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## **Australian Trees for the Rehabilitation of Waterlogged and Salinity-damaged Landscapes**

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### *Abstract*

The revegetation of damaged agricultural landscapes requires a detailed knowledge of appropriate species and their adaptations to cope with the stresses of environments altered by humans. A range of Australian species has a role in the restoration of water and salt balances of catchments and can provide income diversity to agricultural properties damaged by increased frequencies of flooding, rising groundwaters and increased salinities. This review concentrates on the ecologically significant attributes of Australian woody species in waterlogged and saline habitats, and responses of species particularly suited to the restoration of water balance in cleared catchments.

Australian catchments yield little water under natural vegetation, the trees and shrubs being especially resourceful in utilising much of the annual rainfall input. Replacing native, deep-rooted perennial species with annual crops always results in a net gain in catchment water. To redress these problems, cleared landscapes must be partially restored to tree and shrub cover to utilise the excess water remaining when crops are harvested or lie dormant over summer. Upland regions of restored landscapes should be planted to tree crops, particularly those that are luxuriant water users, of commercial value to farmers. Tree plantations for paper pulp, soft-wood timber and eucalypt oils are possibilities. Lowland sites in damaged catchments must be revegetated with trees which have waterlogging adaptations, such as aerenchyma, and tolerance to the products of anaerobic respiration. Areas of waterlogging that are additionally affected by excess salts must have exceptional trees. Australia has a number of native species which are well suited to survive these conditions, produce biomass and utilise excess water, while restricting or coping with the uptake of over-abundant salts. Most tolerant Australian species have a range of anatomical, morphological and physiological attributes to contribute to these adaptive qualities. This review highlights some of these features and describes various combinations that are successful. Australia now has a range of genotypes to bring to bear in the battle to rehabilitate landscapes damaged by disruption of the soil–salt–water balance. Only by redressing these problems can we ensure that future generations will have land capable of retaining economic value and producing potable water.

### **Introduction**

The worldwide land area which has become salt-affected through human causes exceeds  $76 \times 10^9$  ha (Oldeman *et al.* 1991). In Australia, there are more than  $4 \times 10^9$  ha of secondary or human-induced saline soil (Williamson 1990). Secondary salinisation has generally resulted from inappropriate water management of landscapes, especially the clearing of deep-rooted native vegetation in dryland areas (Wood 1924; Schofield 1992). Replacement of eucalypt woodlands with annual, shallow-rooted agricultural crops and pastures has resulted in increased groundwater recharge and rising water tables. Rising water tables mobilise salts stored in the unsaturated soil horizons, transporting the salts to the ground surface and into streams. Increased occurrence of waterlogging and salinity leads to land deterioration and deleterious levels of stream salinity (Williamson *et al.* 1987). Over-irrigation of marginal lands has also been a source of waterlogged and saline lands, especially in the eastern Australian states (Pels 1978; Macumber 1991). Although all Australian states have waterlogging- and salinity-affected lands, the agricultural lands in Western Australia are the most affected of the Australian agricultural landscapes, with more than 9% already unproductive and this value predicted to double in the next 15–20 years (Ferdowsian *et al.* 1996). McFarlane (1991) put the problem into perspective well when he commented that the rate of loss was the equivalent of losing a 2-ha football oval every hour! Human-induced salinity is a major

environmental problem in all semi-arid and arid regions of the world (McKell *et al.* 1986; Dudal and Purnell 1986). Redressing the problem requires the combined knowledge and cooperation of hydrologists, engineers, ecologists and politicians.

Considerable progress has been made in understanding the hydrological parameters involved in the breakdown of the soil–salt–water balance in deforested catchments. Hydrological models of Sivapalan *et al.* (1996a, 1996b, 1996c) have effectively predicted changes in water and salt stores from catchments in south-western Western Australia by considering the rainfall input, the evapotranspiration output and the water fluxes of three soil–water stores: a near-stream perched aquifer system; a deeper, permanent groundwater system; and an intermediate, unsaturated infiltration store. In uncleared vegetation, evapotranspiration typically accounts for more than 75% of rainfall. Williamson *et al.* (1987) estimated transpiration to be about 75–80% of annual rainfall, with another 15% related to interception loss. Sharma (1984) estimated that interception and transpiration in *Eucalyptus marginata* forests account for nearly 90% of annual rainfall. In woodlands near Perth, nearly all the annual rainfall gains were balanced by annual evapotranspirational losses (Dodd and Bell 1993a, 1993b).

Year-round water utilisation is an attribute of native vegetation, while agricultural crop water use is seasonally restricted. Carbon *et al.* (1980) found that the deep-rooted, evergreen, eucalypt vegetation of Western Australia effectively exploits a very large soil volume, transpiring water from deep in the soil profile, especially the soil water at the fringe of the deeper, permanent groundwater table. As a result, the overstorey trees maintain a substantial transpiration rate throughout the arid, Mediterranean-climate summer in spite of severely limiting soil moisture in the upper soil layers. Sharma *et al.* (1987) reported that at least 20% of summer evapotranspiration totals are derived from depths greater than 6 m. Therefore, any major alteration in leaf area index, usually about 2.0 in jarrah forests (Bettenay *et al.* 1980), will cause major changes in the flux of water to the atmosphere. Williamson *et al.* (1987) measured a four-fold increase in streamflow following complete clearance of the forest, average streamflow changing from 10% of rainfall under native forest to more than 30% several years after clearing.

The redressing of the problem of excess catchment groundwater, usually with marked salinities, is now being accomplished in Australia and overseas by re-establishing catchment leaf area index with plantings of trees and shrubs (Schofield 1992). Tree-growing systems can assist in the redevelopment of salt and water balance in both recharge and discharge zones of catchments. In recharge zones, tree-growing systems can include the use of commercial species to assist with water-table control by utilising soil water in the unsaturated infiltration zone water store. Species of commercial value which maximise water use would be the preference for tree plantings in this zone, although species with aesthetic values and those that produce shade and shelter for associated plants and animals have their place in repaired Australian landscapes. In the near-stream, perched, aquifer system and to utilise deeper, subsurface water stores, trees with tolerance of waterlogging and salinity are required. This review surveys the species with the potential to rehabilitate these damaged agricultural catchments, concentrating on the ecophysiological attributes that allow them to survive and function in these environments that have been altered by humans.

## **Species Requirements and Capabilities**

### *Infiltration Zone Species*

Upland recharge and infiltration zones in damaged agricultural catchments should be restored to native plant communities or planted with Australian commercial tree species crops. Greenwood *et al.* (1985) found that the annual evapotranspiration from plantations of *Eucalyptus globulus*, *E. cladocalyx* and *E. maculata* was up to seven times that from grazed pasture landscapes. In addition to their role in water use in recharge zones, genotypes of Australian species can produce on-farm incomes in soft-wood and hard-wood timbers, paper

pulp, particle board, firewood, fodder and oils. Tree plantings are also useful for shelter and shade, wind and water erosion control, wildlife corridors and aesthetic plantings (Prinsley 1992).

*Eucalyptus globulus* has been promoted for revegetation plantations in damaged farmlands in Western Australia as a source of high-quality paper pulp. Exceptional growth is possible, with mean heights in excess of 18 m after 5 years in some areas (Edwards and Harper 1996). Good growth occurs in soils with good nitrogen content and clay contents above 10%, and in regions with higher dry-season rainfall. Poor performance in *E. globulus* has been associated with areas of shallow soil depth which limits water storage (Harper 1994), waterlogged sites (Edwards and Harper 1996) and catchment zones with high soil salinity (Bennett and George 1995). Because *E. globulus* is sensitive to waterlogging and salinity, its effectiveness in utilising excess catchment water is limited to upland, recharge sites.

Plantations of particular *Eucalyptus* species for eucalyptus oil have also been proposed as a means of controlling rising groundwaters (Eastham *et al.* 1993). *Eucalyptus kochii* subsp. *plenissima* and *kochii*, *E. horistes*, *E. radiata* and *E. angustissima* show promise for the production of cineole, but long-term production rates, water-use capabilities, and the markets and economic value of the oil products have not, as yet, been assessed. Also, as the oil eucalypts tend to be sensitive to waterlogging and salinity (van der Moezel *et al.* 1991), their use in agricultural catchments would be in competition with more traditional forms of agricultural land use.

Another tree crop that provides a short-term economic return without markedly altering farming systems that incorporate sheep production is the use of tree fodders such as *Chamaecytisus proliferus* and native legumes such as species of *Acacia*. Biomass production of the exotic *Chamaecytisus* (tagasaste) has been high enough to suggest that it is a suitable option on deep loamy sands of upland catchment sites (Oldham *et al.* 1991; Eastham *et al.* 1993). Native Australian legumes have played only a limited role as fodder species, except as emergency supplementation. No information on water use by tagasaste or the Australian legumes is available and very limited information on the ability of these species to survive in waterlogged and saline environments has been published. Craig *et al.* (1990) found that a range of acacias from naturally saline lands was moderately tolerant of waterlogged and saline conditions in controlled greenhouse trials. Species with good tolerance to waterlogging and salinity included *Acacia* aff. *lineolata* and *A. mutabilis* subsp. *stipulifera*. *Acacia stenophylla* has also proven to be a very tolerant species and *A. auriculiformis*, *A. cyclops*, *A. ligulata*, *A. maconochieana* and *A. sclerosperma* could be considered as moderately tolerant species for use in the revegetation of damaged agricultural catchments (McComb *et al.* 1989; Sun and Dickinson 1995).

Artificially produced hybrids between *E. globulus* and *E. camaldulensis* were superior to purebred *E. globulus* (Oddie *et al.* 1996) in glasshouse waterlogging/salinity trials, and could prove to be suitable for plantation use in mid- to lower-slope regions where the soil is only occasionally waterlogged and moderately saline. Although these hybrids would be typically grown in catchment zones below agricultural crops, their growth rates, pulping quality and economic attributes have yet to be assessed.

Increasing the tree coverage in a catchment cleared in the 1950s, from 35 to 70% by plantations of *Eucalyptus* and *Pinus*, resulted in decreases in groundwater levels up to 5.5 m relative to the ground surface levels, and up to 7.3 m compared with a nearby pasture control site over the period 1980–1989 (Bari and Schofield 1992). The average salinity of the groundwater beneath the plantations also decreased by 11%. Reforestation is therefore a very attractive use of groundwater in recharge areas, but the application of commercial plantation forestry has implications for traditional agriculture because upland plantations utilise the same catchment positions as grain crops and livestock pastures.

#### *Near-stream Perched Aquifer Zone and Discharge Zone Species*

The lower positions in landscapes are usually not as economically valuable for traditional agriculture because crops and pasture species are generally intolerant of waterlogging and salinity. Therefore, the species capable of revegetating these lowland, discharge zones in

damaged agricultural catchments must tolerate seasonal waterlogging and increased soil salinities, as well as provide some farm income. Particular native Australian species that are naturally found on river flood plains have inherent capabilities to rehabilitate the near-stream perched aquifers of damaged agricultural catchments (Bell and van der Moezel 1988; Bell and Williams 1997). In fact, flooding is necessary to maximise growth in *Eucalyptus camaldulensis* (Bacon *et al.* 1993) and a number of species of *Melaleuca* (Watson and Bell 1981). An ability to tolerate flooded conditions is the first prerequisite for species required to rehabilitate recharge zones in catchments. Natural patterns of flood-zone distributions and extensive experimental evidence have indicated that *Eucalyptus* is generally more tolerant of waterlogging and salinity than *Acacia*, but less tolerant than *Melaleuca* and *Casuarina* (Table 1). The performance of particular species, however, provides exceptions to this generalisation (van der Moezel and Bell 1990; Hussain *et al.* 1994). This genetic variation is the key to the selection of tolerant genotypes (Allen *et al.* 1994; Flowers and Yeo 1995).

**Table 1. Relative salt/waterlogging tolerance levels of Australian tree species from a range of published sources**

Very highly tolerant (tolerates waterlogging with 400 mM NaCl)	
<i>Casuarina equisetifolia</i> <sup>1,9</sup>	<i>M. glomerata</i> <sup>1</sup>
<i>C. glauca</i> <sup>1,6,9,11</sup>	<i>M. halmaturorum</i> <sup>1,11</sup>
<i>C. obesa</i> <sup>1,9</sup>	<i>M. lanceolata</i> <sup>11</sup>
<i>Melaleuca acuminata</i> <sup>1</sup>	<i>M. lateriflora</i> <sup>1</sup>
<i>M. bracteata</i> <sup>6</sup>	<i>M. leucadendra</i> <sup>5,11</sup>
<i>M. aff. calycina</i> <sup>10</sup>	<i>M. subtrigona</i> <sup>10</sup>
<i>M. cardiophylla</i> <sup>10</sup>	<i>M. squarrosa</i> <sup>11</sup>
<i>M. cuticularis</i> <sup>11</sup>	<i>M. styphelioides</i> <sup>11</sup>
<i>M. cymbifolia</i> <sup>10</sup>	<i>M. thyoides</i> <sup>1,10</sup>
<i>M. decussata</i> <sup>11</sup>	<i>M. uncinata</i> <sup>11</sup>
<i>M. eleuterostachya</i> <sup>1</sup>	
Highly tolerant (tolerates 300 mM NaCl)	
<i>Acacia stenophylla</i> <sup>1,11</sup>	<i>E. sargentii</i> <sup>1,7,8,11</sup>
<i>Casuarina crista</i> <sup>5,9,11</sup>	<i>E. spathulata</i> <sup>1,7,8,11</sup>
<i>Eucalyptus camaldulensis</i> <sup>1,2,5,6,8,11</sup>	<i>E. intertexta</i> <sup>1</sup>
<i>E. campaspe</i> <sup>11</sup>	<i>E. microtheca</i> <sup>1</sup>
<i>E. cladocalyx</i> var. <i>nana</i> <sup>7,8</sup>	<i>E. raveretiana</i> <sup>1,6</sup>
<i>E. halophila</i> <sup>10</sup>	<i>E. striatocalyx</i> <sup>1</sup>
<i>E. kondininensis</i> <sup>11</sup>	<i>E. tereticornis</i> <sup>1,6</sup>
<i>E. occidentalis</i> <sup>1,8,10,11</sup>	
Moderately tolerant (tolerates 200 mM NaCl)	
<i>Acacia ampliceps</i> <sup>11</sup>	<i>E. leptocalyx</i> <sup>10</sup>
<i>A. aff. lineolata</i> <sup>4</sup>	<i>E. leucoxydon</i> <sup>8</sup>
<i>A. auriculiformis</i> <sup>5</sup>	<i>E. maculata</i> <sup>2</sup>
<i>A. mutabilis</i> subsp. <i>stipulifera</i> <sup>4</sup>	<i>E. moluccana</i> <sup>2,6</sup>
<i>A. salicina</i> <sup>11</sup>	<i>E. ovata</i> <sup>11</sup>
<i>Casuarina cunninghamiana</i> <sup>5,6,9,11</sup>	<i>E. patens</i> <sup>8</sup>
<i>Eucalyptus aggregata</i> <sup>11</sup>	<i>E. platypus</i> var. <i>heterophylla</i> <sup>7,8</sup>
<i>E. argophloia</i> <sup>2</sup>	<i>E. redunca</i> <sup>8</sup>
<i>E. camphora</i> <sup>11</sup>	<i>E. robusta</i> <sup>2,6,8,11</sup>
<i>E. cladocalyx</i> <sup>8</sup>	<i>E. rudis</i> <sup>11</sup>
<i>E. drepanophylla</i> <sup>2</sup>	<i>E. tereticornis</i> <sup>11</sup>
<i>E. floctoniae</i> <sup>8</sup>	<i>E. uncinata</i> <sup>10</sup>
<i>E. goniantha</i> <sup>10</sup>	<i>E. wandoo</i> <sup>8</sup>

**Table 1.** (continued)

Mildly tolerant (tolerates 100 mM NaCl)	
<i>Acacia cyclops</i> <sup>4,11</sup>	<i>E. melliodora</i> <sup>6</sup>
<i>A. brumalis</i> <sup>4</sup>	<i>E. paniculata</i> <sup>2</sup>
<i>A. patagiata</i> <sup>4</sup>	<i>E. pellita</i> <sup>2</sup>
<i>A. redolens</i> <sup>4</sup>	<i>E. urophylla</i> <sup>2</sup>
<i>Eucalyptus angulosa</i> <sup>10</sup>	<i>Grevillea robusta</i> <sup>2</sup>
<i>E. citriodora</i> <sup>2</sup>	<i>Melaleuca quinquinervia</i> <sup>5,11</sup>
<i>E. grandis</i> <sup>2,6</sup>	
Mostly intolerant (intolerant of 100 mM NaCl)	
<i>Acacia aulacocarpa</i> <sup>5</sup>	<i>E. polycarpa</i> <sup>2</sup>
<i>Casuarina decaisneana</i> <sup>3</sup>	<i>E. saligna</i> <sup>2</sup>
<i>Eucalyptus cloeziana</i> <sup>2</sup>	<i>Lophostemon confertus</i> <sup>2</sup>
<i>E. intermedia</i> <sup>2,6</sup>	<i>Pinus caribaea</i> var. <i>hondurensis</i> <sup>2</sup>
<i>E. pilularis</i> <sup>2</sup>	

<sup>1</sup>van der Moezel and Bell (1990); <sup>2</sup>Sun and Dickinson (1993); <sup>3</sup>Clemens *et al.* (1983); <sup>4</sup>Craig *et al.* (1990); <sup>5</sup>Sun and Dickinson (1995); <sup>6</sup>Dunn *et al.* (1994); <sup>7</sup>Greenwood *et al.* (1994); <sup>8</sup>Greenwood *et al.* (1995); <sup>9</sup>van der Moezel *et al.* (1989a); <sup>10</sup>van der Moezel and Bell (1987b); <sup>11</sup>Marcar *et al.* (1995).

*Eucalyptus camaldulensis*, the most widespread of Australian eucalypts, has the ability to tolerate both waterlogging and salinity, and contains considerable genotypic variation (Sands 1981; Bell *et al.* 1994; Farrell *et al.* 1996a, 1996b). This species has been promoted extensively for discharge zone plantings (Morris and Thomson 1983; Fox *et al.* 1990; Marcar 1993), although particular genotypes are considerably more tolerant than others (Bell *et al.* 1994). Other eucalypt species ranked with *E. camaldulensis* for waterlogging- and salt-tolerance in field trials are *E. moluccana*, *E. reveretiana* and *E. tereticornis* (Dunn *et al.* 1994). *Eucalyptus camaldulensis*, *E. robusta* and *E. argophloia* were the highest ranked eucalypts in a study of freely drained seedlings in a glasshouse (Sun and Dickinson 1993). *Eucalyptus microtheca*, *E. striatocalyx*, *E. occidentalis*, *E. spathulata* and *E. sargentii* are also eucalypts with known tolerance to saline water, and they grow on occasionally waterlogged sites (Fox *et al.* 1990; van der Moezel and Bell 1990; van der Moezel *et al.* 1991; Marcar *et al.* 1995). *Eucalyptus* species with the capability to produce aerenchyma in root tissues can be used to rehabilitate the lower regions of catchments affected by increasing periods of soil anoxia. These species, however, must also tolerate salinised soil to be effective in the rehabilitation of secondary salinised sites. In secondary salinised sites in Western Australia, deaths of *E. rudis* were attributed to the combined effects of increasing salinities and prolonged inundation (Froend *et al.* 1987).

Particular species of the genera *Melaleuca* and *Casuarina* are considerably more tolerant than the best acacias and eucalypts (van der Moezel and Bell 1987b, 1990; van der Moezel *et al.* 1991; Denton and Ganf 1994). Highly tolerant *Melaleuca* species include *M. acuminata*, *M. cymbifolia*, *M. eleuterostachya*, *M. glomerata*, *M. halmaturorum*, *M. lanceolata*, *M. lateriflora* and *M. thyoides* (Table 1). Casuarinas are among the most tolerant of Australia species to condition of waterlogging and salinity. *Casuarina obesa* and *C. glauca* occur naturally on the margins of inland salt lakes and estuaries (Doran and Hall 1983). *Casuarina equisetifolia* occupies coastal sites exposed to ocean water inundation and salt spray. *Casuarina cristata* and *C. cunninghamiana* occur on low-lying river flats and banks of fresh-water rivers and streams. Glasshouse trials have related the severity of natural environments with the ranking of species in order of tolerance to waterlogging and salinity: *C. obesa* > *C. glauca* > *C. equisetifolia* > *C. cristata* > *C. cunninghamiana* (van der Moezel *et al.* 1989a). Dunn *et al.* (1994) showed that *C. glauca* was highly tolerant of waterlogged and saline

conditions. *Casuarina equisetifolia* was among the most tolerant of species trialled in India (Hussain *et al.* 1994; Singh *et al.* 1994). Deaths of *Melaleuca strobophylla* and *Casuarina obesa* at Lake Toolibin in Western Australia, a lake in the wheatbelt that is affected by increased inundation and secondary salinisation, appear to be caused by salinity concentration rather than increased frequency and duration of flooding (Froend *et al.* 1987; Bell and Froend 1990). Deaths of *Melaleuca ericifolia* in the Gippsland Lakes region have also been attributed to increasing salinity (Ladiges *et al.* 1981). *Melaleuca* and *Casuarina* are therefore capable of surviving extended periods of waterlogging, but suffer from the effects of increased salinity.

### **Anatomy, Morphology and Physiology of Tolerant Species**

#### *Tolerance at Seed Germination*

Understanding the anatomy, morphology and physiology of tolerant genotypes can improve the practice of placing 'the right tree in the right place'. The timing of planting and the understanding of tolerance at different stages of the life cycle are also important in the design of revegetation. Direct seeding into zones of winter soil saturation and salinity presents major environmental stress for germination. Seeds of *Melaleuca ericifolia* can germinate while submerged and are therefore metabolically adapted to anaerobic conditions (Ladiges *et al.* 1981). Germination is also strongly influenced by the osmotic pressure of salts in the soil solution. Seeds of *Eucalyptus occidentalis*, *E. eremophila* and *Melaleuca cardiophylla* withstand the osmotic pressure effects of salts in the soil or toxic ion effects after imbibition and germinate in 200 mM NaCl, but in most species germination is severely limited at these concentrations (van der Moezel and Bell 1987a). Although some species have developed tolerance at the germination phase of the life cycle, most germinate at less stressful periods of the year. Dormancy is generally maintained until rainfall dilutes external osmotic potentials to levels which allow imbibition (Bell *et al.* 1993a). Furthermore there is no relationship between waterlogging and salt tolerance during germination and subsequent tolerances as seedlings (Ayers 1952; Rozema 1975; Ladiges *et al.* 1981; Clemens *et al.* 1983; Pearce-Pinto *et al.* 1990) or adult plants (Morris 1984). In summary, planting of established seedlings of species with known tolerance in discharge zones of damaged agricultural catchments is preferred to direct seeding of waterlogged and saline sites.

#### *Mechanisms of Waterlogging Tolerance*

The physiological consequences of waterlogging of the soil are changes in stomatal aperture, transpiration, permeability of root membrane, levels of abscisic acid, cytokinins and gibberellins, and the absorption of water (Drew and Lynch 1980; Bradford and Yang 1981; Kozlowski 1984). Resistance is likely to relate to a complex mix of relevant traits inter-relating to enhance survival and growth (Flowers and Yeo 1995). Therefore, genotype selection requires knowledge of a range of attributes and their importance in the ecological approach to redressing land loss due to waterlogging and salinity. Adventitious roots, stem hypertrophy and the production of aerenchyma tissue are induced by flooding in seedlings of *Eucalyptus viminalis*, *E. ovata* and *E. robusta* (Clemens and Pearson 1977; Ladiges and Kelso 1977). The greater flooding tolerance of *E. camaldulensis* compared with *E. globulus* has been attributed to an ability of the former to produce adventitious roots on submerged portions of the stem (Sena Gomes and Kozlowski 1980a; Blake and Reid 1981; Marcar 1993). The capacity to produce adventitious roots was also associated with the comparative flooding tolerances of *E. grandis*, *E. robusta* and *E. saligna* (Clemens *et al.* 1978). Flooded plants show transient water deficits, reduced stomatal conductance and transpiration, and limited growth rates when roots suffer oxygen deficits immediately after waterlogging (Sena Gomes and Kozlowski 1980a, 1980b). However, the development of adventitious roots above the level of flooding restores gas exchange capacity, and returns water relations and growth rates to those existing prior to waterlogging (Sena Gomes and Kozlowski 1980a,

1980b; van der Moezel *et al.* 1989b; Akilan *et al.* 1997b). Salinity has profound effects on the capacity of waterlogged plants to produce adventitious roots. Akilan *et al.* (1997a) found that *E. camaldulensis* exposed to saturated soil conditions with 300 mM NaCl could not produce adventitious roots. A lack of adventitious roots in *E. lesouefii* was previously noted in saline waterlogged plants by van der Moezel *et al.* (1989b). Anatomical adaptations to increase oxygen levels in root tissues also facilitate the oxygen required by respiration to control ion uptake under conditions of anoxia as a prerequisite for tolerance of saline water tables.

#### *Mechanisms of Salinity Tolerance*

Although tolerance to waterlogged and saline environments involves the integration of numerous physiological processes, species capable of tolerating these habitats show (1) reduction of salt uptake at the root/soil interface; (2) reduction of salt transport to shoots and leaves; (3) effective localisation of salts in lower senescent leaf tissues to limit salinity concentrations in developing leaves; (4) tissue tolerance to salinity and osmotic adjustment; and/or (5) enzyme tolerance to NaCl. Tissue concentrations of NaCl also influence stomatal conductance, evapotranspiration and net gas exchange. Most tolerant species present several of these mechanisms simultaneously to the stresses of high soil salt solutions.

Salt exclusion from the shoot is a major mechanism of salt-tolerance in non-halophytes (Greenway and Munns 1980). Studies by van der Moezel *et al.* (1988) showed the most salt-tolerant species among a range of *Eucalyptus* and *Casuarina* exclude  $\text{Na}^+$  and  $\text{Cl}^-$  from young growing shoots. The site of exclusion appears to be in the roots and intolerant species with high  $\text{Na}^+$  uptake also had low  $\text{K}^+$  root concentrations. In other comparative studies, salinity resistance in a range of Australian eucalypts has been strongly related to an ability to restrict the uptake of ions (van der Moezel *et al.* 1989b; Marcar and Termaat 1990; Marcar 1993). When waterlogging involves saline water, the ability to maintain membrane control of ion uptake and selectivity is a major consideration in the success of particular species (Morris 1984; Rogers 1985; Marcar 1993; Marcar *et al.* 1995).

Salinity tolerance can also relate to an ability to sequester excess ions already absorbed into senescent, lower leaves (van der Moezel *et al.* 1988). There is considerable worldwide evidence that the ability to exclude  $\text{Na}^+$  and  $\text{Cl}^-$  from young leaves is an important attribute of salinity-tolerant trees (Allen *et al.* 1994). Salinity resistance in *E. camaldulensis* is related to tolerance of increased concentrations of  $\text{Na}^+$  and  $\text{Cl}^-$  in leaf tissues (Sands 1981).

Biochemical adaptations to waterlogging and salinity are less well known, especially in woody plants. While salinity causes substantial damage to membranes, lesions in the plasma-membrane, and changes to the structure and permeability of the bimolecular lipid layer of root cells (Kalaji and Pietkiewicz 1993), these changes have not been confirmed in waterlogged and salinised Australian trees.

Growth restrictions due to waterlogging and salinity can also be affected through particular physiological processes. Growth reductions in waterlogged and salinised *E. camaldulensis*, *E. lesouefii*, *E. tereticornis*, *E. robusta* and *E. globulus* were related to reduced relative water content, stomatal conductance, whole-plant transpiration and net photosynthesis (van der Moezel *et al.* 1989b; Marcar 1993). Under increasing levels of salinity, *E. lesouefii* maintained a higher growth rate and had a smaller reduction in these physiological processes compared to *E. camaldulensis*, yet accumulated more  $\text{Na}^+$  and  $\text{Cl}^-$  in plant tissues. In a wider range of eucalypts, however, stomatal conductance and salt uptake were not related (van der Moezel and Bell 1990). The most tolerant species, *E. microtheca*, had higher relative growth, stomatal conductance, percentage survival and lower foliar  $\text{Cl}^-$  content than the most sensitive species, *E. robusta*. In the more tolerant species, *E. microtheca* and *E. camaldulensis*, stomatal closure preceded salt uptake. In the more sensitive species, *E. robusta* and *E. lesouefii*, stomatal closure was the result of salt uptake. Concentrations of foliar nutrients in *E. microtheca* before and after salinity and waterlogging stress were similar, which indicates an ability to control the uptake of salts or to sequester toxic ions in lower leaves that are subsequently senesced.

However, the ability of *E. microtheca* to retain leaves already enhanced growth potential. Clones of *E. camaldulensis* with the greatest tolerance that were stressed for salinity and drought (Farrell *et al.* 1996a) and waterlogging/salinity and alkalinity (Farrell *et al.* 1996b) maintained leaf area and continued to transpire water, even while under stress. Water use in a plantation of *E. camaldulensis* and *E. tereticornis* in southern India was strongly influenced by total leaf area index (Roberts and Rosier 1993).

Tolerance to waterlogging and salinity is usually related to combinations of both morphological and physiological adaptations. The morphological changes are usually preceded by changes in stomatal aperture, transpiration and net photosynthesis (Kozłowski 1984). Long-term tolerance to waterlogging and salinity may therefore be related to the degree to which morphological–physiological interactions to stress are affected (van der Moezel *et al.* 1989b). A genotype may take up salts in the transpiration stream, yet shunt excesses into senescent tissues, and allow younger leaf tissue to maximise photosynthesis and net carbon gain, and grow with periodic bursts of activity. Other genotypes may restrict water and, therefore, salt uptake, retain all leaves with increased salt concentrations through osmotic adjustment and produce a more constant, but slower rate of instantaneous growth. In the search for genotypes to de-water agricultural catchments, those that retain leaf area and maintain high stomatal conductance under saline conditions, but exclude salts from their roots, would be favoured.

#### *Root Expanse Differences and Regrowth Potential*

In addition to attributes of above-ground structures and function influencing water uptake from waterlogged and saline environments, attributes of the root structure and water and salt uptake functions differ between species (Passioura 1988). Plants naturally fringing permanent wetlands or inhabiting ephemeral swamps must regrow root tips when groundwater again becomes available. *Eucalyptus camaldulensis* has long been known to possess both a surface root system and a deep, tap and sinker root system (Awe *et al.* 1976; Bell *et al.* 1993b). Mensforth and Walker (1996b) have shown that the dynamic root development system of *Melaleuca halimifolium* adjusts root growth and water uptake to parts of the profile where soil water is readily available and in this way maintains transpiration at a rate required for continued growth. This species absorbs salts, reducing plant water potentials to almost  $-7$  MPa; it can then utilise saline groundwater during summer when surface soils are too saline for water uptake (Mensforth and Walker 1996a). Akilan *et al.* (1997b) have shown that differences in the ability to regrow root tissues account for the relative seasonality of water use in clones of *Eucalyptus camaldulensis*. In alley-farming treatment comparisons in marginally saline landscapes near Katanning, Western Australia, *Casuarina obesa* was found to have less of an effect on associated pasture grasses than some species of *Eucalyptus*. The implication from the pattern of water use was that *C. obesa* exploits a more vertical volume of soils than do eucalypts (Scott and Crossley 1996). Recent studies using carbon isotope discrimination on water-use efficiency for a range of eucalypts found that the deeply rooted phreatophytes were clearly distinguished from those species that depend solely upon soil moisture derived from rainfall (Anderson *et al.* 1996). The ability to access groundwater tables allows phreatophytes to be more profligate in water use to maximise carbon gain. However, comparisons of carbon isotope discrimination between several phreatophytic eucalypts in an attempt to relate dry mass allocation and water-use efficiency as the basis for selecting specific genotypes was less successful (Le Roux *et al.* 1996). In the search for high-water-use species to rehabilitate damaged agricultural catchments, low-water-use efficiency (large amounts of water transpired in relation to the amount of carbon fixed) would be an attribute for selection of trees to perform the task of transpiring excess catchment water.

#### *Effect of Waterlogging and Salinity on Nitrogen Fixation in Acacia*

Species with tolerance to waterlogging and salinity, plus high protein content, have appeal for use in agricultural catchments as sheep fodder. However, species of *Acacia* tend to be only

moderately tolerant (Table 1). In the nitrogen symbiosis between legumes and *Rhizobium* strains, although free-living rhizobia are able to grow in high soil salinity (Bhardwaj 1975; Singleton *et al.* 1982), it appears that the effectiveness of the symbiotic relationship is limited by the salt sensitivity of the host plant (Wilson 1970; Craig 1991a). With a highly salt-tolerant *Acacia redolens* provenance acting as host, nodule number and mass, specific nodule activity and total nitrogen content did not vary between controls and those grown in solutions up to 160 mM NaCl, although the infectivity of *Rhizobium* strains and total effectiveness of the nodules decreased as the external concentration of NaCl was increased (Craig *et al.* 1991a). The ability to symbiotically fix nitrogen, the nitrogen content of the phyllodes and, therefore, the fodder value of acacias growing in discharge zones will be determined by the tolerance of the legume host rather than by the tolerance of the strains of *Rhizobium*.

In salt/waterlogged treatments, tolerance of *Acacia* species was related to an ability to control concentrations of Na<sup>+</sup> in phyllodes (Craig *et al.* 1990). Decreased concentrations of K<sup>+</sup> and Ca<sup>2+</sup> under both waterlogged and salt-waterlogged treatments compared with freely drained controls suggest that maintenance of membrane integrity and Na<sup>+</sup>:K<sup>+</sup> selectivity were also related to tolerance in *Acacia*. Crude protein values of 6–25% with reasonable digestibility values (Craig *et al.* 1991b) mean that acacias could provide maintenance forage in times of drought, although high concentrations of Na<sup>+</sup> and Cl<sup>-</sup> generally mean a greater requirement of water supplementation for grazing sheep. With the recent findings that sheep production from grazing on species of *Atriplex* has been poor (Warren and Casson 1992; Warren *et al.* 1995), tolerant species of *Acacia* deserve further examination for moderately affected regions of salinised catchments.

#### *Effects of Waterlogging and Salinity on Water Use*

Of major importance for the restoration of catchment water balance is the ability of rehabilitation species to extract, transport and transpire water. However, water use under waterlogged and saline conditions can be limited. Streamside trees of *E. camaldulensis* use stream water, but further than 15 m from the bank they use a combination of groundwater and surface-soil water (Mensforth *et al.* 1994). In summer, groundwater is the only source, but this species opportunistically uses recharge water when it is available in winter. High groundwater salinity (40 dS m<sup>-1</sup>) did not prevent the trees from using groundwater. A positive correlation between midday leaf conductance and pre-dawn water potential indicated that as water is drawn from drier and more saline soil, transpiration is influenced by both indirect and direct effects on stomatal aperture. Closure of stomata in response to a decrease in plant water potential has also been observed in *E. camaldulensis* in pot experiments (Pereira and Kozlowski 1976). Although the influence of environmental stress on stomatal closure varies among *E. camaldulensis* provenances (Gibson *et al.* 1991; Roberts and Rosier 1993), in the most tolerant genotypes, the stomata close at lower leaf-water potentials than in other flooding-tolerant eucalypt species (Quraishi and Kramer 1970; Pereira and Kozlowski 1976).

Species-specific differences in water use by flood-plain forest eucalypts in South Australia were found by Thorburn *et al.* (1993), with rates of water use by *E. largiflorens* being substantially lower than those by *E. camaldulensis*. However, leaf area index of *E. camaldulensis* was up to three times that of *E. largiflorens* and higher soil salinities at the *E. largiflorens* sites were implicated in the reduced transpiration rates. There were also differences in the rooting patterns between the two species, with *E. camaldulensis* taking up water from shallow soil water and groundwater simultaneously and *E. largiflorens* being more restricted to groundwater. Variation in the use of shallow soil water and groundwater has also been observed in clones of *E. camaldulensis* (Akilan *et al.* 1997b).

#### **Variation in Tolerance within *Eucalyptus camaldulensis***

*Eucalyptus camaldulensis* is the most widespread species of this large genus and contains considerable genetic variation (Midgley *et al.* 1989). Understanding the way particular geno-

types respond to the environment, especially in relationship to tolerance to the combined stress of waterlogging and salinity, is essential to the reclamation process and for the eventual marketing of particular clones. Australian genotypes of *E. camaldulensis* have international marketing potential, but efforts should be made to retain the profits in the country of origin. Seeds have been sold freely or given to overseas organisations, and extensive foreign plantations now compete for world markets in saw timber, paper pulp and oils. More than 500 000 ha of *E. camaldulensis* are planted overseas. Even the species' own epitaph comes from the Camalduli Monastery in Italy where it was cultivated early last century.

Provenance-specific characteristics of *E. camaldulensis* growing in north-eastern Australia have been exploited to compare details of physiological response to arid, semi-tropical habitats and more mesic, monsoonal habitats (Gibson *et al.* 1991). Provenance differences were most marked during periods of drought stress. Trees from arid sites respond to drought by rapidly limiting shoot growth, an early senescence of older leaves and the production of new leaves with a relatively greater ratio of dry weight to area (Gibson and Bachelard 1994; Gibson *et al.* 1994). Seedlings from dry-site provenances produce comparatively more fine root growth relative to shoot growth and reduce allocation to leaves relative to stems (Gibson *et al.* 1994). Reduced dry weight allocation to stems and leaves in seedlings of dry-habitat provenance is accomplished by the shedding of lower leaves and initiating axillary shoots with small leaves at lower nodes. Maintenance of root production during stress periods in the dry provenance seedlings allows longer maintenance of transpiration rate when exposed to water limitation compared with seedlings from the humid tropics. On the other hand, seedlings from the humid tropics are less responsive to the induction of drought conditions, continuing to produce similar leaf morphologies under induced drought conditions, and maintain carbon allocation patterns similar to those under more mesic conditions. Lower transpiration rates in humid tropic seedlings were associated with stomatal closure, increased water-use efficiency and decreased carbon isotope discrimination (Hubick and Gibson 1993).

In addition to provenance selections, a range of highly tolerant clones of *Eucalyptus camaldulensis* genotypes has been selected (McComb *et al.* 1989; van der Moezel and Bell 1990) and field-trialled (Bell *et al.* 1993c, 1994) for reclamation purposes. The two clonal lines, M66 and M80, from the Marrinup Nursery of Alcoa of Australia Ltd, have been used in a range of studies related to the rehabilitation of waterlogged and saline land. The comparison provides insights into the anatomical, morphological and physiological interactions which lead to an ability to cope with waterlogged and saline habitats. The M66 line originated from a tree growing near Erudina, South Australia, and M80 originated from Wooramel, Western Australia (Table 2). Both habitats are arid, but Erudina has lower annual rainfall and a higher ratio of evaporation to rainfall. James and Bell (1995) found that these two genotypes share one enzyme locus (MDH-2), but differ in four others (PGI, PGM, SDH and SOD). Of a number of clones compared in detail, M66 and M80, in addition to being genetically the most dissimilar, are the most dissimilar in terms of leaf anatomy and morphology. The leaf of the M66 clone is shorter than that of M80, but wider and thicker (Table 2). M66 leaves tend to be more glaucous and blue-green, with M80 showing a more true green to yellow-green. Cuticle thickness in M66 is nearly double that of M80. M66 tends to have fewer but larger stomata although stomatal density for both clones tends to be high in comparison with other species of *Eucalyptus* (Cameron 1970; Ridge *et al.* 1984; Kumar and Rao 1985). M66 is, therefore, more typical of plants growing in xeric, high-light habitats, producing leaves with smaller area, but a greater thickness (Abrams *et al.* 1994), with a high ratio of volume to leaf surface (Bolhar-Nordenkampf 1987). Cuticle thickness is most often associated with high light environments (Igboanugo 1992). In general, the greater the density of stomata, the smaller they will be (Tisha 1985). Increased number and smaller-sized stomata allow for more flexible regulation of water loss; carbon dioxide uptake is therefore maintained when the relative humidity of the air is low (Bolhar-Nordenkampf 1987).

**Table 2. Comparison of clones M66 and M80 of *Eucalyptus camaldulensis***

	Clone M66	Clone M80
Clone origin and environmental features		
Provenance latitude	31°29'S	25°45'S
Provenance longitude	139°21'E	114°16'E
Provenance rainfall (mm)	195	214
Provenance evaporation-to-rainfall ratio	14.4	13.7
Anatomical features <sup>A</sup>		
Leaf length (mm)	106	148
Leaf width (mm)	60	31
Leaf thickness (mm)	388	328
Total cuticle thickness (mm)	12.1	7.0
Stomatal area (%)	7.9	6.3
Stomatal density (mm <sup>-2</sup> )—adaxial	237	354
Stomatal density (mm <sup>-2</sup> )—abaxial	315	456
Length of stomatal pore (mm)—adaxial	16.6	15.7
Length of stomatal pore (mm)—abaxial	15.7	14.7
Leaf orientation <sup>B</sup>		
Average leaf/stem angle (°)	20	-20
Average blade angle (°)	56	43
Response during fresh-water waterlogging stress trial <sup>C</sup>		
Specific weight of old leaves (g cm <sup>-2</sup> )	0.31	0.14
Specific weight of new leaves (g cm <sup>-2</sup> )	0.19	0.08
Total leaf area (cm)	1 580	1 794
Root dry weight (g)	12.8	17.4
Total plant dry weight (g)	43.5	90.0
Total water uptake (kg tree <sup>-1</sup> )	9.64	11.78
Water uptake per leaf area (kg m <sup>-2</sup> day <sup>-1</sup> )	2.57	2.82
Response during salt-water waterlogging/salinity stress trial <sup>D</sup>		
Total water use (kg)	1.88	3.54
Daily water use (g)		
Total	44	82
0 mM NaCl	73	144
100 mM NaCl	65	109
200 mM NaCl	48	84
300 mM NaCl	13	34
Leaf numbers	29	73
New leaf numbers	4	18
Specific weight old leaves (g cm <sup>-2</sup> )	0.60	0.33
Specific weight new leaves (g cm <sup>-2</sup> )	0.18	0.11
Total leaf area (cm)	844	1338
Root dry weight (g)	27.6	35.7
Shoot/root ratio	0.6	1.1
Total plant biomass (g)	51	75
Stomatal conductance (mmol m <sup>-2</sup> s <sup>-1</sup> )		
After 5 days waterlogged in 0 mM NaCl	195	107
After 12 days waterlogged, 3 days 100mM NaCl	140	119
After 22 days waterlogged, 3 days 200mM NaCl	146	62
After 35 days waterlogged, 8 days 300mM NaCl	64	45

**Table 2.** (continued)

	Clone M66	Clone M80
Net gas exchange ( $\text{mmol m}^{-2} \text{s}^{-1}$ )		
After 5 days in 0 mM NaCl	16.7	8.8
After 12 days waterlogged, 3 days 100mM NaCl	8.7	7.2
After 22 days waterlogged, 3 days 200mM NaCl	21.4	7.6
After 35 days waterlogged, 8 days 300mM NaCl	10.0	4.2
Response during fresh and salt waterlogging trials <sup>E</sup>		
Leaf Na <sup>+</sup> (%)—control	0.36	0.54
Leaf Na <sup>+</sup> (%)—fresh waterlogged	0.33	0.48
Leaf Na <sup>+</sup> (%)—salt waterlogged	2.61	3.04
Leaf Cl <sup>-</sup> (%)—control	1.15	0.81
Leaf Cl <sup>-</sup> (%)—fresh waterlogged	0.57	0.75
Leaf Cl <sup>-</sup> (%)—alt waterlogged	4.36	5.37
Root Na <sup>+</sup> (%)—control	0.48	0.51
Root Na <sup>+</sup> (%)—fresh waterlogged	0.55	0.65
Root Na <sup>+</sup> (%)—salt waterlogged	2.34	2.53
Root Cl <sup>-</sup> (%)—control	0.36	0.96
Root Cl <sup>-</sup> (%)—fresh waterlogged	0.65	0.86
Root Cl <sup>-</sup> (%)—salt waterlogged	2.78	3.35
Field response to gradient of waterlogging and salinity <sup>F,G</sup>		
Upland slope—9-year-old trees		
Mean height of all trees (m)	17.6	22.4
Height of water use measurements tree (m)	15	15
Diameter of water use tree (cm)	18	21
Leaf area of water use tree ( $\text{m}^2$ )	14	35
Conducting wood area ( $\text{cm}^2$ )	173	176
Annual water uptake per land area (mm)	1334	1680
Water uptake per conducting wood area ( $\text{L cm}^{-2}$ )	69	86
Water uptake per leaf area (mm)	857	432
Lowland slope—9-year-old trees		
Mean height of all trees (m)	12.5	17.4
Height of water use measurements tree (m)	9	10
Diameter of water use tree (cm)	12	11
Leaf area of water use tree ( $\text{m}^2$ )	12	11
Conducting wood area ( $\text{cm}^2$ )	109	62
Annual water uptake per land area (mm)	968	610
Water uptake per conducting wood area ( $\text{L cm}^{-2}$ )	80	89
Water uptake per leaf area (mm)	726	499
Leaf ion content and osmotic adjustment <sup>H</sup>		
Nine-year-old plants growing in upper landscape positions		
Na <sup>+</sup> (%) of leaves	0.17	0.05
Cl <sup>-</sup> (%) of leaves	0.48	0.53
Leaf osmotic potentials (MPa)	-1.75	-1.44
Nine-year-old plants growing in lower landscape positions		
Na <sup>+</sup> (%) of leaves	0.26	0.05
Cl <sup>-</sup> (%) of leaves	0.56	0.52
Leaf osmotic potentials (MPa)	-1.91	-1.64

<sup>A</sup>James and Bell (1995); <sup>B</sup>James and Bell (1996); <sup>C</sup>Farrell *et al.* (1996a); <sup>D</sup>Farrell *et al.* (1996b); <sup>E</sup>Akilan *et al.* (1997a); <sup>F</sup>Akilan *et al.* (1997b); <sup>G</sup>Marshall *et al.* (1997); <sup>H</sup>Unpublished data of Akilan *et al.*

Leaf displays of young plantlets of M66 and M80 are also markedly different (James and Bell 1996). M66 plantlets tend to have more vertically tilted and rotated leaf blades than M80 plantlets (Table 2). The more vertical orientation of the leaf blades enables the M66 clone to maximise interception of morning and afternoon light while reducing exposure to midday sun. M66 was also found to intercept a greater proportion of total daily photosynthetically active radiation (PAR) than M80.

The comparative orientation of leaves of these two clones is also linked to their respective features of leaf anatomy. M66 with the thicker leaves, greater development of cuticle, spongy and palisade mesophyll, and larger chloroplasts intercepts a greater proportion of total daily sunlight than M80. It is apparent that M66 is better adapted to higher PAR flux densities, and thus has developed more 'sun-leaf' characteristics. It is well documented that leaves developed under high light intensities are thicker, have well-developed palisade and spongy mesophyll, and develop thicker epidermal layers (Chabot and Chabot 1977; Sims and Pearcy 1992). Leaves that display these anatomical features have higher photosynthetic rates per unit area because of the greater proportion of leaf tissue per unit leaf area, increased quantities of enzymes and higher stomatal conductances, than leaves developed under lower light conditions (Sims and Pearcy 1992). Vertical leaf orientation results in substantial reduction in leaf temperatures and transpiration (DeLucia *et al.* 1991). Thus, M66 would appear better adapted to arid conditions and high-light habitats. It may not, however, be capable of utilising soil water under more mesic conditions.

The contrasting morphology of these two clones influences their responses to conditions of waterlogging stress with fresh (Farrell *et al.* 1996a) and salt water (Farrell *et al.* 1996b). Under conditions where soil was waterlogged with fresh water to half the pot height, M66 continued to produce much heavier leaves than M80 during the period of waterlogging (Table 2). The leaves of the plantlets at the start of the experiment (old leaves) were  $0.31 \text{ g cm}^{-2}$  for M66 and  $0.14 \text{ g cm}^{-2}$  for M80. At the end of 30 days of waterlogging, the specific weights of new leaves were  $0.19 \text{ g cm}^{-2}$  (M66 clone) and  $0.08 \text{ g cm}^{-2}$  (M80 clone). This indicates that genetic control of leaf morphology is strong, and only moderately influenced by short-term environmental stress. By the end of the trial, M80 plantlets had greater total leaf area, root dry weight and total plant dry weight. This greater productivity under waterlogged conditions was associated with greater total water uptake, on both a per tree and per leaf area basis. An ability to produce and retain leaf and root tissue while under waterlogging stress is clearly an attribute of *E. camaldulensis*, resulting in its success in waterlogged habitats. M80 appears to be better adapted than M66 to conditions of waterlogging with fresh water. The ability to produce and retain leaf area contributes to productivity in flood-plain species (e.g. *Populus*; Michael *et al.* 1988; Dickmann *et al.* 1990). In plantation eucalypts in India, leaf area index was the most important variable in the prediction of total tree water use, while differences in stomatal conductance and leaf water potential were of only minor influence (Roberts and Rosier 1993). The ability to produce and retain leaf surface area is, therefore, an important attribute in trees used to reclaim waterlogged regions in agricultural landscapes.

Under conditions of waterlogging with progressively greater salinity, both *E. camaldulensis* clones again proved to be very tolerant (Farrell *et al.* 1996b), with M80 transpiring more water because of its greater numbers of leaves, and total leaf, root and plant biomass (Table 2). As salinity of the waterlogging conditions increased, daily water use on a whole plant level was always greater for M80 than for M66. However, stomatal conductance and net gas exchange are generally measured on the basis of leaf surface area, and both were greater for M66. The superiority of response of M66 is undoubtedly due to its greater stomatal area per unit leaf area (and therefore greater conductance) and greater leaf thickness. This stress experiment therefore confirmed the superior ability of M80 to utilise water under waterlogged conditions, but there was some indication that M66 was more tolerant of anoxic conditions where salinity was also involved.

Further glasshouse trials on the effects of waterlogging by fresh and salt water indicated that adventitious roots formed earlier in M80 than in M66 under waterlogging with fresh water (Akilan *et al.* 1997a). Clone M80 also used more water after prolonged waterlogging. In contrast, M66 was better suited to more saline conditions; greater water uptake by M80 was associated with increased concentrations of Na<sup>+</sup> and Cl<sup>-</sup> (Table 2). Sands (1981) also indicated that differences in tissue tolerance to Na<sup>+</sup> and Cl<sup>-</sup> could explain differences in salinity tolerance in *E. camaldulensis*.

Year-long measurements of water use on 9-year-old trees of M66 and M80 on a gradient of waterlogging and salinity at Wubin, Western Australia, indicated the capabilities of these trees to de-water damaged agricultural catchments because average annual water uptake (1148 mm) exceeded rainfall (432 mm) by about 2.7-fold and approached 56% of pan evaporation for the area (Marshall *et al.* 1997; Akilan *et al.* 1997b). Growth and water uptake, however, varied with genotype, season and position on the slope. In upslope positions where depth to groundwater was greatest and soil and groundwater salinities were least, M80 trees were larger and produced more than twice the leaf area of the M66 trees (Table 2). However, in downslope positions where depth to groundwater was considerably less and soil and groundwater salinities were much greater, the two clones were more similar in size and leaf area. As in the controlled, short-term experiments, water use by M80 was facilitated by greater leaf surface area, a factor partially compensated for in M66 by greater stomatal pore area per leaf surface area.

Water uptake varied seasonally, with water use by M80 being greater over the entire year, except during winter when water was taken up from the unsaturated portion of the profile. M66, on the other hand, used more of the saline groundwater table in summer. Only M66 produced new root terminals at depth during the warmer, drier months (Akilan *et al.* 1997b). These studies again suggest that M80 is more tolerant of waterlogging by relatively fresh water, but that M66 is more capable of using water of higher salinity. Concentrations of Na<sup>+</sup> and Cl<sup>-</sup> and osmotic potentials in leaves of the 9-year-old field-grown trees confirmed the greater ability of the leaves of M66 to take up saline groundwater (Table 2). The high root-to-leaf ratios of Na<sup>+</sup> and Cl<sup>-</sup> (>1) suggest that both of these *Eucalyptus camaldulensis* clones sequester ions in roots. However, in M80, the significantly lower concentration of Na<sup>+</sup> in leaves and higher root-to-leaf ratios of Na<sup>+</sup> suggests that the roots of M80 possess a greater capacity to exclude Na<sup>+</sup>. In contrast, the ability of M66 to accumulate greater concentrations of ions in leaf tissue ensures that water uptake continues further into the summer as soil solute concentrations increase. M80 would therefore be better suited to higher slopes in partially cleared catchments, where rainfall provides relatively fresh soil water. M66 is better suited to lower catchments positions owing to its ability to utilise more saline groundwaters. Successful restoration of the water balance in damaged agricultural catchments can therefore be maximised by matching specialised species and genotypes to particular catchment positions.

Despite the availability of a range of highly tolerant tree species and particularly productive genotypes, the economic requirements for rehabilitating large areas of damaged agricultural land with trees and shrubs are difficult to overcome. Costs are estimated to be \$400–1000 ha<sup>-1</sup> (Bartle 1992) and the very large numbers of highly tolerant tree seedlings required cannot be produced in existing nurseries. To be effective on a large scale, some presently productive agricultural land must be converted to tree crops, an economic system where the profit on the crop is realised only every 8–10 years. However, the restoration of damaged agricultural land is possible, and it is essential if we are to ensure the long-term productivity of the land and the quality of the water for future generations.

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