20/10/2002, when it was possible to borrow a sand bucket-type auger with extension handles from CSIRO Land & Water (SA Govt) to obtain the floodplain soil-water $\delta^{18}O$ measurements described below).

Riverbank soil samples were collected each trip to measure matric potential (Greacen *et al*. 1989) and gravimetric soil water content. On each sampling date, four replicate soil samples for each depth class were collected at increasing depths within the soil profile (i.e. 0.25, 0.5 m and then every 0.5 m to water table). The water table was intercepted at depths between ~1.0 to 1.5 m. Samples were placed into 250 ml sampling jars with one 55 mm diameter, number 42 Whatman® ashless filter paper (Whatman International Ltd, England) in full contact with the soil (but not touching the sides of the jar) before sealing with electrical tape. The water content of the filter paper was used to calculate the matric water potential (kPa), based on the calibration curve described by Greacen *et al*. (1989). The soil samples were weighed immediately once opened, placed in alfoil trays and dried for 72 hr at 80°C. Samples were then reweighed to calculate gravimetric soil water content of each sample according to equation 5.1 below:

Equation 5.1:

$$Gravimetric\ soil\ water\ content = \left\{\frac{W_{initial} - W_{final}}{W_{initial}}\right\}\ (g)$$

Where:

$W_{initial}$ = initial weight of soil sample (g)

W_{final} = final weight of soil sample (g)

5.2.3.3 Seasonal water source determination ($\delta^{18}O$): Salix babylonica

Water sources used by *S. babylonica* were determined using stable isotope oxygen analysis (δ^{18}O). This analysis was restricted to *S. babylonica* due to costs and because δ^{18}O data for *E. camaldulensis* within the LRM is already available in the literature for comparsion (see Mensforth *et al.* 1994).

Salix babylonica stem tissue, soil water, groundwater and river water samples were collected from the riverbank for stable oxygen isotope analyses (δ^{18}O) on three occasions ((1/9/2002, 20/10/2002 and 5/1/2003). At each sampling time, three replicate river water samples were collected from randomly selected positions. Soil samples were also collected from three randomly selected positions, at depths of depths of 0.1 m, 0.25 m, 0.5 m and 1 m and then every 0.5 m until the groundwater was intercepted. At each depth approximately 200 g of soil was obtained. Groundwater samples were collected at a depth of 0.25 m below the oint where the water table was intercepted. Composite samples of *S. babylonica* non-green stem tissue (n = 10; diameter ~0.01 m) was collected. All representative samples of stem tissue, soil, groundwater and/or river-water were placed in 250 ml airtight glass jars or in 50 ml glass McCartney vials, then sealed with electrical tape to prevent water loss and stored in a cooler until laboratory analysis, as described in Walker *et al.* (2001).

Oxygen isotope analysis (δ^{18}O) values of the water extracted from each sample was determined using a Europa Geo 20-20 gas isotopic ratio mass spectrometer at the CSIRO Land and Water, Isotope Analysis Laboratory (Adelaide, Australia). The procedure used is described in Walker *et al*. (2001) but briefly, samples are compared with secondary standards, which are used to determine δ^{18}O of the sample on the SMOW-SLAP scales.

Oxygen isotope analysis involves equilibration of oxygen in water samples with that in CO_2. The error of analysis was ± 0.3‰ for $\delta^{18}O$ (Thorburn *et al.* 1993). Only $\delta^{18}O$ was selected to test for water source because often δ^2H is highly correlated with $\delta^{18}O$ so that in most instances $\delta^{18}O$ provides essentially identical information (Walker *et al.* 2001).

In addition, on 5/1/2003 a piezometer was installed within the floodplain site as part of a Department of Land, Water and Biodiversity Conservation (SA Govt) project (Bore name: LOX 02109) so on the 11/3/2003, 3 groundwater samples were collected to measure electrical conductivity.

5.2.3.4 Seasonal long term Water Use Efficiency ($\delta^{13}C$)

To assess long-term WUE of *S. babylonica*, *E. camaldulensis* and *A. stenophylla*, mature leaf samples were collected from the riverbank and floodplain sites to measure stable carbon isotope ratios (Farquhar *et al.* 1989). Enriched stable carbon istope analysis ($\delta^{13}C$) values (less negative) usually relate to some environmental moisture stress, while depleted values (more negative) are usually indicative of non-stressful growing conditions (Buhay *et al.* 2008). At the beginning of the growing season (01/09/2003), 20 newly developing and expanding leaves were tagged on individual trees, per species (n=5). This was done to ensure that the leaves selected for $\delta^{13}C$ analyses represented the growing season examined. By the end of the growing season (1/5/2003), a final subset of 10 leaves were then randomly selected from 3 of the individual trees per species (due to the loss of some tags) to make up a composite sample per replicate. Samples were then oven-dried at 70ºC for 72 hr. Dried leaf samples were ground to a fine powder using liquid nitrogen from which 1.1 – 1.5 mg subsamples were taken. Samples were analysed at the Western Australian Centre for Biogeochemistry Isotope Analysis Laboratory (University of Western Australia). Carbon isotope ratios ($\delta^{13}C$) were determined relative to the Pee Dee Belemite (PDB) standard as outlined in Leffler and Evans (1999) and expressed in parts per thousand (‰) as per Equation 5.2.

Equation 5.2:

$$\delta^{13}C = \left\{\left({R_{sample}}/{R_{standard}} \right) - 1\right\} \times 1000\ ‰$$

where R_{sample} and $R_{standard}$ are the molar ratios of ${}^{13}C/{}^{12}C$ of the sample and standard, respectively.

Tissue $\delta^{13}C$ can be considered a time-averaged estimate of water status over the lifetime of the tissue (Farquhar *et al*. 1988). $\delta^{13}C$ is related to water-use efficiency because low water availability causes stomatal closure and a concomitant decline in the ratio of substomatal [CO_2] to ambient [CO_2] (i.e. c_i/c_a). More specifically, intercellular CO_2 concentrations become lower relative to ambientCO_2 concentrations, that discrimination against the heavier carbon isotope by Rubisco declines and tissue values are then closer to ambient. (Farquhar *et al.* 1988). A detailed description of the process involved in determining $\delta^{13}C$ is outlined in Leffler and Evans (1999).

5.2.4 Precipitation

Mean annual precipitation for the field site region at the time of the study was 265.1 mm yr^{-1} (closest locality: Berri Weather Station #024025: 44 yr recorded data period. Data provided courtesy of Bureau of Meteorology, South Australia). Total rainfall across the investigated growing season was 61 mm; approximately one third of the mean rainfall (i.e. 187 mm) that normally falls in that region over that period (Fig. 5.2). The most significant rain event was on 20/2/2003 (i.e. 17.6 mm). During October and January there was no precipitation (Fig 5.2).

NOTE:
This figure is included on page 142 of the print copy of the thesis held in the University of Adelaide Library.

Figure 5.2. Daily precipitation recorded at Berri (Weather Station #024025) from July 2002 to July 2003. Data provided courtesy of Bureau of Meteorology, SA Govt).

5.2.5 Statistical Analysis

Individual trees were randomly selected across the site, per sampling trip, therefore a two factor analysis of variance (2-way ANOVA) was used assess the differences in predawn and midday $\psi_{shoot,}$ between riverbank *S. babylonica* and natives species (*E. camaldulensis* and *A. stenophylla*) and sampling months. A three factor analysis of variance (3-way ANOVA) was also used to determine differences in shoot water potentials ($\psi_{predawn}$ and ψ_{midday}) between the riverbank and floodplain sites and sampling months for the species *A. stenophylla* and *E. camaldulensis*, but not *S. babylonica* since they do not grown on floodplains. Due to low replicate numbers at some sampling times, no statistical analysis of g_s, A and E between species within the riverbank site was made. A further co-variate analysis was used to determine how assimilation rates relate to stomatal conductance between species (ANCOVA, JMP-IN version 4.0.3). A 2-way ANOVA was used to assess differences in soil readings (gravimetric water content and soil ψ_{matrix}) between depths within the riverbank site across the months. Source of water used by *S. babylonica* was identified by plotting $\delta^{18}O$ values for the possible plant water sources (i.e. river-water, soil-water and groundwater) against the isotopic composition of *S. babylonica* twig water (Thorburn *et al.* 1993b). Simple ANOVAs were used to assess whether firstly, there was a difference in foliar $\delta^{13}C$ between sites, then whether differences existed in foliar $\delta^{13}C$ between species at each site and also to assess whether there were any differences in the elevation of each riverbank species relative to the water level. Means were compared by Tukey-Kramer honestly significant difference (Tukey's HSD) test when appropriate. Data were log transformed to meet assumptions of normality and homoscedasticity and for all statistical tests $\alpha = 0.05$. Data were analysed using JMP-IN (vers. 3.2.6 or 8.0).

5.3 Results

5.3.1 Pilot study of diurnal ψ_{shoot} and tree position on the riverbank

All three species followed similar diurnal patterns of ψ_{shoot}, with less negative predawn ψ_{shoot} readings (mean: *S. babylonica* = -0.22 ± 0.037 MPa, *E. camaldulensis* = -0.78 ± 0.047 MPa and *A. stenophylla* = -0.78 ± 0.08 MPa). Shoot water potentials gradually became more negative until reaching a minimum value close to midday (Fig. 5.4). After midday, ψ_{shoot} slowly became less negative in all species and had almost reached the maxima pre-dawn values by 2000 hr (Fig. 5.3). Although the species had similar patterns of diurnal ψ_{shoot}, *S. babylonica* had significantly less negative predawn and midday ψ_{shoot} ($F_{2,\ 242}$ = 50.91. p<0.0001) than *A. stenophylla* followed by *E. camaldulensis*. The most negative ψ_{shoot} occurred at 1200 hr for both *S. babylonica* (mean = -1.49 ± 0.04 MPa) and *A stenophylla* (mean = -2.01 ± 0.61 MPa) and at 1100 hr for *E. camaldulensis* (mean = -2.86 ± 0.022 MPa) (Fig. 5.3). Thus, all midday water potential measurements were subsequently made between 1100-1300 hr.

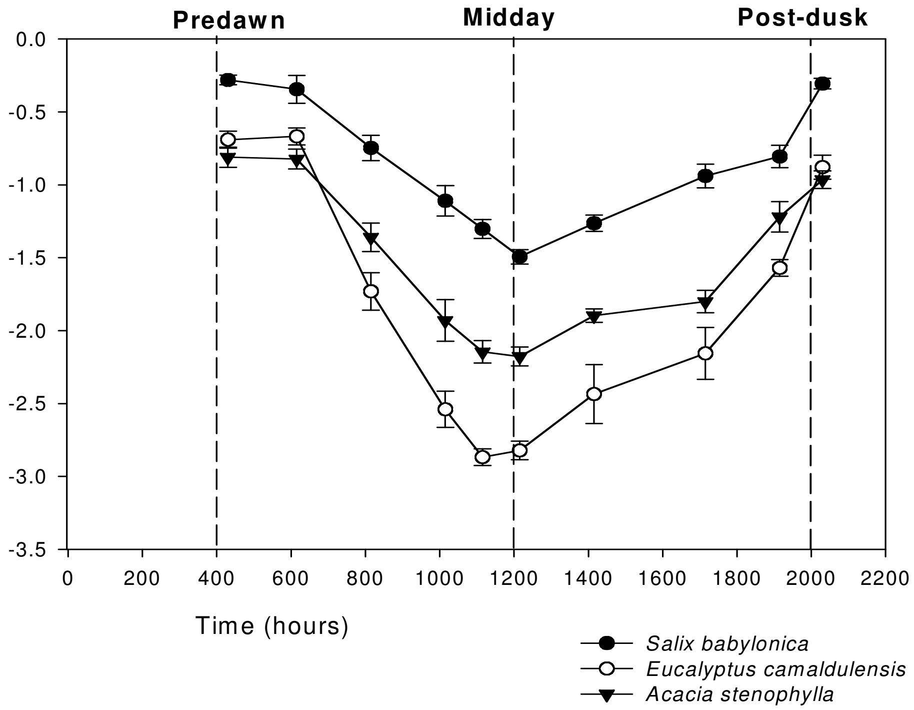

Figure 5.3. Diurnal ψ_{shoot} for *S. babylonica*, *E. camaldulensis* and *A. stenophylla,* growing along the riverbank at Loch Luna Reserve (18th January 2002). Data points are mean ± SE (n = 4).

Elevation

Measurements of the relative position of each species growing along the riverbank edge of the main channel show that there were significant differences between species ($F_{2,\ 36}$ = 15.49, $p<0.001$) where *S. babylonica* are only found at very low elevations relative to the river-water level whereas *A. stenophylla* tend to be at slightly higher riverbank positions (relative to water-level) and *E. camaldulensis* are intermediate (Table 5.2).

Table 5.2. Height above river level of the dominant riparian trees that line the main channel riverbank edges on the Lower River Murray. Data points represent means ± SE (n = 12). The same letters are not significantly different at α =0.05 level according to Tukey-Kramer honestly significant different test.

Species	**Height above river level (m)**
S. babylonica	$+0.47 \pm 0.15^{A}$
E. camaldulensis	$+1.13 \pm 0.14^{B}$
A. stenophylla	$+1.65 \pm 0.15^{C}$

5.3.2 Changes in ψ_{shoot} across seasons

There was a significant month × species interaction ($p < 0.001$) for predawn shoot water potentials at the riverbank site, indicating that differences between species change over time (Table 5.3). Across most sampling dates ψ_{predawn} tended to be less negative in *S. babylonica*, followed by *E. camaldulensis*, then *A. stenophylla.* Except in December, when ψ_{predawn} for *S. babylonica* was much less than *E. camaldulensis*, which was comparable to *A. stenophylla* (Fig. 5.4a). There was also a significant month × species interaction ($p < 0.001$) in riverbank ψ_{midday} values, although once again *S. babylonica* ψ_{midday} tended to be consistently less negative then *A. stenophylla*, followed by *E. camaldulensis, except in* October 2002, when ψ_{midday} was more negative in *E. camaldulensis* than the other two species (see Table 5.3; Fig 5.4b).

Table 5.3. F statistics and p-values ($\alpha = 0.05$) for predawn shoot water potential ($\psi_{predawn}$) and midday shoot water potential (ψ_{midday}) for adult trees (i.e. *Salix babylonica, Eucalyptus camaldulensis andAcacia stenophylla)* within the riverbank sites (2-way ANOVA).

Site	**Factor**	**Predawn shoot water potential ($\psi_{predawn}$)**	**Midday shoot water potential (ψ_{midday})**
Riverbank	month	$F_{4,178} = 28.74$, $p<0.0001$	$F_{4, 178} = 51.07$, $p< 0.0001$
	species	$F_{2,178} = 456.15$, $p<0.0001$	$F_{2, 178} = 1648.84$, $p<0.0001$
	Month × species	$F_{8,178} = 6.15$, $p<0.0001$	$F_{8, 178} = 5.70$ $P<0.0001$

In terms of predawn shoot water potentials ($\psi_{predawn}$) the significant species × months × site interaction ($p < 0.0001$, see Table 5.4) suggests there were no consistent trends in predawn shoot water potentials ($\psi_{predawn}$) between native species and the riverbank and floodplain sites arcross the monitoring period. In the riverbank site, *E. camaldulensis* had slightly less negative $\psi_{predawn}$ than *A. stenophylla,* yet slightly more negative $\psi_{predawn}$ on the floodplain (Figure 5.4 a, b). In the riverbank, $\psi_{predawn}$ in *E. camaldulensis* were most negative in early spring (September 2002), while the most negative $\psi_{predawn}$ measurements for *E. camaldulensis* trees on the flooplain were in March 2003 (Fig. 5.4 a, b). For *A stenophylla*, the least negative $\psi_{predawn}$ were in December 2002 in both the riverbank and flooplain sites (Fig. 5.4 a, b).

The overarching significant interaction ($p = 0.008$), which suggests that the midday shoot wate potentials (ψ_{midday}) for the native species were not consistent between species, months or sites (Table 5.4) In general the flooplain native trees had more negative ψ_{midday} than the riverbank trees (mean ψ_{midday} for floodplain *E camaldulensis* was -3.03 ± 0.021 MPa and for *A. stenophylla* was -2.49 ± 0.021 MPa) (see Fig. 5.4 c & d). *E. camaldulensis* tended to have less negative ψ_{midday} than *A. stenophylla* within both sites across the monitoring period. In the riverbank site, ψ_{midday} measurements for *E. camaldulensis* and *A. stenophylla* were the most negative in the months of early spring (i.e. September 2002 and October 2002) (Fig. 5.4 c & d). However, in the floodplain site, while ψ_{midday} for *A. stenophylla* remained fairly consistent across the sampling months, *E. camaldulensis* had the most negative ψ_{midday} in September 2002 and March 2003 (Figure 5.4 c, d).

Table 5.4. F statistics and p-values ($\alpha = 0.05$) for predawn shoot water potential (ψ_{predawn}) and midday shoot water potential (ψ_{midday}) for adult native trees (i.e. *Eucalyptus camaldulensis andAcacia stenophylla)* across the monitoring period, between the riverbank and flooplain sites (3-way ANOVA).

Factor	**Predawn shoot water potential (ψ_{predawn})**	**Midday shoot water potential (ψ_{midday})**
month	$F_{5, 279} = 38.46$, $p < 0.0001$	$F_{5, 283} = 27.60$, $p < 0.001$
species	$F_{1, 279} = 0.51$, p = 048	$F_{1, 283} = 714.83$, $p < 0.001$
Site	$F_{1, 279} = 1440.53$, $p < 0.0001$	$F_{1, 283} = 1287.11$, $p < 0.0001$
Month × species	$F_{5, 279} = 7.05$, $p < 0.0001$	$F_{5, 283} = 5.280$, $p < 0.001$
Month × site	$F_{5, 279} = 5.07$, $p = 0.0002$	$F_{5, 283} = 11.95$, $p < 0.001$
Species × s ite	$F_{1, 279} = 74.81$, $p < 0.0001$	$F_{1, 279} = 2.19$, $p = 0.14$
Month × species × site	$F_{5, 279} = 5.50$, $p < 0.0001$	$F_{5, 283} = 3.21$, $p = 0.008$

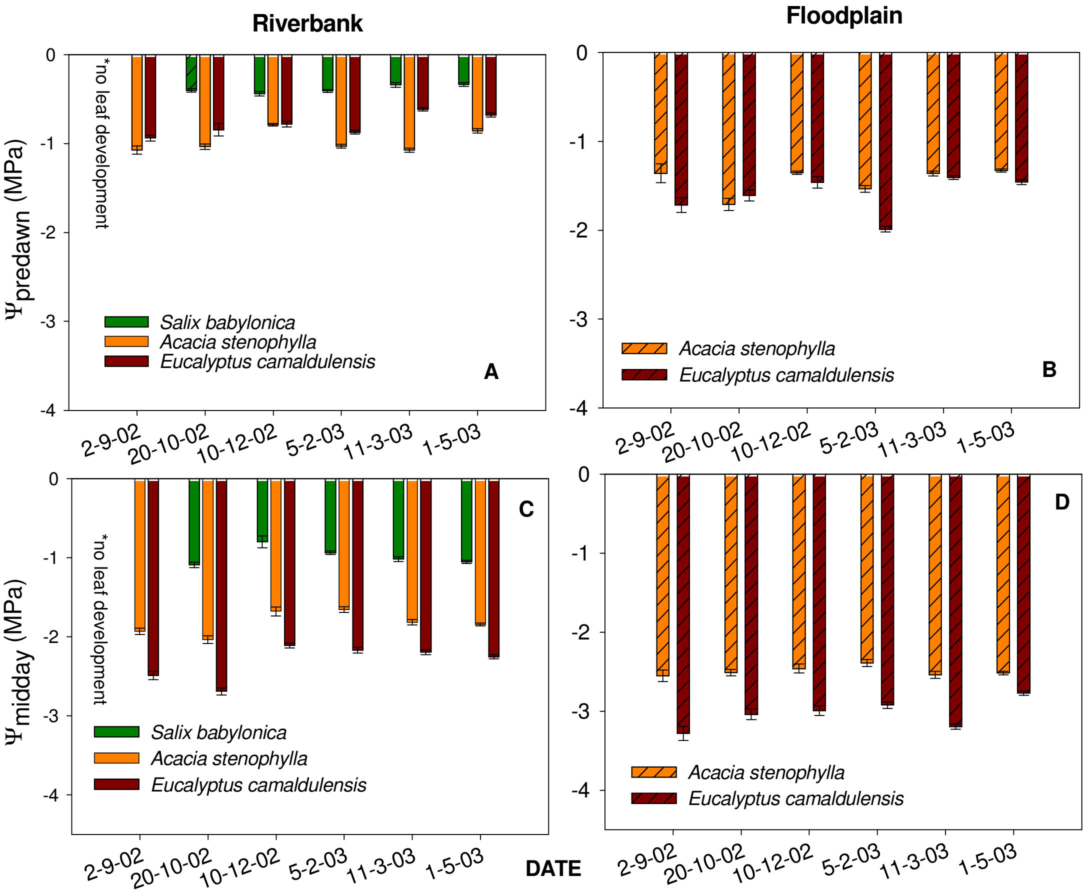

Figure 5.4. Comparison of riverbank (A) and floodplain (B) $\psi_{predawn}$ (MPa) and riverbank (C) and floodplain (D) ψ_{midday} for *S. babylonica*, *E. camaldulensis* and *A. stenophylla*. Katarapko National Park, Lower Murray River (SA). Measurements were taken every six weeks across the growing season September (2002) to May (2003). Mean ± S.E (n = 3).

5.3.3 Gas Exchange and chlorophyll fluorescence

Assimilation rates (A) were higher in all trees in spring (September 2002 & October 2002) than in late summer (March 2003) (Fig. 5.5 a). Riverbank *E. camaldulensis* recorded the highest mean A values in September 2002 (17.1 µmol m^{-2} s^{-1}), followed by *A. stenophylla* (15.3 µmol m^{-2} s^{-1}). In October 2002, *S. babylonica* leaves were still not fully developed, so assimilation rates were markedly lower (mean 9.7 µmol m^{-2} s^{-1}) than the native trees (Fig 5.5a). There were no significant differences in the slopes of the lines comparing g_s and A across species (ANCOVA, $p = 0.25$) suggesting similar photosynthetic capacities (Fig. 5.6), although the range for *S. babylonica* was much smaller than the other two species. Transpiration rates were similar across all months for all species on the riverbank except in March 2003 when mean leaf temperatures for *S. babylonica*, *A. stenophylla* and *E. camaldulensis* were higher than those during other months (i.e. leaf temperature ranges in September 2002: 17 -21°C, October 2002: 16 -28°C compared with March 2003: 35 - 40°C) (Fig. 5.5b) Stomatal conductance was generally greater in riverbank trees than floodplain trees. Native trees on the riverbank had much higher stomatal conductances in early spring compared with riverbank *S. babylonica* and natives on the floodplain (Fig 5.5d). Across the remaining months of the study period, stomatal conductance in *S. babylonica* was similar to the native trees on the riverbank and floodplain. Overall though, floodplain trees had lower A, E and g_s than the riverbank trees across all months (see Fig. 5.5a, c and d). Since gas exchange measurements were unable to be taken during December 2002 and May 2003sampling trips, measurements of predawn F_v/F_m were made instead. Predawn F_v/F_m for all three species at the riverbank and floodplain sites was close to 0.8 suggesting that the trees were not significantly photodamaged, which might be expected if they were water stressed (Fig 5.5c).

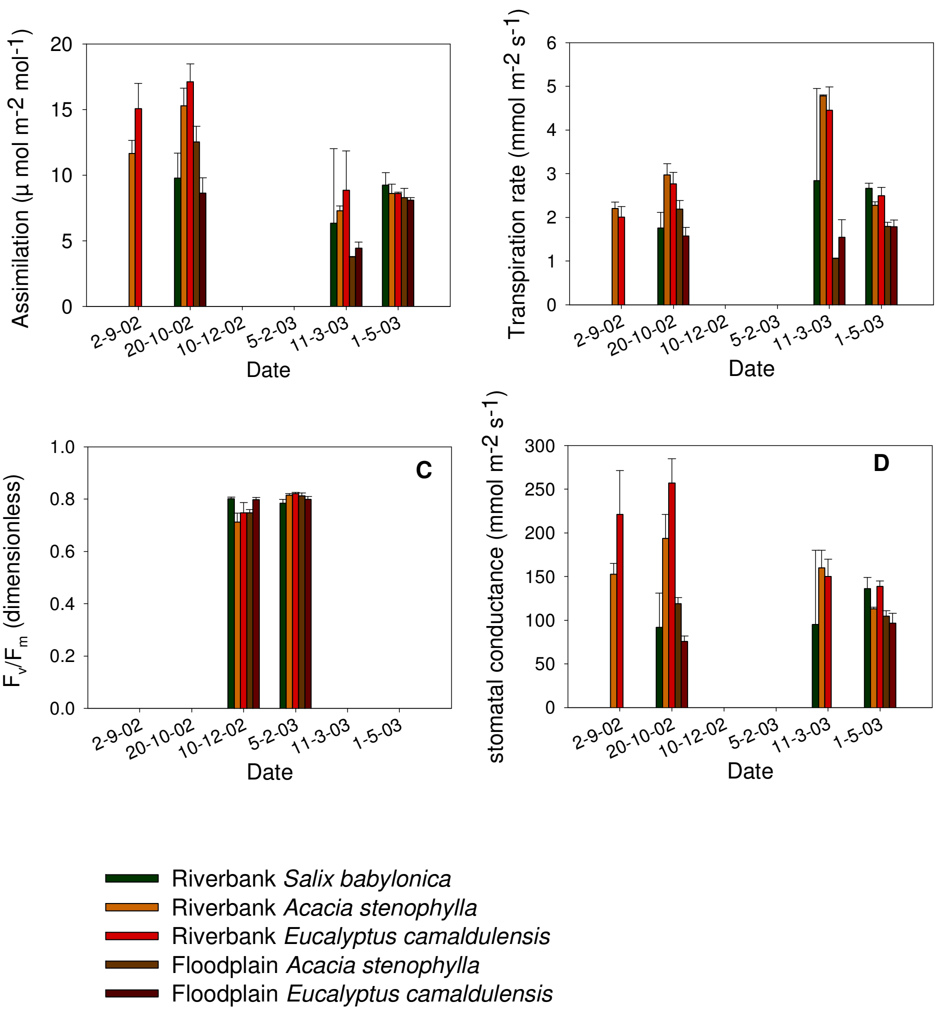

Figure 5.5. Comparison of assimilation rates (A), transpiration rates (B), F_v/F_m, (C) and stomatal conductance (D) for *S. babylonica*, *A. stenophylla* and *E. camaldulensis*, on riverbank (i.e. high water availability) versus floodplain (i.e. low water availability) sites. Katarapko National Park, Lower Murray River (SA). For A, C and D, measurements were taken every six weeks across the growing season September- 2002 to May- 2003 (excluding sampling dates during December and February due to instrument failure. Measurements of predawn photosynthetic yield were taken instead as an indicator of plant stress). Mean ± S.E (n = 2 - 4). *data for floodplain tree

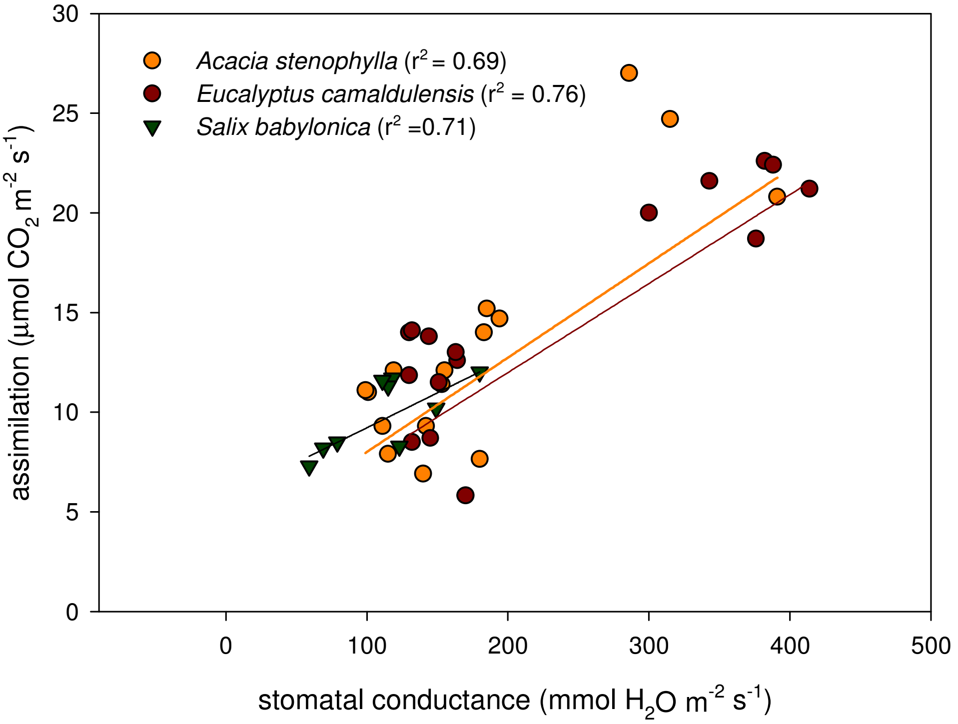

Figure 5.6 (a-d). Relationships between stomatal conductance (g_s) and photosynthetic rates (A) for *S. babylonica, A. stenophylla* and *E. camaldulensis* from the riverbank site. Data were collected across the period 2/9/2002 to 1/5/2003.

5.3.4 Soils

Soil water content (g g^{-1}) was similar across depths at the riverbank site and remained relatively constant throughout the months (Fig. 5.7a). A number of trends were evident in the soil matric potential despite considerable variability. While there was no significant difference in ψ_{soil} across months ($F_{7,\ 47}$ = 2.86, p = 0.054), there were differences between depths ($F_{7,\ 47}$ = 4.31, p = 0.019). Soil matric potential was more negative in the upper 0.25 m depth than the lower depths. This was most pronounced in the December 2003, when mean ψ_{soil} at this depth reached -5.04 ± 2.43 MPa ($F_{7,\ 47}$ = 3.41, p = 0.005) (Fig. 5.7b). Overall soil matric potential became less negative with increasing depth and at depths between 1.0 - 1.5 m was similar to $\psi_{predawn}$ (range -0.3 to -1.0 MPa) for all species across the months.

In December trees may have accessed soil water deeper than 0.25 m, in February, any depth may have been accessed. In March and May, 2003 all plants may have accessed water at depths >0.75 m and > 1m, respectively (Fig. 5.7b and Fig. 5.4a).

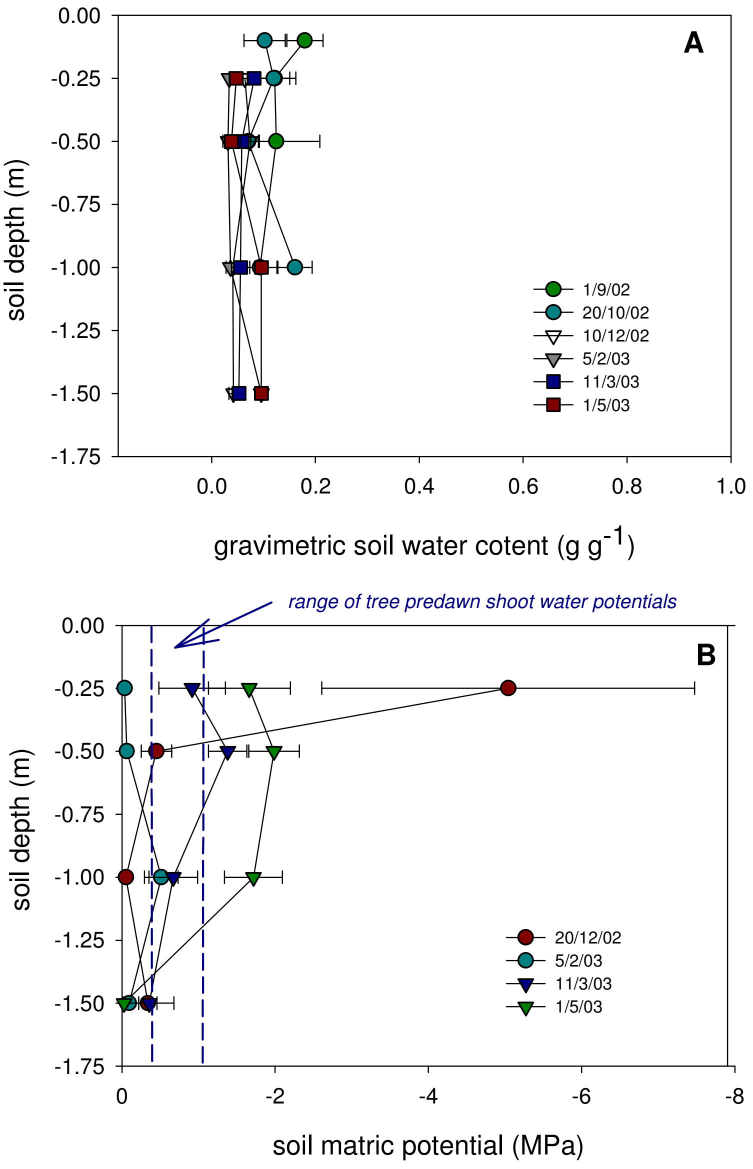

Figure 5.7. Gravimetric soil water content g g^{-1} (A) and soil matric potential (MPa) (B) throughout the soil profile at the riverbank site (Katarapko National Park, South Australia) across the spring to autumn monitoring period (September 2002 to May 2003). Data points represent means ± SE (n = 3 - 4 for each depth).

5.3.5 Water Source for S. babylonica

S. babylonica $\delta^{18}O$ stem tissue values were a similar to the $\delta^{18}O$ soil-water measured at the 0.25 m depth in early spring (Figure 5.8a). In October 2002, *S. babylonica* $\delta^{18}O$ were closer to the $\delta^{18}O$ river-water values, suggesting they were deriving their water from a mixture of both soil-water and river water (Fig. 5.8b). During October 2002 measurements of $\delta^{18}O$ floodplain groundwater and $\delta^{18}O$ river-water were similar suggesting that mixing occurred or possibly interception of the alluvial groundwater with the main river channel. Groundwater within the floodplain site had a salinity of 4.97 ± 0.88 dS m^{-1} when measured in spring. $\delta^{18}O$ values of soil-water within the floodplain soil profile suggest there was isotopic enrichment in the upper depths (<-0.5 m) and again at between 2.5 to 2.75 m depths. In mid-summer (February 2002) *S. babylonica* $\delta^{18}O$ and $\delta^{18}O$ river-water were closely matched, although there were indications that *S. babylonica* were deriving their water from both the river- and soil- water sources (Fig5.8c). In general, isotopic enrichment occurred in both the upper and lower regions of the profile (<0.5 m and between 1.0 m respectively).

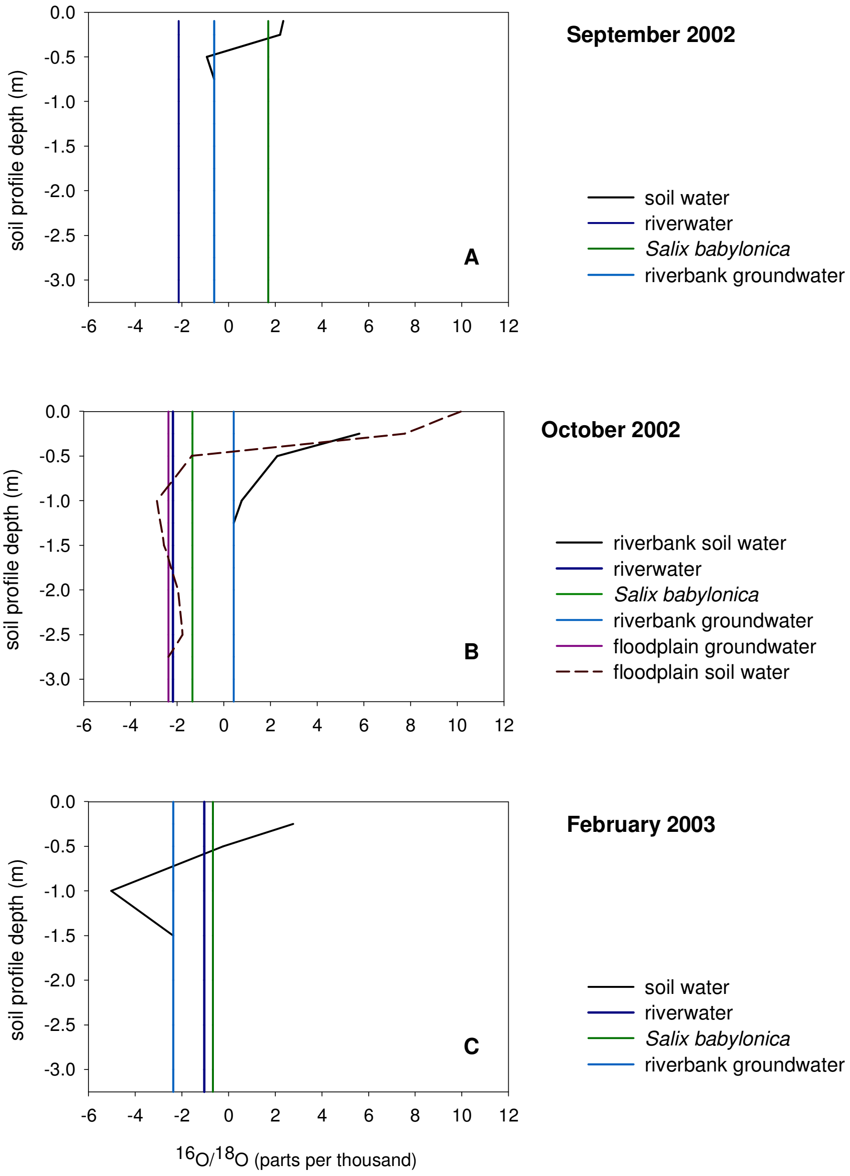

Figure 5.8. $\delta^{18}O$ values for *S. babylonica* stem tissue, river-water, groundwater and soil water (-0.1 to -2.75 m) from *riverbank* and *floodplain* sites of Lower River Murray (Katarapko National Park, South Australia) in September 2002 (A), October 2002 (B) and February 2003 (C).

5.3.6 Carbon isotope discrimination: long term water-use-efficiency

δ^{13}C values for *A. stenophylla* and *E. camaldulensis* on the floodplain were significantly higher ($F_{1, 15} = 19.18$, $p = 0.0007$) than the δ^{13}C values of *A. stenophylla*, *E. camaldulensis* and *S. babylonica* on the riverbank suggesting more conservative water use for the floodplain species (Fig. 5.9).

There were slight differences in foliar δ^{13}C among species at each site ($F_{2, 9} = 5.42$, $p = 0.045$). *A. stenophylla* had the lowest δ^{13}C value followed by *S. babylonica* and *E. camaldulensis* which were similar. There were no significant differences in foliar δ^{13}C values between species on the floodplain ($F_{1, 6} = 6.79$, $p = 0.06$) implying that both *A. stenophylla* and *E. camaldulensis* were equally conservative in their water usage on the floodplain (Fig. 5.9).

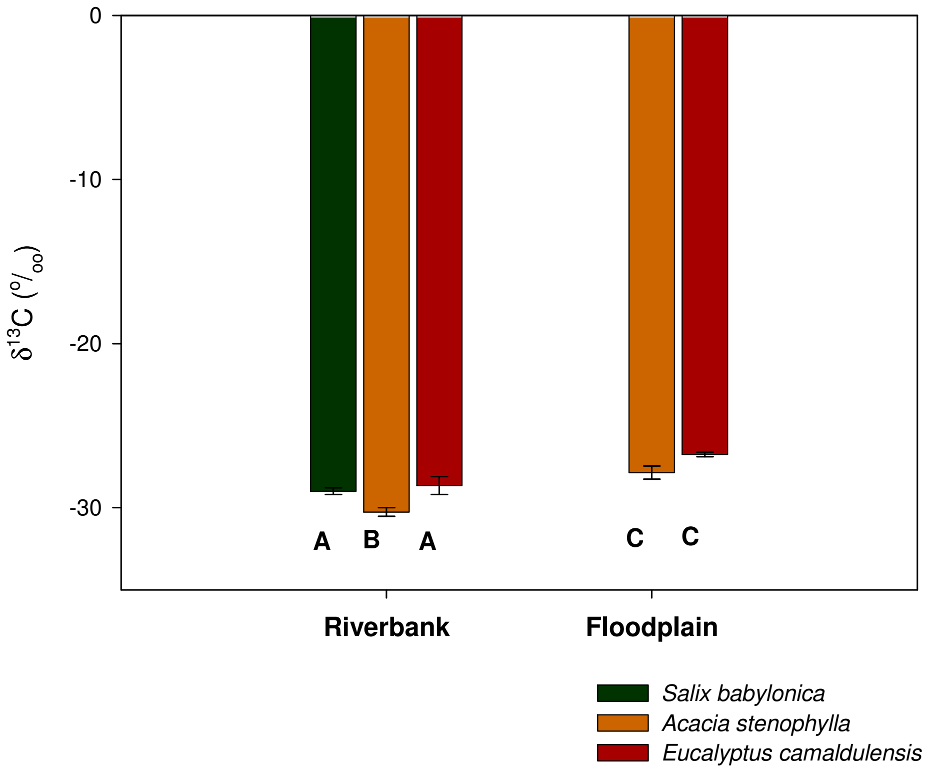

Fig 5.9. Seasonal (September 2002 – May 2003) foliar $\delta^{13}C$ values for *S. babylonica*, *E. camaldulensis* and *A. stenophylla* from *riverbank* and *floodplain* sites of Lower River Murray (Katarapko National Park, South Australia). The same letters are not significantly different at α =0.05 level according to Tukey-Kramer honestly significant different test.

5.4 Discussion

Water relations of willows and natives

Shoot $\psi_{predawn}$ is often compared with measurements of ψ_{soil} at different soil depths to infer where plants may be sourcing their water (Flanagan *et al.* 1992). However, at different depths ψ_{soil} is often highly variable and, while an individual plant may have consistent $\psi_{predawn}$ across a season, a gradual switch from surface water to groundwater sources could go undetected (Smith *et al.* 1991, Ehleringer and Dawson 1992). *S. babylonica* had consistently less negative $\psi_{predawn}$ (i.e. ~0.35 MPa) than the two native species suggesting that its roots were in contact either with the saturated region of the riverbank soil (water table depths of ≥1.0 m) and/or river-water itself. Nevertheless $\delta^{18}O$ values suggested that riverbank *S. babylonica* were sourcing their water either directly from the river, or the upper 0.25 m of the soil profile, since $\delta^{18}O$ stem tissue values were always a closer match to these two water sources. However since *S. babylonica* $\psi_{predawn}$ did not correspond with ψ_{soil} at the upper 0.25 m depths, it is most likely that *S. babylonica* is reliant on access to a consistent supply of river-water, and does not generally access deeper soil-water sources. In contrast, the range of $\psi_{predawn}$ for native species consistently matched ψ_{soil} at deeper depths (>0. 5 m) across most of the study period, which suggests natives were using the deeper soil water sources.

The differences in $\psi_{predawn}$ between *S. babylonica* and natives on the riverbank presumably reflect their elevation relative to river-water levels, and the source of water they are accessing. *A. stenophylla* grow at the highest positions and had the most negative $\psi_{predawn}$ across the study period, whereas *S. babylonica* had the lowest position and the least negative $\psi_{predawn}$. This is also consistent with *S. babylonica* relying directly on river water from the main channel.

Given that it can access river-water, it might be expected that *S. babylonica* would be somewhat more profligate with its use of water than the native species. However *A. stenophylla* had the lowest $\delta^{13}C$ on the riverbank, suggesting lower water use efficiency than *E. camaldulensis* and *S. babylonica*. These differences in water use may occur because of differences in tree age, tree height, sex (Farquhar *et al.* 1988, Calder and Dye 2001) or variability in microclimatic and topographic features (Leffler and Evans 1999). Donovan and Ehleringer (1994) found that small juveniles of the shrub *Chrysothamnus nauseosus*, had lower $\delta^{13}C$ than larger adults. The lower $\delta^{13}C$ of juveniles was often accompanied by relatively high rates of photosynthesis and stomatal conductance compared with adults, even though juveniles generally had more negative $\psi_{predawn}$.

Riverbank trees had a lower $\delta^{13}C$ than floodplain trees. However, on the riverbank there was no significant difference in $\delta^{13}C$ between *S. babylonica* and *E. camaldulensis,* and *A. stenophylla* had significantly lower $\delta^{13}C$ than *S. babylonica.* This appears to contradict the widely held view that invasive riparian trees (*Salix* included, see Cremer *et al.* 1995) are profligate water users compared with natives. Indeed, in the western United States, introduced *Tamarix* spp. aggressively compete with the surrounding native vegetation for water and in doing so disrupt ecosystem processes by lowering water-tables and drying out waterholes (Zavaleta 2000). On average, *Tamarix* spp. was shown to consume 3000 – 4600 m3 ha^{-1} yr^{-1} more water than the native vegetation they replace. But although some plants are able to decrease transpiration during water deficit, when they have access to continually saturated zones or deep water sources, they can transpire continuously (Domingo *et al.* 1999). A study by Bodribb and Hill (1994) investigated the possible factors limiting the distribution of southern hemisphere conifers and found that when seedlings were grown under well-watered conditions, their $\delta^{13}C$ did not provide any indication of the drought tolerance that is observed in the field, because if the water was there – they used it. This contradicted the assumption that trees with higher $\delta^{13}C$ and supposedly greater water use efficiency would be better adapted to field conditions of low rainfall and drought. This concurs with a review by Calder and Dye (2001) on the hydrological impacts of invasive plants. They concluded that greater water usage by an invasive species was more likely to occur in water-limited conditions as opposed to riparian or water-unlimited conditions. Thus, it is possible that riverbank natives were just as profligate in their water use as *S. babylonica*, simply because more water was available.

Another factor to consider is that the volume of water used by vegetation, especially in aquatic systems, may be related more to the total area of space colonised, plus the structure and composition, of the vegetation. Studies on the water use of reed and sedge communities in four different lake systems in Poland found that if total leaf biomass was substantial, then the volume of water used by the vegetation exceeded the amount of water that would be otherwise lost from the open water-body via evaporation (Bernatowicz *et al.* 1976). As mentioned in Chapter 3, on the main channel of the LRM, the regions where native vegetation flourishes tend to be structurally complex and species rich (Roberts and Ludwig 1991) compared with the regions where *Salix* taxa flourish (Kennedy *et al.* 2003). The emergent reed *Phragmites australis* commonly co-occurs with *Eucalyptus* sp. lined reaches on the LRM (Roberts and Ludwig 1991). *P. australis* can reach heights of <6 m and produce high leaf biomass so transpiration rates can also be high (<300 g H_2O h^{-1} m^{-2} leaf area) (Moro *et al.* 2004). This suggests that comparing the amount of water consumed by invasive *Salix* compared with natives may prove futile since even if *Salix* are removed, the area may be replaced by other species, such as *Typha*, that also have high rates of water use. It may be more useful to compare the total amount of vegetation between river reaches, as opposed to differences in individual species water-use patterns (Dahm *et al.* 2002)

The more negative $\psi_{predawn}$ and ψ_{midday} and higher $\delta^{13}C$ in floodplain trees versus riverbank trees does suggest lower water availability in this habitat and possible signs of water stress (Rood *et al.* 2003). In the current study, assimilation rates and stomatal conductances were also lower in floodplain natives compared with riverbank trees. In addition, lower assimilation rates and stomatal conductances observed in late summer for both native species, corresponded with the lowest soil water contents and matric potentials across the study period; although these data were for riverbank soils only. In another study on the floodplains of the LRM, *E. camaldulensis* trees showing severe visual signs of water stress (>90% canopy reduction) and extremely low $\psi_{predawn}$ of -4.25 MPa were still able to transpire as seen in sap flow measurements made on the same day (DWLBC 2005). In this same study, *A. stenophylla* were not assessed as having visual signs of water stress like *E. camaldulensis*, but they too recorded highly negative $\psi_{predawn}$ measurements of -3.5MPa. Despite the indications of possible water stress in floodplain trees (and riverbank trees in late summer) in this study, measurements of F_v/F_m suggested none of the trees at either site were particularly stressed. However, F_v/F_m can have its limitations when assessing water stress. For example, Crawford and Wilkens (1996) found that abscised *E. camaldulensis* leaves had deformed palisade mesophyll, which was indicative of severe water stress; however the chloroplasts remained intact and functional. This suggests they may be able to retain photosynthetic efficiency even under water stress. A study assessing the health of *E. camaldulensis* growing on sites of decreasing water availability in eastern Australia also found confusing data (Chisholm and Stone 2003). On the site with least water availability, *E. camaldulensis* showed apparent signs of water stress with markedly negative $\psi_{predawn}$ of

-2.5 MPa. Yet measurements of F_v/F_m made on the same day were still > 0.75, suggesting the trees were not severely water stressed. The data from this study and previous research are consistent with natives being tolerant of a wide range of soil conditions and/or being able to access water at greater depths when soils dry in the upper profile.

Cavitation Risk

Lack of *S. babylonica* on floodplains may also reflect an inability to access sufficient quantities of groundwater to maintain growth. For *S. babylonica* to survive in floodplain habitats they would need to generate $\psi_{predawn}$ lower than -1.3 MPa (minimum seasonal $\psi_{predawn}$ recorded by native trees) – a value they did not attain on the riverbank - in order to extract groundwater from these soils. *S. babylonica* may not be able to do this since many other willows are reportedly prone to xylem cavitation; which occurs when xylem sap is under tension (Pockman *et al.* 1995) and reaches critically low pressures pulling air bubbles into xylem conduits (Tyree and Sperry 1988). Previous studies have found that a 100% loss of water transport occurs in *S. gooddingii* and *Populus fremontii* when ψ_{xylem} falls within the range of – 2 to –3 MPa (Pockman and Sperry 2000). Similarly Synder and Williams (2000) found that the same species (*P. fremontii*, *S. goodingii*) appeared to regulate midday water potentials to -1.5 MPa in the field. In contrast, *E. camaldulensis* trees only suffer a 50% hydraulic conductivity loss in the ψ_{xylem} range of – 3.8 to – 4.2 MPa as a result of cavitation (Pammenter and vander Willigen 1998). This vulnerability to cavitation in other *Salix* taxa may explain the narrow distribution of *S. babylonica* along riverine corridors. Braatne *et al.* 1996 (cited by Rood *et al.* 2003) found that distribution of *Populus* spp. (Salicaceae) is limited to areas where they can gain access to supplemental water provided by a stream or river. More specifically, they are restricted to bands up to 3 – 4 m along the riverine corridor, above the lowest base flow level of the river in late summer. It is believed that their distribution is a function of elevation from groundwater as opposed to their distance from the river (Stromberg *et al.* 1996, Horton *et al.* 2001*b*).

Root Morphology

Access to water may be further constrained by root system development since my data suggest *S. babylonica* would require a root system that penetrates up to 2.5 to 2.75 m to access groundwater sources on floodplains. High $\psi_{predawn}$ for *S. babylonica* along riverbanks most likely reflects their ability to produce numerous adventitious roots that can tolerate the saturated soil zone and persist just under the water surface. $\psi_{predawn}$ were slightly lower for riverbank *E. camaldulensis* (± -0.3 MPa) and *A. stenophylla* (± -0.3 MPa) and may reflect a preference for soil conditions that are less anoxic. Although *E. camaldulensis* are able to produce adventitious roots in response to flooding their overall growth can be inhibited if waterlogging is prolonged (Marcar 1993). *Salix* taxa in many riparian systems throughout Australia exhibit some distinct morphological differences in rooting structure and depth compared to the dominant native trees. Willows form large, fine, lateral root mats (Ladson 1997, Serena and Williams 1997) and are capable of producing numerous adventitious roots (that are distinctly pinkish coloured, Chapter 4). In the field they are either in direct contact with the water and/or distributed throughout the saturated zone of the soil profile. Perhaps because of their ability to form adventitious roots, that appear to be tolerant of water-logged conditions, *S. babylonica* can tolerate the lower elevations and even grow in of the channel, thereby tapping directly into river-water sources. *E. camaldulensis* and *A. stenophylla* may be limited to slightly higher elevations because many *Eucalyptus* and *Acacia* spp. produce bimodal root systems; where shallow-buried roots allow for the uptake of surface water, precipitation and nutrients, and sinker roots are produced to access deeper groundwater sources (BenDavid-Novak and

Schick 1997). Although measuring $\delta^{18}O$ values for the native species was outside of the scope of this project, previous research by Thorburn and Walker (1993) established that riparian *E. camaldulensis* were only using river water when at distances shorter than 15 m from the river's edge, beyond that they use precipitation derived soil-water and alluvial groundwater sources.

Salinity Tolerance

Another aspect restricting the establishment *S. babylonica* on floodplains may be saline groundwater, since the decline of dominant LRM floodplain trees has been linked to soil salinisation (Overton *et al.* 2006). On the floodplains, groundwater salinities are highly variable on temporal and spatial scales, but may be as high as 55 dS m^{-1} (Slavich *et al.* 1999), which is considerably greater than the floodplain groundwater values measured in this study (~5 dS m^{-1}). A field survey along the Murray River from Wellington to Mannum (below Lock 1) by Kennedy *et al.* (2003) showed soil-water conductivities along the riverbank varied between 2.2 and 11.4 dS m^{-1} with a median value of 6.0 dS m^{-1}. Although mature *S. babylonica* and *S. fragilis*, were present along the entire length of the LRM surveyed, experimental glasshouse trials in the same study showed that seedling growth was severely limited when exposed to soil conductivities between 3 - 7 dS m^{-1}. In contrast Rawat and Banerjee (1998), who exposed potted *E. camaldulensis* seedlings to increasing salinity levels of 0, 4, 8, 12 and 16 dS m^{-1} found seedling height, biomass production and photosynthetic rates were stimulated at conductivities between 4 – 12 dS m^{-1} relative to other concentrations used. In addition survival of *E. camaldulensis* seedlings was not significantly affected at 16 dS m^{-1}. Similar trends were found in maturing (5 – 7 years old) *E. camaldulensis* and *A. stenophylla* trees growing on a saline discharge site (Marcar *et al.* 2003), where tree height and diameter at breast height (DBH) were improved under saline conditions (6 -10 dS m^{-1}). Maturing *E. camaldulensis* showed a degree of decline in tree height with increasing salinity, but *A. stenophylla* showed no decline in growth even at 10 dS m^{-1}. These results correspond with a set of guidelines produced by Rural Industries Research and Development Corporation (2000) recommending the use of *E. camaldulensis* in slightly saline conditions of 2 – 4 dS m^{-1} and the planting of *A. stenophylla* for extreme saline conditions of 16 dS m^{-1}.

In-stream salinity values for the LRM were relatively low (<0.7 dS m^{-2} s^{-1} (DWLBC 2005) across the study period (see Chapter 6). The ability of developing (see Chapter 3) and mature (see Chapter 4) *S. babylonica* to produce adventitious roots that directly tap river-water sources, may therefore alleviate the stress that saline groundwater poses to *S. babylonica* growth, yet at the same time this would restrict them to the river's edge. For example, the emergent reed, *Phragmites australis* survived daily inundations of saline water >35 ppt if their roots and rhizomes were located in relatively fresh and brackish water of less than 15 ppt (Adams and Bate 1999).

Chapter 6

Responses of *Salix babylonica* and native *Eucalyptus camaldulensis* to a Lower River Murray drawdown.

6.1 Introduction

Rivers impounded along longitudinal gradients have suffered from the effects of successional changes in aquatic vegetation and a decline in vegetation health as well as diminishing fauna and invertebrate populations (Junk 1989, Poff *et al.* 1997, Kingsford 2000, Bunn and Arthington 2002, Nilsson and Berggren 2000, Walker 2001) because flow stabilisation can occur as a result of weirs and dams - creating artificially constant environments that lack natural extremes (Maheshwari *et al.* 1995, Poff *et al*. 1997). These alterations to flow regimes as a result of weir operations (Obedzinkski *et al.* 2001) have resulted in compositional shifts in riparian and littoral vegetation (Roberts and Ludwig 1991, Walker 1994a, Blanch *et al.* 2000, Walker 2001, Norris *et al.* 2001) because flow stabilisation favours some species at the expense of others that were adapted to variability in flow (Walker 1994a, Gehrke *et al.* 1999, Blanch *et al.* 1999, Blanch *et al.* 2000, Kingsford 2000).

Under natural regimes, periods of low flow are generally a seasonal phenomenon taking place during the dry seasons in many rivers (Welling *et al.* 1988, Pettit *et al.* 2001). Depending on the timing, extent and duration of a low flow episode (Wood and Pfitzer 1960) there may be beneficial or detrimental effects (Poff *et al.* 1997) on aquatic communities. Low flows may cause spatial shifts in zooplankton (Marques *et al.* 2007) and fish communities (Jackson 1966, Kuznetsov 1971, cited in Benejam *et al.* 2008) and/or decreased water quality (Caruso 2002). In xeric environments, the duration of low flow events is a strong influence in shaping vegetation patterns along main channels (Stromberg *et al.* 2007). Vegetation communities may be altered (Thomaz *et al*. 2006) by limiting the establishment and growth of less water-stress tolerant species. For example, in the United States where riparian plants on stream reaches with low flow (due to water diversions) had reduced shoot water potentials and stomatal conductance compared with plants on reaches with natural flow (undiverted reaches) (Smith *et al.* 1991). Yet low flow may increase the regeneration of other species by offering favourable windows of opportunity for germination, colonisation and establishment (Thompson and Grime 1983, Pettit and Froend 1999, Hölzel and Otte, 2004b).

Under the natural regimes along the Lower River Murray (LRM), water levels would have dropped during low flow periods between floods, allowing low lying floodplain areas and wetlands to dry out (Walker 2001) and colonisation by terrestrial flora and fauna to occur; but a series of locked weir structures have now stabilised flow (Chapter 3). Approximately half of the floodplain wetlands that were once seasonally inundated are now permanently inundated (Walker 2001), and the elimination of low flow periods on the LRM is believed to have reduced opportunities for the regeneration of native trees, but created conditions that favour introduced *Salix* (Roberts and Marston 1999, Walker 2001, George *et al.* 2005, Jensen *et al.* 2008). To mimic more natural water levels in the Murray River, manipulation of river water levels using the locks and weirs, has been proposed (DWLBC: Factsheet #21). In 2000, a trial was carried out that raised water levels above normal operating levels to inundate floodplains (Siebentritt *et al.* 2001) but as yet, no manipulative trials involving the lowering of water below designated pool levels have occurred (DWLBC: Factsheet #21). However, a natural river-water drawdown was predicted to occur below Lock 1 on the LRM from late 2002 into 2003. Since 1996, dry conditions have prevailed across much of the Murray-Darling Basin watershed (Murphy and Timbal 2007). While dry years are not unprecedented for the LRM in recorded history (e.g. extremely low rainfall years occurred from 1918-1919 and again in the mid 1960's (http://www.bom.gov.au), this recent period was characterised by significantly higher air temperatures than usual, leading to increased evaporation and reduced water availability (Murphy and Timbal 2007). Several years of drought across the Murray-Darling Basin catchment meant that from November 2001 the river was maintained below 'entitlement flow' levels. Entitlement flow is set at 1850 GL yr^{-1} under the Murray-Darling Basin Agreement and relates to the minimum of water guaranteed to flow down the Murray River each year into South Australia from the upriver states. Typically South Australia receives flows well in excess of entitlement flow, but in 2002/03, flows to South Australia were constrained to 1835 GL (i.e. 15 GL below entitlement levels) (DWLBC 2006). The drawdown was predicted to particularly affect the LRM region below Lock 1 – an area of approximately 648 km^2 inclusive of 200 km of main river channel (Lock 1 to Wellington) (see Chapter 1, Fig. 1.2), the adjoining wetlands, and Lakes Alexandrina and Albert (DWLBC 2006).

The predicted sustained low river flows provided an opportunity to compare the responses of native riparian trees and introduced trees, since water levels were predicted to fall below designated pool levels, despite regulation practices. On the LRM invasive *Salix babylonica* and native *Eucalyptus camaldulensis* co-occur on riverbanks, but *S. babylonica* are more likely to be present in regions upstream of weirs where water-levels remain relatively stable, whereas the distribution of *E. camaldulensis* is uniform along weir pools (Chapter 3). *S. babylonica* also appear constrained to low elevations along the main channel banks whereas *E. camaldulensis* are widely distributed along longitudinal and lateral gradients (see Chapter 5). Results from Chapter 5 show *S. babylonica* extracts water directly from the river itself or from soil-water in the upper 0.25 m. It was therefore predicted that a river-water level drawdown >0.3 m and minimal annual precipitation would induce signs of water stress (i.e. low ψ_{shoot} and low leaf gas exchange rates) in the exotic *S. babylonica,* but not in *E. camaldulensis*.

6.2 Methods

6.2.1 Field Site

Forster Island, below Lock 1 (34° 44′19.1″S, 139°32′21.9″E) (Fig 6.1), where *S. babylonica* and *E. camaldulensis* co-occurred, was used as the study site. It is approximately 4 km in length, flanked by the main river channel on the eastern side and separated from the mainland by small channels that feed into and out of a lagoon on the other side. Riparian vegetation at the study site includes: *E. camaldulensis*, *S babylonica*, *Acacia stenophylla* and *Eucalyptus largiflorens* plus reeds such as *Cyperus gymnocaulos, Phragmites australis* and *Typha domingensis*. Soil types within the island range from alluvial sands to grey, cracking floodplain clays.

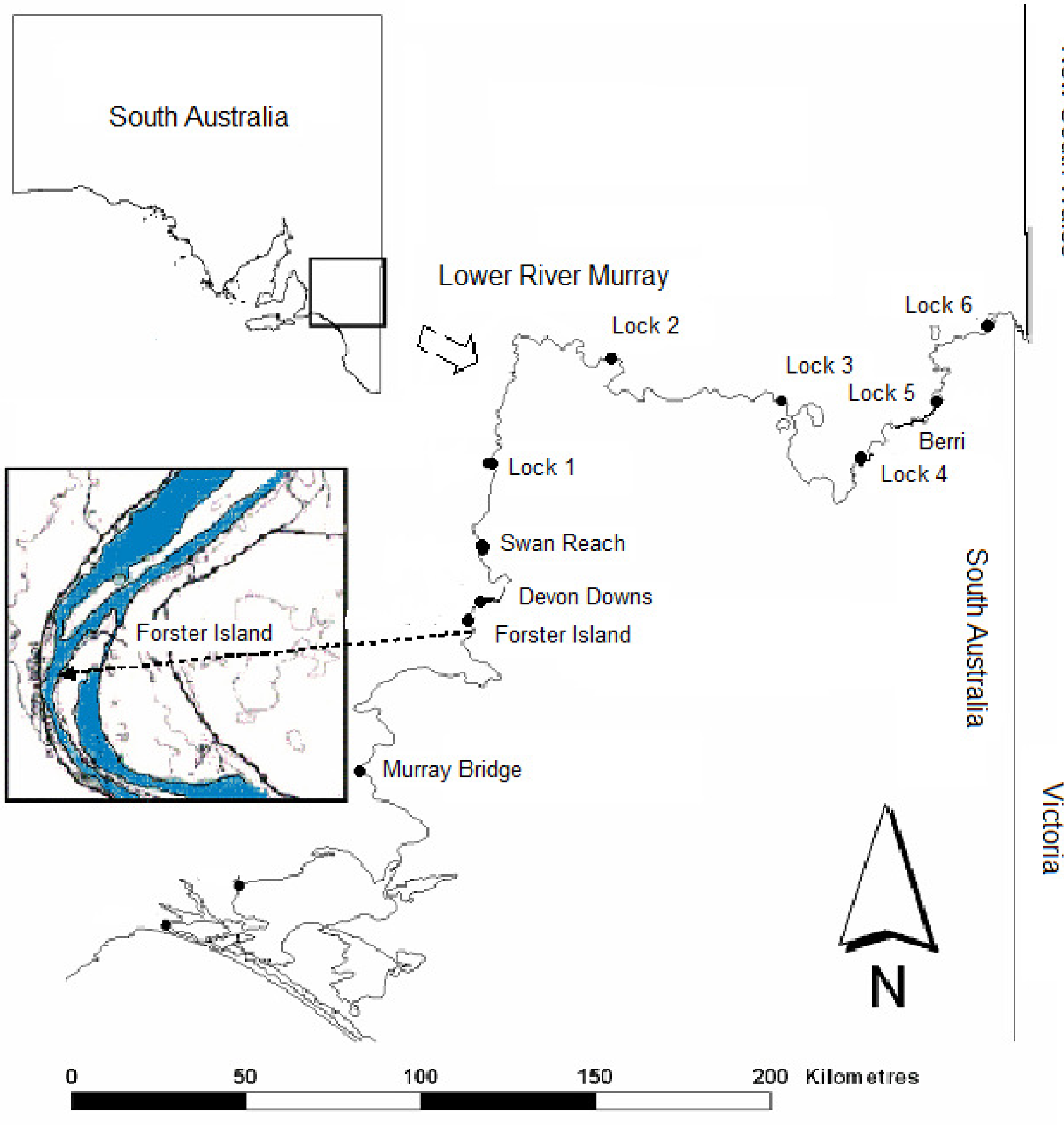

Figure 6.1. Map of the Lower River Murray, South Australia, showing the location of the Forster Island study site.

6.2.2 River water levels

From November 2002, river-water levels receded to a minimum pool level of 0.28 mAHD on 18/5/2003; 0.42 m below the designated pool level for Lock 1 (i.e. 0.7 m) (Fig. 6.1 & Fig. 6.2). Overall drawdown rate was slow (~ 2 – 2.5 mm day^{-1}) yet receding river-water levels caused obvious signs of riverbank exposure (Fig. 6.3). After June 2003, water levels started to rise, suggesting the end of the drawdown and the start of the recovery phase. A maximum pool level of 1.24 mAHD was recorded in September 2003 and river water levels remained above the designated pool level until February 2004 when they started to decline again (Fig. 6.2).

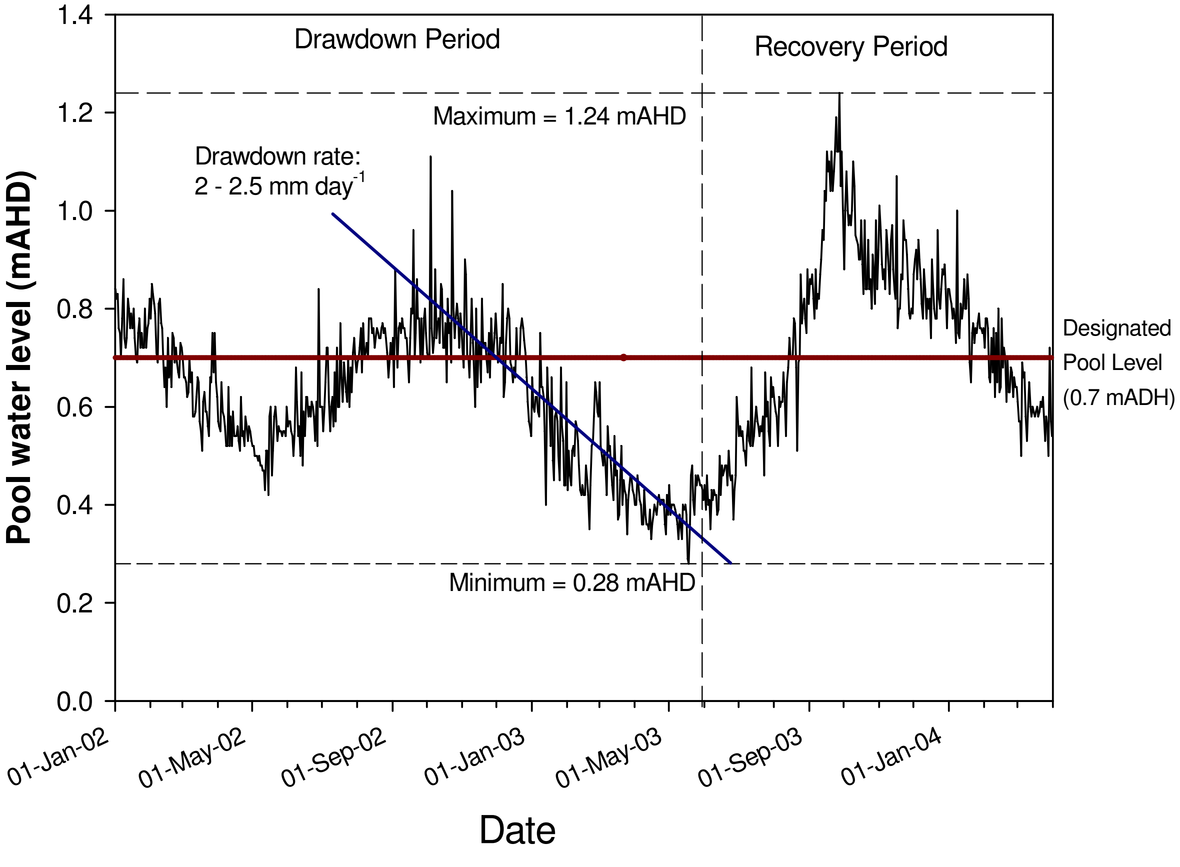

Figure 6.2. Daily river water levels (mAHD) for the Lower Murray River downstream of Lock 1 over the period January 2002 to May 2004. The blue line shows the mean drawdown rate for the period between September 2002 to May 2003.

Figure 6.3. Exposed riverbank mudflats (foreground) at Devon Downs on the Lower River Murray, ~8 km upstream of the Forster Island field site, as a result of the drawdown (March 03). Note how the *E. camaldulensis* (left) are found growing at a higher bank elevation than the *S. babylonica* (centre).

6.2.3 Precipitation

Continuous rainfall data (Bureau of Meteorology, South Australia) was available for the nearby Swan Reach locality (~30 km upstream from Forster Island) (Fig 6.1). In 2002, the total yearly rainfall (121 mm) was well below the yearly rainfall average of 271.7 mm y^{-1} (1898 – 2005) and monthly rainfall totals were consistently low from month to month (9.3 ± 6.3 mm $month^{-1}$) (Fig. 6.3). During the drawdown (November 2002 to May 2003), the average monthly rainfall increased markedly (26.7 ± 26.7 mm $month^{-1}$). Monthly rainfall was erratic with a considerable rainfall (84.6 mm) in February 2003 which occurred across a two day period followed by virtually no rainfall the following month (Figs. 6.2 & 6.4). From June 2003, river-water levels started to increase, and monthly rainfall was more consistent (mean monthly rainfall 26.1 ± 16.2 mm $month^{-1}$) (Figs. 6.2 & 6.4), but dropped again over the summer and autumn of 2004 (average monthly rainfall was 7.8 ± 8.9 mm $month^{-1}$) (Fig. 6.4).

NOTE:
This figure is included on page 175 of the print copy of the thesis held in the University of Adelaide Library.

Figure 6.4. Total monthly precipitation recorded at Swan Reach (weather station # 024535), ~30 km upstream from the study site at Forster Island, from January 2002 to June 2004 (Bureau of Meteorology, SA Govt).

6.2.4 Temperature

Murray Bridge was the closest locality (township ~70 km downstream of field study site) (Fig. 6.1) from which temperature data (Bureau of Meteorology, South Australia) across the study period was available. Mean monthly temperatures across the drawdown (November 2002 to May 2003) ranged from 19 - 30°C; however maximum summer temperatures often exceeded 40°C, especially during summer (Figure 6.5).

NOTE:
This figure is included on page 176 of the print copy of
the thesis held in the University of Adelaide Library.

Figure 6.5. Mean, maximum and minimum monthly temperatures recorded at Murray Bridge locality (weather station # 024521), ~70 km from Forster Island field site,from January 2002 to June 2004 (Bureau of Meteorology, SA Govt).

6.2.5 Sampling Protocol

Monthly measurements of soil water status and plant performance were made from February 2003 to May 2003. In the recovery phase, two more trips were undertaken in December 2003 and February 2004.

6.2.6 Soils

Gravimetric soil water content and matric potential were measured as described in Chapter 5 (Greacen *et al*. 1989). On each sampling trip, four replicate soil samples (~ 200 g per sample) were collected at random positions across the riverbank sites, to depths of 0.25 and 0.5 m and then every 0.5 m to the water table or a maximum 1.5 m.

6.2.7 ψ_{shoot}

Predawn (0430 - 0600 hrs) and midday (1130 - 1300 hrs) ψ_{shoot} were measured on 5 replicate trees of each species on the riverbank per sampling trip with a Scholander Pressure Chamber (Scholander *et al.* 1965). Three shoot samples (~ 3-5 leaves per shoot) were collected from each replicate tree (n = 15 per species) from a height of ~1.5 m and transported back to the pressure chamber in a sealed plastic bag so that measurements could be made ≤10 min following harvesting.

6.2.8 Leaf gas exchange

Assimilation (A: μ mol CO_2 m^{-2} s^{-1}), transpiration (E: mmol H_2O m^{-2} s^{-1}), stomatal conductance (g_s: mol H_2O m^{-2} s^{-1}) and leaf temperature (T_L °C) were measured on 3 replicates trees of each species along the riverbank. Measurements were made at midday (1300 - 1400 hrs) when photon flux density (PFD) reached a diurnal maximum > 1000 μ mol m^{-2} s^{-1}, using an open-system Infra Red Gas Analyser (LCA-4: ADC Bioscientific Ltd) on one fully, expanded mature leaf for each replicate. Leaf gas exchange data were used to calculate instantaneous water use efficiency (i.e. A/E mmol CO_2 mol H_2O).

6.2.9 Statistical Analysis

A two-factor analysis of variances (2-way ANOVA) was used to assess differences in soil gravimetric water content and ψ_{soil} across months and between depths. A 2-way ANOVA was also used to determine differences in shoot water potentials ($\psi_{predawn}$ and ψ_{midday}) and leaf gas-exchange (i.e. A, E, $g_{s,}$ T_L, A/E) between sampling months and species. Similarly a 2-way ANOVA was conducted to determine differences in $\psi_{predawn}$ and ψ_{midday} between drawdown and recovery periods and species. Means were compared by Tukey-Kramer honestly significant difference (Tukey's HSD) test when appropriate. Data were log transformed to meet assumptions of normality and homoscedasticity and for all statistical tests $\alpha = 0.05$. Data were analysed using JMP-IN (vers. 3.2.6 or vers. 8.0).

6.3 Results

6.3.1 Soils

Soil water content increased significantly with increasing soil depth ($F_{3,\ 96}$ = 58.8, $p<0.0001$) (Fig. 6.6). There were also significant differences in soil water content across sampling trips ($F_{5,\ 96}$ = 18.19, $p<0.0001$) with the lowest soil water content recorded in February 2003 (Fig. 6.6). In general soil matric potential (ψ_{soil}) was very high (i.e. close to zero) throughout the study period indicating high soil water availability. While there were no significant differences in ψ_{soil} with depth ($F_{3,\ 96}$ = 2.19, p = 0.122), there were significant differences in the ψ_{soil} across sampling months ($F_{5,\ 17}$ = 3.01, p = 0.018). There was a significant month × soil interaction ($F_{5,\ 17}$ = 2.82, p = 0.0072), and ψ_{soil} was markedly lower (-1.08 ± 0.6 MPa) at the depth of 0.25 m in February 2003 than for any of the other months (Fig. 6.7). During the drawdown, the depth at which the water table was intercepted fluctuated between depths of 1.10 and 1.25 m (Fig. 6.6 & 6.7). By the recovery phase, there was a slight increase in water table height (~0.20 m), and water was intercepted at depths of ~0.95 m in December 2003 and then at depths ~1.0 m by February 2004 (Fig. 6.6 & 6.7).

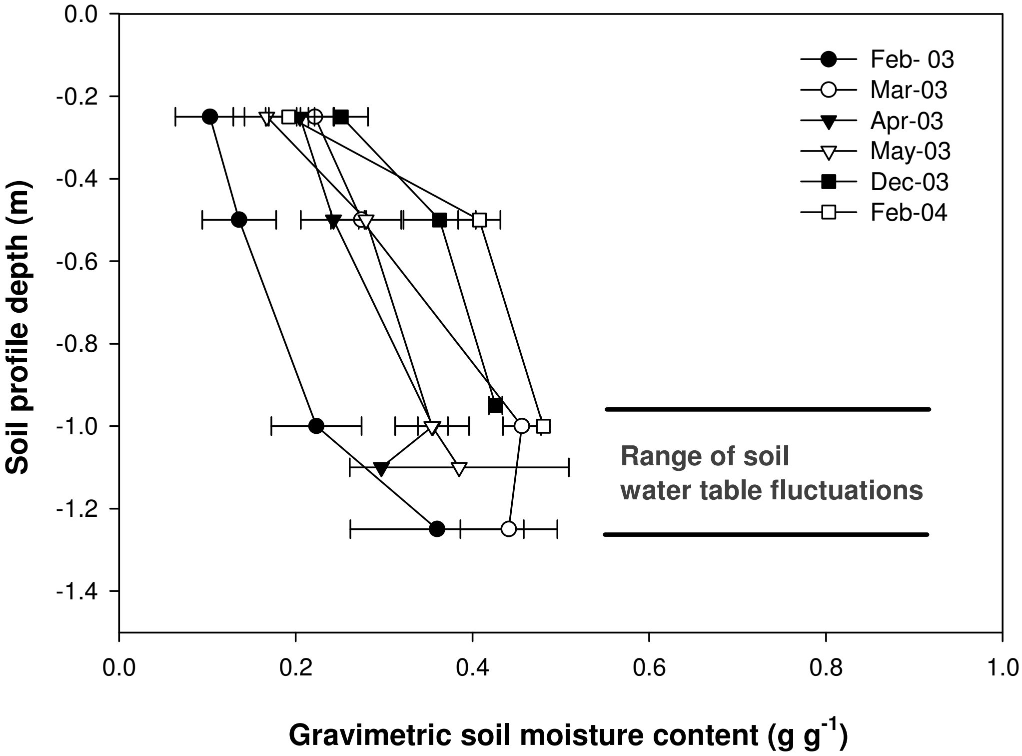

Figure 6.6. Change in gravimetric soil moisture content (g g-1) throughout the riverbank soil profile at Forster Island (Lower River Murray, South Australia) across the drawdown (February 2003 to June 2003) and recovery phase (June 2003 to February 2004). Data points represent means ± SE (n = 4 for each depth).

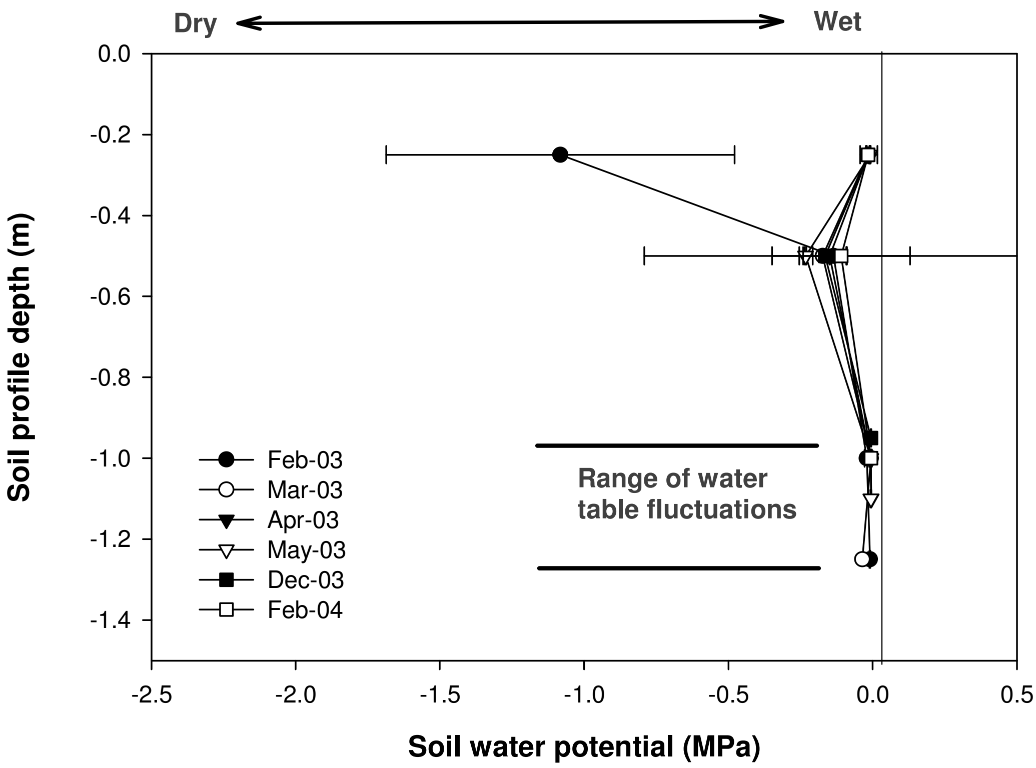

Figure 6.7. Soil water potential (MPa) throughout the riverbank soil profile at Forster Island (Lower River Murray, South Australia) across the drawdown (February 2003 to June 2003) and recovery phase (June 2003 to February 2004). Data points represent means ± SE (n = 4 for each depth).

6.3.2 Shoot water potential (ψ_{shoot})

ψ_{shoot} varied across the drawdown and recovery phases. In general, *S. babylonica* had a consistently higher ψ_{predawn} than *E. camaldulensis* ψ_{predawn} across the entire study period (Fig. 6.8a), but the significant month × species interaction ($F_{5,\ 180} = 9.33$ $p<0.0001$) shows that *S. babylonica* had less negative ψ_{predawn}, but reached their most negative ψ_{predawn} in March 2003, and then returned to similar February ψ_{predawn} values for the remainder of the drawdown. On the other hand, *E. camaldulensis* recorded their most negative ψ_{predawn} in February 2003, and then ψ_{predawn} gradually became less negative, remaining fairly consistent across the remaining months of the drawdown.

A significant period × species interaction ($F_{1,\ 180} = 68.46$, $p =0.013$) shows that although *S. babylonica* and *E. camaldulensis* had slightly more negative ψ_{predawn} (-0.31 ± 0.014 and -0.64 ± 0.015 MPa respectively) during the drawdown compared with the recovery period (*S. babylonica*: -0.24 ± 0.018 MPa and *E. camaldulensis*: -0.50 ± 0.019 MPa), and it was *E. camaldulensis* that showed the greatest recovery (Fig 6.6a).

Similarly, *S. babylonica* had significantly higher ψ_{midday} (- 0.975 ± 0.0134 MPa) than *E. camaldulensis* (- 2.203 ± 0.034 MPa) (Fig. 6.6b) ($F_{1,\ 180} = 2804.3$, $p<0.0001$). Differences between months were also significant ($F_{5,\ 180} = 66.63$, $p < 0.0001$); however there was also a significant month × species interaction ($F_{5,\ 180} = 22.14$, $p < 0.0001$). During the drawdown months both *S. babylonica* and *E. camaldulensis* had similar responses in ψ_{midday} with both species recording their lowest ψ_{midday} values during April 2003 when water levels were low and ranged between 0.35 to 0.46 mAHD. However, the interaction showed there were differences in ψ_{midday} between species across the drawdown and recovery periods. Further analysis shows there were significant differences in ψ_{midday}

between species ($F_{1,\ 180}$ = 1766.7, $p<0.0001$) and between the drawdown and recovery periods ($F_{1,\ 180}$ = 235.8, $p<0.0001$) with a significant period × species interaction ($F_{1,\ 180}$ = 89.3, $p<0.0001$) highlighting that during the recovery phase ψ_{midday} became a little less negative in *S. babylonica* (by <0.15 MPa), but markedly so in *E. camaldulensis* (by more than 0.5 MPa) (Figure 6.6b).

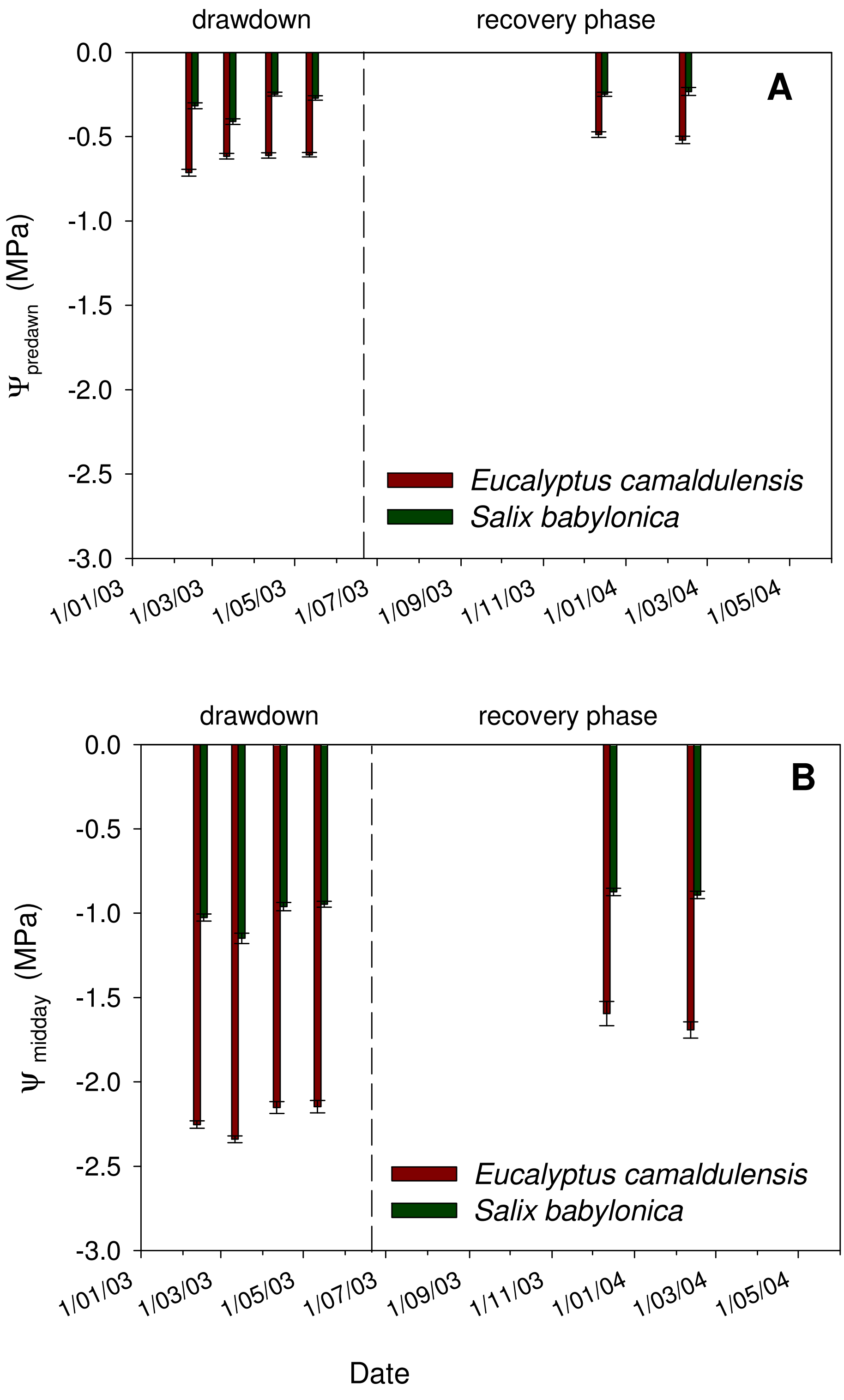

Figure 6.8. $\psi_{predawn}$ (A) and ψ_{midday} (B) for *S. babylonica* and *E. camaldulensis*. Trees were monitored at Forster Island (Lower River Murray, South Australia) during the drawdown (January 2002 to May 2003) and subsequent recovery phase (December 2003 to February 2004). Data points represent mean ± SE (n = 15).

6.3.3 Leaf gas exchange

Overall, mean assimilation for *S. babylonica* (8.08 ± 0.17 µmol CO_2 m^{-2} s^{-1}) was significantly greater than *E. camaldulensis* (7.49 ± 0.17 µmol CO_2 m^{-2} s^{-1}) ($F_{1,\,36}$ = 6.32, p=0.019) and there were significant differences between months ($F_{5,\,36}$ = 6.49, p = 0.0006). However, differences were due to a significant month × species interaction ($F_{5,\,36}$ = 6.427, p = 0.048) (Fig 6.9) because for *S. babylonica* assimilation ranged from 7.6 to 8.4 µmol CO_2 m^{-2} s^{-1} during the drawdown and recovery phases, but for *E. camaldulensis* assimilation was initially low (~4.8 µmol CO_2 m^{-2} s^{-1}) in February 2003, but by March 2003, following a large rainfall event in late February, assimilation almost doubled, and remained consistently high across the remainder of the drawdown and recovery phases (7.7 to 8.6 µmol m^{-2} s^{-1}) (Fig.6.9a).

Mean transpiration for *S. babylonica* (3.25 ± 0.348 mmol H_2O m^{-2} s^{-1}) was also significantly greater than in *E. camaldulensis* (2.47 ± 0.14 mmol m^{-2} s^{-1}) ($F_{1,\,36}$ = 13.73, p = 0.0011) (Fig. 6.9b). Differences were also significant between months ($F_{5,\,36}$=23.43, p<0.0001); but a significant month × species interaction ($F_{5,\,36}$ =4.68, p = 0.004) showed transpiration in *S. babylonica* was greatest (~7 mmol m^{-2} s^{-1}) on the February 2003 sampling trip. In contrast, transpiration rates in *E. camaldulensis* were comparatively consistent between months (Fig. 6.9a, b).

Stomatal conductance was significantly greater in *S. babylonica* (mean: 0.13 ± 0.008 mol H_2O m^{-2} s^{-1}) than in *E. camaldulensis* (mean: 0.097 ± 0.006 mol H_2O m^{-2} s^{-1}) (Fig. 6.9c) ($F_{1,\,36}$ = 11.59, p=0.0023) and significantly different across months ($F_{5,\,36}$ = 3.09, p = 0.027), but again a significant month × species interaction ($F_{5,\,36}$= 4.69, p = 0.004) showed

S. babylonica had a much higher stomatal conductance (~0.23 mol m^{-2} s^{-1}) in February 2003 than did *E. camaldulensis* (Fig. 6.9c).

Because of the significant interactions in leaf gas exchange between species and across months, the calculations of instantaneous water use efficiencies (A/E) also highlight that *S. babylonica* had significantly lower mean A/E (2.77 ± 0.25 mmol CO_2 mol^{-1} H_2O) than *E. camaldulensis* (3.64 ± 0.24 mmol CO_2 mol^{-1} H_2O) ($F_{1, 36}$= 6.32, p = 0.019) (Fig 6.9, Table 6.1). There were also significant differences between months ($F_{5, 36}$= 8.53, $p < 0.0001$) with both species recording significantly lower A/E during February 2003 (Table 6.1). Overall, mean leaf temperatures (T_l) were not significantly different between species ($F_{1, 36}$=0.05, p = 0.65), but were significantly different between months ($F_{5, 36}$ = 224.35, $p < 0.0001$) with much higher leaf temperatures recorded in midsummer (i.e. February 2003, and again in February 2004) (Table 6.1).

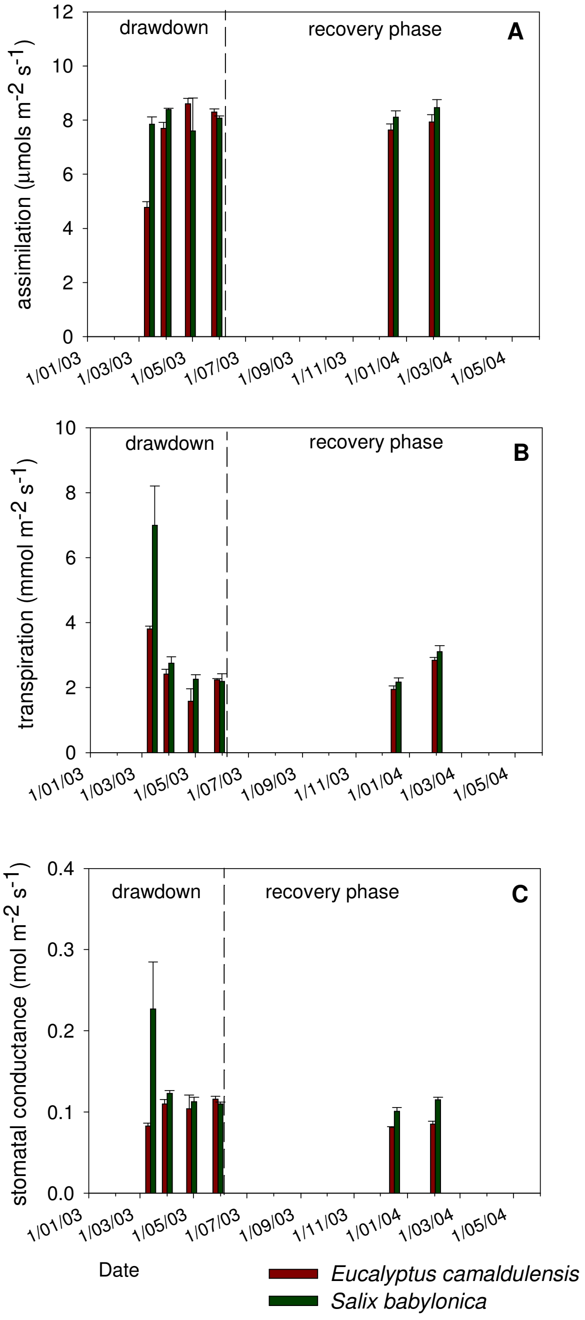

Figure 6.9 (a-c). Midday assimilation rates (A), transpiration rates (B) and stomatal conductance rates (C) for *S. babylonica* and *E. camaldulensis* when photon flux density was >1000 μmol m^{-2} s^{-1}. Trees were monitored at Forster Island [Lower River Murray, South Australia] during a drawdown (February 2003 to May 2003) and subsequent recovery phase (December 2003 to February 2004). Data points represent means ± SE (n = 3).

Table 6.1 Instantaneous water use efficiency (A/E mmol CO^2 mol^{-1} H_2O) and leaf temperature (T_l °C) for *S. babylonica* and *E. camaldulensis*. The trees were monitored at Forster Island [Lower River Murray, South Australia] during a river drawdown (February 2003 to May 2003) and subsequent recovery phase (December 2003 to February 2004). Numbers are means ± SE (n =3).

	Species	*Salix babylonica*		*Eucalyptus camaldulensis*	
Parameters		A/E (mmol mol^{-1})	T_l (°C)	A/E (mmol mol^{-1})	T_l (°C)
DRAWDOWN	Feb-03	1.20 ± 0.22^{A}	30.31 ± 0.41^{A}	1.60±0.04^{A}	30.62 ± 0.23^{A}
	Mar-03	3.08 ± 0.21^{B}	28.81 ±0.35^{B}	3.21±0.15^{B}	28.82 ± 0.29^{B}
	Apr-03	3.32 ± 0.36^{B}	24.33 ± 0.34^{B}	6.20±1.67^{B}	23.67 ± 0.34^{B}
	May-03	3.67 ± 0.01^{B}	24.33 ± 0.34^{B}	3.71±0.01^{B}	25.0 ± 0^{B}
RECOVERY	Dec-03	3.74 ± 0.13^{B}	26.96 ± 0.18^{B}	4.68±0.18^{B}	27.15 ± 0.04^{B}
	Feb-04	3.19 ± 0.23^{B}	30.67 ± 0.14^{A}	2.79±0.09^{B}	30.60 ± 0.28^{A}

6.4 Discussion

Water stress

Contrary to initial predictions there was no evidence of short-term water stress, such as low $\psi_{predawn}$ in either species. In fact, mean $\psi_{predawn}$ for both species in this particular study was even less negative (~0.1 MPa) than the riverbank trees measured in Chapter 5 that were not experiencing a drawdown. However, this may be due to differences between the two study sites, since the field site in Chapter 5 was >100 km upstream and further inland. A climatic gradient exists along the river, and annual rainfall tends to decrease, while maximum temperatures increase, further upstream from the river mouth, increasing potential evaporation further upstream (Table 2.4, Chapter 2).

There were only slight decreases in $\psi_{predawn}$ in both species in response to receding water levels during the drawdown. This was probably due to the lack of any effect of the drawdown on riverbank ψ_{soil}, which remained high (i.e. close to 0 MPa) at depths below 0.25 m, suggesting riverbank soil water availability was not limited across the drawdown. Despite a drop of river-water levels of ~0.40 m, the riverbank water table only dropped ~0.15 m during the drawdown. The disparity in river-water levels against water table levels may reflect the effects of wind/wave action. Webster *et al.* (1997) found that river-water levels at Devon Downs North (~8 km upstream of the study field site) are strongly affected by winds. The presence of Lock 1 upstream creates a river region that is more like a long, thin lake. As a consequence, wind blowing upstream forces river-water up against the weir, generating significant fluctuations in river water levels of up to 0.3 m. The stage hydrograph for river-water levels below Lock 1 (Fig. 6.1) reflects a high degree of daily variability and explains the slow drawdown rate (~2 – 2.5 mm day^{-1}), which probably contributed to the stable riverbank water table levels.

S. babylonica and *E. camaldulensis* were unlikely to be adversely affected by alterations in water quality parameters as a result of low flow. In terms of plants, root processes become more active at higher temperatures (Ruter 1996, Schwarz *et al.* 1997) which could improve plant growth. Yet it has been shown that temperatures exceeding 30°C can decrease root growth in avocado plants (Lahav and Trochoulias 1982) and adventitious roots may also be more prone to pathogenic infections at higher temperatures (Hodges and Campbell 1995), which may alternatively impede growth. During periods of low flow there is potential for increased water temperatures and the development of persistent thermal stratification (where a warm, surface-heated layer persists for more than one day). However, during the drawdown, surface water temperatures were moderate and consistent, remaining at 18-25°C across the drawdown (DWLBC 2006) and although isolated incidents of diurnal stratification occurred, no episodes of persistent stratification occurred. Therefore temperature was unlikely to be a factor affecting the trees.

Nor was in-stream salinity likely to have negatively impacted upon the trees since levels remained low across the drawdown (DWLBC 2006). Although there is a clear relationship indicating that the lower the river flow in the LRM, the higher the level of in-stream salinity (MDBDC 1999) this was not observed during the drought and low flow conditions across 2002-2004. Indeed, low in-stream salinity was a feature of the entire River Murray system because the main source of water entering the system came from fresh head-waters. Prior to the drawdown salinity levels in the LRM was as high as 0.7 dS m^{-1}, but progressively decreased to around 0.3 dS m^{-1} in March 2003 and continued to remain low (<0.4 dS m^{-1}) during the recovery phase (DWLBC 2006).

There is also potential that changes in nutrient levels can affect tree growth, but it is often very difficult to describe 'typical' nutrient conditions in the LRM given the multiple sources and differences in seasonal availability of nutrients at any given time (Mackay *et al.* 1988). Yet the possibility exists that receding water levels can create a hydraulic gradient, and a net transfer of nutrient rich water from associated wetlands, that then enter the main river channel (DWLBC 2006). However during the drawdown, nutrient levels (e.g. phosphorus, nitrogen and carbon) within the main channel of the LRM remained unchanged across the period and relatively nutrient-poor (DWLBC 2006), therefore nutrient levels were also unlikely to have had a profound affect on the trees.

Response to rainfall

Overall, the results do suggest that *S. babylonica* and *E. camaldulensis* were affected by the drawdown in different ways. The above average rainfall in February 2003 significantly increased ψ_{soil} in the upper 0.25 m of the riverbank which correlated with a significant increase in $\psi_{predawn}$ for *E. camaldulensis* but a significant decrease in *S. babylonica*. This suggests that *E. camaldulensis* were able to use this available precipitation derived water-source whereas *S. babylonica* were not. Once again the lower position of *S babylonica* on the river-floodplain elevation gradient relative to *E. camaldulensis* may make them more sensitive to surface-water drawdown (Odland and del Moral 2002). As discussed in Chapters 4 & 5, root architecture between the species differs and *S. babylonica* produce dense mats of pink-coloured adventitious roots that lie in direct contact with the river-water (see Fig 6.10), although the reason for doing so is unclear. Therefore, the declining $\psi_{predawn}$ may reflect their response to declining river-water levels, despite the increase in soil water availability. Thus, a drawdown characterised by faster drawdown rates and a greater drop in water level (> 0.5 m), may inhibit growth because available surface-water sources would rapidly fall below the active root zone for *S. babylonica*. On the other hand, *E. camaldulensis* develop substantial volumes of fine roots (< 2 mm diameter) (Jonsson *et al.* 1988, Nasra *et al.* 2005), with more than 50% of the total volume concentrated in the upper 10 cm of the soil profile (Tedala 2004). This enables them to respond to shallow soil water sources and makes them potentially less sensitive to diminishing surface water sources.

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Figure 6.10. Surface root systems of *E. camaldulensis* (left) and *S. babylonica* (right). *E. camaldulensis* have bimodal root systems with volumes of fine surface roots concentrated in the upper surfaces and deep tap roots (>2 m). Photo taken in at Devon Downs (~8 km upstream of Forster Is) during the study period. In contrast, *S. babylonica* produce dense lateral root mats and masses of pinkish-coloured adventitious roots (visible here just below water line). Photo taken at Forster Island during the study period.

Leaf Gas Exchange Characteristics

In midsummer (February 2003), *S. babylonica* had considerably higher rates of assimilation and transpiration than *E. camaldulensis*. However, *S. babylonica* also had lower instantaneous water-use efficiencies (i.e. less carbon biomass produced per unit water transpired), because of a relatively higher increase in transpiration than in assimilation. On that particular sampling day, conditions were hot (~30°C) with intermittent cloudy periods, which may explain the discrepancies. It is also possible that some of the leaves sampled for *E. camaldulensis* were predominantly shaded for most of the morning and therefore leaf gas exchange was low because of stomatal closure, yet at the time measurements were made, leaves were selected from sunny positions and light conditions were likely to be saturating (i.e. photon flux density > 1300 µmol m^{-2} s^{-1}), (Meinzer *et al.* 1999).

These differences in leaf gas exchange may be related to differences in leaf anatomy. Eucalypt leaves are likely to be relatively thicker, as a study by James and Bell (1995) found leaf thickness in *E. camaldulensis* trees from different localities across southern Australia from ranged from 300 to 425 µm, which is more than double the leaf thickness of *Salix* taxa leaves (*S. viminalis* clones, *S. burjatica*, *S.* × *dasyclados*) that ranged from 95 to 125 µm in a study by Patton *et al.* (1989) (also see Chapter 4). In addition structural tissue in *E. camaldulensis* may be as high as 40%, whereas *S. babylonica* has relatively soft leaves and may only contain 25% structural tissue (Janssen and Walker 1999). These differences may influence their response to heat stress induced by high temperatures and/or high irradiance. Heat stress may initially lead to an increase in transpiration and assimilation rates until a species-dependent critical temperature is reached. Prolonged leaf heat stress may even cause short to long-term damage to leaves (Zhang *et al.* 2001). Mean monthly temperatures across the summer months in this region of the LRM are typically warm (~26 - 29°C) however temperatures may exceed 40°C during the summer. It is possible that *S. babylonica* maintain high transpiration rates on hot days as a means of cooling the leaf, so that assimilation can be maintained (Wuenscher and Kozlowski 1970). On the sampling day in February 2003, when *S. babylonica* showed markedly higher rates of transpiration, similar leaf temperatures were recorded for both species. Higher transpiration rates in *S. babylonica* are likely to result in consumption of larger volumes of water than *E. camaldulensis* per unit leaf area, if access to water is maintained. Although further investigation is needed before firm conclusions can be drawn, this may have important management implications since there is a growing interest in quantifying the water budgets of regional systems (Scott *et al.* 2000) so that both anthropogenic demands and native vegetation water use requirements are satisfied (Stromberg 2001, Walker 2001).

Dispersal

In this study, only the short-term response of the mature riverbank trees was monitored, but droughts can have long-term effects on the demography of populations, community composition and diversity and hence ecosystem processes (Lake 2003). Particular variables of a drawdown may affect the population dynamics of both species by either benefiting or inhibiting the reproductive and recruitment potential of mature trees.

Flowering in *E. camaldulensis* does not necessarily occur every year, but prolific flowering may occur (Boland *et al.* 1980) following flooding (Roberts and Marston 2000). If flowering does not arise, seeds are often retained in a canopy seed bank (as opposed to a soil seed bank) (Jensen *et al.* 2008). In healthy trees, seed-release often peaks in December to February, but yield is highly variable from year to year (Jensen *et al.* 2008). Therefore the timing of a drawdown may benefit *E. camaldulensis* recruitment since receding water levels could potentially provide recruitment sites (Roberts and Marston 2000). The timing of this drawdown coincided with seedfall in *E. camaldulensis* and seedlings established on exposed edges of lagoons (DWLBC 2006). Germination was apparently greatest under the canopy drip-lines of mature trees and on exposed substrate as water levels receded during the drawdown. However, as water levels rose during the recovery phase most seedlings were inundated to depths of up to 0.3 m (DWLBC 2006), thus the duration of the drawdown can significantly influence seedling establishment. By January, 2004 none of these recruits had survived suggesting that they were susceptible to submergence and inundation, which supports the results found in the pond experiment in Chapter 4. Had established seedlings survived, the drawdown and drought conditions may have actually benefited population and community persistence of *E. camaldulensis*.

On the LRM, it appears that *S. babylonica* only reproduce exclusively via asexual means (i.e. layering and/or shoot fragmentation) (see Chapter 2). The growth of establishing recruits is often greater in continually saturated conditions (0 cm day^{-1}) or with slow water drawdown rates (1 - 2 cm day^{-1}) (Chapter 3). The slow drawdown rates that occurred during this study period (of ~2.5 mm day^{-1}) may therefore have provided the potential for *S. babylonica* establishment, as newly created habitat space became available. However, major dispersal events of *Salix* propagules are more likely to occur during floods, although other disturbances, such as wind or accidental mechanical damage, could facilitate the breaking up of shoots and dispersal. The results from Chapter 4 suggest that even if *S. babylonica* propagules arrived at a recently exposed site during a drawdown, establishment of such recruits would be likely to be impaired by the effects of submergence and inundation as water levels rise during the recovery phase. However, since mature, established *S. babylonica* are capable of layering, it is possible that they could colonise the newly exposed space during a drawdown later resulting in persistent in-stream growth; but this was not observed in the current study.

Management

Overall, the results neither signify that a slow drawdown in river-water levels is likely to detrimentally affect the growth of invasive *S. babylonica* nor established native *E. camaldulensis*. To favour regeneration of *E. camaldulensis* the timing of a drawdown should coincide with seedfall (e.g. December – February), but be of sufficient duration to allow recruits to avoid submergence or inundation so that they may successfully establish, at least at the higher elevation positions. Faster drawdown rates (i.e. > 1- 2 cm day^{-1}) and a greater drop in water level (i.e. > 0.5 m) may possibly inhibit *S. babylonica* growth since they appear more reliant on surface-water and less able to respond to alternative water sources than *E. camaldulensis*.

Chapter 7

General Discussion

7.1 Overview

One explanation for the susceptibility of riparian zones to invasion by exotic species is that they are highly dynamic because repeated flooding reduces the intensity of competitive interactions and periodically re-sets portions of the riparian community to early successional stages (Décamps & Tabacchi 1992). Along temporal scales in their native habitats, *Salix* and *Populus* (Salicaceae) are often considered pioneer species that colonise barren riparian habitats following flood disturbances (Rood *et al.* 2003, Kuzovkina and Quigley 2005, Fierke and Kauffman 2006). This appears to contradict the current distribution of invasive *S. babylonica* on the LRM since they are likely to be restricted to regions above weir structures where water regimes are stable (daily water variations of <0.1 m day^{-1}) and disturbance is minimal. More specifically *S. babylonica* are positioned at the very margins of the river-land interface; occupying the lowest position on the river-floodplain elevation gradient relative to co-occurring native trees (*Eucalyptus camaldulensis, E. largiflorens* and *Acacia stenophylla*). The area they occupy is similar to the littoral zone occupied by aquatic macrophytes *Typha domingensis, Juncus aridicola* and *Schoenoplectus validus* along weir pools of the LRM (Blanch *et al.* 1999), but is not shared by other native woody species; suggesting that *S. babylonica* could be thought of as amphibious and/or aquatic trees. Similar descriptions were used before in other Australian woody tree species such as *Melaleuca* spp., *Casuarina cunninghamiana* and *Cryptocarya hypospodia,* since in southern Australia, they are predominantly found growing on creeks and river banks and in stationary and/or slowly flowing wetlands, swamps and creeks (Kahn 1993, Denton and Ganf 1994, O'Grady *et al.* 2006, Salter *et al.* 2008).

However, the mortality of other invasive *Salix* seedlings (e.g. *S. nigra*) compared with *Salix* on the LRM is that in other regions of southern Australia, was found to be greatest at lower elevations of a reservoir because they were subjected to greater degrees of inundation in their first few growing seasons (Stokes 2008). Yet on the LRM *Salix* occupy the lowest position on the river-floodplain elevation gradient relative to co-occurring natives despite evidence from this study that growth and survivorship of establishing *S. babylonica* propagules in the experimental ponds were impaired by the effects of water-logging and top-flooding. This susceptibility of juveniles to water-logging and top-flooding possibly explains why in the field, mature *S. babylonica* are found at elevations >0.25 m relative to baseline river-water levels. Also, because *S. babylonica* are capable of layering, allowing a substantial allocation of roots outside of the water-logged zone, means the detrimental effects of prolonged inundation on mature trees is further alleviated.

However, why aren't native trees occupying these same positions? Especially since results from this study suggest that the distribution of native trees is independent of water regimes created by weirs (Chapter 3) and that seedling establishment is just as successful as seedling establishment in *S. babylonica*, at elevations where water-logging and top-flooding is minimal (Chapter 4). It is likely that *S. babylonica* are competitively superior within these regions since in the experimental pond study, the relative growth rates (RGR) of establishing propagules were significantly greater than RGR of native seedlings. Establishing propagules also had greater secondary and tertiary growth (i.e. denser, complex canopy architecture) that could potentially crowd out other species and repress establishment of native flora. Competitive displacement in the field is not uncommon, such as in the marshes of North America where although *Typha angustifolia* and *T. latifolia* can co-exist, they will often segregate along a water depth gradient; with *T. latifolia* in shallow water and *T. angustifolia* in deeper water (Grace and Wetzel 1981). The reasons being, Grace and Wetzel (1981) surmised, because the traits permitting *T. angustifolia* to grow in deep water did not confer a competitive advantage in shallow waters.

To some extent the restricted distribution of *S. babylonica* on the LRM reflects traits, which while appearing favourable for riverbank environments concurrently restricts their capacity to successfully compete with co-occurring native trees at higher elevations. In riverbank environments they had comparable leaf gas-exchange with co-occurring natives, but significantly higher ψ_{shoot} under analogous temperature and irradiation. For *S. babylonica* to expand their range beyond river margins and into floodplain regions, they would need to exhibit greater physiological plasticity; generating ψ_{shoot} lower than -1.3 MPa in order to extract groundwater from floodplain soils (i.e. the minimum seasonal $\psi_{predawn}$ recorded by native trees), which is a value they did not attain in the riverbank habitats. ψ_{shoot} is generally considered a good index of water extraction capacity by the root system of plants (Aranda *et al.* 2000), thus *S. babylonica* may have an inferior ability to tract enough water for growth under water stress.

S. babylonica were also found to predominantly use river-water or very shallow groundwater sources (< 0.5 m) hence another factor restricting their distribution to river margins where the availability of these water sources are continuous. Over large geographic areas, plant distribution is often related to climate influenced variables like rainfall, temperature and solar radiations (Austin *et al.* 1984), but at a site level plant distribution is often related to the local environmental characteristics like water availability. In a wetland system in Pennsylvania (USA) dominant plant species are used as indicators of water sources (Goslee *et al.* 1997) since deciduous trees *Nyssa sylvatica* and *Betula alleghaniensis* were associated with continuous groundwater sources while annual wildflower *Symplocarpus foetidus* were associated with seasonal surface-water sources. Several aquatic macrophytes *Potamogeton pectinatus* and *Nymphaea odorata* were associated with permanent surface-water sources (Goslee *et al.* 1997). Alterations to water sources as a result of natural events like flooding and/or drought or river management protocols mean plants may have to adjust where they source their water. However, an ability to shift water sources was not something observed in *S. babylonica* when, in this study, they did not even appear to take advantage of a short rain pulse in the dry season to improve tree water status. This conflicts with other woody species, studied elsewhere, like *Casuarina cunninghamiana* and *Acacia auriculiformis* in the Daly River in northern Australia that primarily used groundwater when it was shallow but otherwise used shallower soil-water at higher positions in the landscape (Lamontagne *et al.* 2005). Similarly in southern Portugal woodlands, as upper soil layers dried out over the dry season, water uptake in the dominant *Quercus suber* trees shifted to deeper, moister soil layers (Otieno *et al.* 2006).

This reliance on shallow alluvial groundwater sources that are linked to permanent surface water sources has been observed before in other *Populus* and *Salix* taxa in North America (Snyder and Williams 2000, Horton *et al.* 2001b, Rood *et al.* 2003). Similar observations were made on the Swan Coastal Plains in Western Australia, where *Banksia ilicifolia* appear restricted to environments with shallow depths to groundwater and *Melaleuca preissiana* to wetlands because of their greater vulnerability to cavitation (relative to other co-occuring *Banksia* spp.) at higher xylem water potentials (Froend and Drake 2006). Yet this obligate water use strategy of *S. babylonica* contrasts sharply with the facultative water use strategies of co-occurring native trees, *E. camaldulensis* and *E. largiflorens*. As previously mentioned (Chapter 5), on the LRM floodplains, these two species will access deep, saline groundwater sources, yet switch to fresher soil water and/or surface water sources following high rainfall, flooding and/or bank recharge (Jolly and Walker 1996, Mensforth *et al.* 1994, Holland *et al.* 2006). For *E. largiflorens* in particular, the water sources used by stands of healthy trees were low-salinity soil-water overlying highly saline groundwater (>40 dSm−1) (Holland *et al.* 2006). Bank recharge (i.e. horizontal infiltration from surface water) was an important means for maintaining this supply of deep low-salinity soil-water for trees growing within ~50m of water bodies whereas vertical infiltration of rainfall and/or floodwaters through cracking clays was important for *E. largiflorens* trees positioned further away.

This suggests that current river management protocols that have eliminated small floods and reduced the frequency and duration of medium floods (Walker and Thoms 1993) or created weir pool water regime gradients (Chapter 3) are generally drying out floodplains. This not only facilitates the growth of *S. babylonica* at river margins, but also restricts the distribution and health of native trees. Indeed, survival of the common floodplain *E. largiflorens* is in jeopardy because populations are skewed towards an abundance of over-mature trees, but few that can regenerate adequately (George *et al.* 2005). A similar situation was observed in eastern England; where intense land clearing and agricultural activities led to regeneration of riparian and floodplain trees and an over abundance of mature trees (Harper *et al.* 1997).

Consequently, although *S. babylonica* are successful at displacing native flora along river margins, current river management practices are also contributing to water stress and a subsequent decline in the health, persistence and regeneration of dominant native riparian and floodplain trees. The protection of groundwater-dependent ecosystems – a term that describes the facultative native tree communities of the LRM, is now recognised as an important aspect of water management in Australia (Mackay 2006). Especially since ‘environmental flows’ sometimes only consider allocating water directly to the river itself and neglect to replenish the floodplains (Eamus *et al.* 2006). Yet river management strategies that frequently replenish low-salinity soil-water sources beyond the immediate zone of river margins are just as important for the persistence and regeneration of both native riparian and floodplain communities (George *et al.* 2005, Otieno *et al.* 2006, Jensen *et al.* 2008).

7.2 Management Implications

Hybrid Threats

On the LRM *S. babylonica* reproduce exclusively via asexual means (i.e. layering and/or shoot fragmentation and dispersal by water). The dominance of asexual reproduction in aquatic vegetation is not uncommon and encourages long-term colonisation of riparian zones (Shafroth *et al.* 1994, Khudamrongsawat *et al.* 2004, Douhovnikoff *et al.* 2005). However, confirmation of overlapping flowering times between the abundant female *S. babylonica* and male *S. matsudana* × *alba*, in the same locality, does provide hybridisation potential should the current distance (> 10 km) separating the two taxa be diminished following accidental or deliberate introduction. This concern is that hybridisation may facilitate invasiveness by producing novel genotypes, increasing genetic variability, producing heterotic genotypes, or by reducing the frequency of detrimental alleles by recombination (Ellstrand & Schierenbeck 2000) and allow new hybrids to outcompete their parent taxa (Bímová *et al.* 2004). Also, since the rate of spread of seeding *Salix* taxa in Australia is estimated to be far greater than the rate of vegetative spread

(Ladson 1997), if the current LRM *Salix* taxa were to sexually reproduce, their distribution range could also rapidly increase. For instance, a cross between *S. babylonica* and more water- and salt-tolerant *S. matsudana* × *alba* may alleviate the possible barriers that exclude *S. babylonica* from establishing on floodplains of the LRM (e.g. inability to access alternative deep groundwater, salinity intolerance and/or vulnerability to erosion). From a management perspective, it is highly recommended that current populations of *S. matsudana* × *alba* in the surrounding Riverland district be completely removed (or at least seasonally pruned each year back to prevent flowering) in order to prevent a seeding outbreak. In addition, *S. babylonica* should be added to the 'Weeds of National Significance' register in Australia.

Response to climate change

Climate change threatens to alter the composition of riparian forests (Hultine *et al.* 2007) since CO2 concentrations will increase worldwide as a result of carbon (and other climate relevant trace gas) emissions into the atmosphere (Schonwiese 1992, Hulme *et al.* 1999, Arnell *et al.* 2002) causing warmer sea temperatures and changes in precipitation patterns (Palmer and Ralsanen 2002, Dukes *et al.* 2005). In Australia, mean annual temperatures are predicted to increase by 0.4 to 2°C in the next two decades, hence potentially increasing evaporation and heatwaves and causing fewer frosts (Hughes 2003). Since the bio-geographic ranges of many plants are primarily set by climate (Simberloff 2000) and temperature affects factors such as flowering times (Fitter and Fitter 2002), even a global warming of 1°C could threaten the survival of species currently pushing the upper limits of their temperature thresholds. At present, the occurrence of *Salix* in the southern regions of Australia reflects their climatic suitability and possibly already at the upper limits of their temperature threshold (http://www.weeds.org.au) so it is plausible that the predicted increases in mean annual temperatures of 0.4 - 2°C could actually restrict their distribution.

Especially as a study by He and Dong (2003a) found that a small atmospheric temperature rise of 0.5 - 1°C may be detrimental to the growth and maintenance of *S. matsudana* in semi-arid regions of China. Another concern may be the implication that under hot, dry conditions *S. babylonica* can use more water than co-occurring native species, at smaller time scales per unit leaf area, and this may also require careful examination. Especially considering that in some regions of Australia, water resources are already stressed (AGO 2003, Arnell 1999) intensifying competition between public users and threatening future allocations for environmental flows (AGO 2003). In addition there is also the implication that low genetic diversity in LRM *Salix* taxa (i.e. since they only reproduce asexually) and their clumped distribution in the field may also increase their susceptibility to atypical climate events, which could assist management strategies.

On the other hand, climate change may increase the distribution of some species (Cheal and Coman 2003 as cited in AGO 2003), since elevated CO_2 can increase the water-use efficiency of some species such as *Eucalyptus macrorhyncha* and *E. rossii* (Roden and Ball 1996), *Pinus radiata* (Kirschbaum 1999) *Acacia nilotica* (Kriticos *et al.* 2003) and some *Populus* and *Salix* taxa (Johnson *et al*. 2002). Given that certain species may be able to capitalise on some aspects of climate change, like increasing [CO_2] (Dukes and Mooney 1999); determining how the interactions of elevated temperatures and [CO_2] will potentially affect biological aspects like flowering times, photosynthetic capacity and/or dispersal of introduced *Salix* taxa, compared with co-occurring natives would be useful.

Dispersal

An alternative explanation for the exclusion of *S. babylonica* from floodplains is that propagules are merely not arriving to these regions. In their native ranges, *Salix* propagules are widely dispersed by floods, but as yet the factors governing natural dispersal in *Salix* taxa on the LRM have not been determined; although hydrograph data do confirm that there were substantial floods post regulation (see Chapter 3). Numerous *Salix* taxa have brittle stem bases that provide effective dispersal mechanisms (Beismann *et al.* 2000) which suggests arrival to floodplain sites is possible, even if not highly frequent. However, establishing *S. babylonica* juveniles may also be particularly vulnerable after arrival because on floodplains they would be subjected to limited soil-water sources in the upper soil regions (< 1 m) for at least the first growing season. However, if *S. babylonica* seedlings were able to find sufficient water, the results from Chapter 4 suggest that there is potential for their growth rates and biomass accumulation to exceed that of the native species.

Successful germination of seedling recruits tends to be rare and relates to a suite of variables such as length of growing season, timing of seed dispersal, flood duration and depth to water source (Mahoney and Rood 1998, Scott 1998 and Ahn *et al.* 2007) whereas unseasonal floods may assist asexual recruitment (Barsoum 2007). Although no floods occurred on the LRM throughout this study period, their occurrence would provide opportunities to investigate a) the timing and/or magnitude of a flood needed to break up *Salix* propagules from a parental source and disperse them across the floodplain, b) distances dispersed from parent source, c) the longevity of propagules following flood and d) the influence of field microsite characteristics (i.e. riverbank versus floodplain in relation to elevation, soil type, wave action, and light, nutrient and water availability) on growth and survival.

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Appendices

Appendix 2-1. List of *Salix* taxa that are listed as weeds of national significance in Australia. Data provided by Agriculture & Resource Management Council of Australia & New Zealand Environment and Conservation Council and Forestry Ministers (2000).

Taxon	**Common Name**	**Origin**	**Dispersal Mechanisms**	
S. aegyptiaca	Asian sallow	Iran, Armenia, Asia	?S	?V
Salix alba var. alba	White willow	Europe		V
Salix alba var. vitellina	Golden upright willow	Europe	S	V
Salix alba var. alba ×S. matusdana (syn. S. babylonica var. pekinensis)	NZ Hybrid willow	Hort. (NZ)	S	V
Salix alba var. vitellina ×S. matsudana 'Tortuosa'	Golden Tortured willow	In situ hybrids		?V
Salix alba var. vitellina ×S. ×sepulcralis var. chrysocoma	Willow	In situ hybrids	?S	?V
Salix babylonica	Weeping willow	China	S	V
Salix calodendron (S. caprea ×S. purpurea ×S. viminalis)	Pussy willow	Europe		V
Salix chilensis 'Fastigata'	Chilean Pencil willow	Chile	?S	V
Salix cinerea ssp. cinerea	Grey sallow, pussy willow	Europe-Siberia	S	V
Salix cinerea ssp. oleifolia	Rusty willow	Europe, N. Africa	S	?V
Salix cinerea ssp. cinerea ×S. ×reichardtii	Pussy willow	In situ hybrids	S	?V
Salix fragilis var. fragilis	Crack willow	W. Europe		V
Salix fragils var. furcata	Forked –catkin crack willow	W. Europe		V
Salix fragilis var. fragilis ×S. matsudana 'Tortuosa'	Willow	In situ hybrids	S	?V
Salix fragilis var. fragilis ×S. nigra	Willow	In situ hybrids	S	?V
Salix glaucophylloides	Dune willow	N. America	S	?V
Salix glaucophylloides ×S.? ×riechardtii	Willow	In situ hybrid	S	?V
Salix matsudana (syn. Salix babylonica var. pekinensis)	Peking willow	China, Mongolia, Korea		V
Salix matsudana 'Tortuosa'	Tortured willow	Hort. (location?)	S	V
Salix ×mollissima (S. triandra ×S. viminalis)	Willow	Europe		V
Salix nigra	Black willow	N. America	S	V
S. nigra ×S. matsudana 'Tortuosa'	Willow	In situ hybrid	?S	
S ×pendulina (S. babylonica ×S. fragilis var. fragilis)	Weeping willow	Hort. (Europe)		V
Salix purpurea (and several cultivars)	Purple Osier	Europe, Asia	S	V
Salix reichardtii (S. caprea ×S. cinerea)	Pussy willow	Europe		V
Salix ×rubens (S. alba ×S. fragilis)	Basket willow	Europe/ In situ hybrid	S	V
Salix ×rubra (Salix purpurea ×S. viminalis)	Osier	Europe	S	V
Salix ×sepulcralis var. chrysocoma (S. alba var. vitellina ×S. babylonica)	Golden weeping willow	Hort. (Europe)	S	V
Salix ×sepulcralis var. sepulcralis (S. alba var. alba ×S. babylonica)	Weeping willow	Hort. (Europe)		V
Salix viminalis	Osier	Europe –Russia	S	V

*Hort. = horticultural hybrid

**S = seeding. V = vegetative (rooting of detached twigs/branches or layering)

Appendix 2.2 Field Identification Key for *Salix* taxa on the Lower River Murray (South Australia) (modified from Cremer 1995)

NOTE:
This appendix is included on page 234 of the print copy
of the thesis held in the University of Adelaide Library.