

**An ecophysiological approach to determine problems  
associated with mine-site rehabilitation: a case study in  
the Great Sandy Desert, north-western Australia**

by  
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## Summary

Establishment of vegetation and ecosystem functioning is central to the mitigation of environmental impacts associated with mining operations. This study investigated the ecophysiological functioning of mature plants in natural vegetation and applied this knowledge to diagnose problems affecting plant health and causes of poor plant cover at a mine-rehabilitation site. Ecophysiological parameters, including plant water relations and mineral nutrition, were studied in conjunction with soil physical, hydraulic and chemical properties.

The natural ecosystem at the study location in the Great Sandy Desert is characterised by sand dunes and interdunes with distinct plant communities on each. One of the most notable features of the vegetation is the presence of large *Corymbia chippendalei* trees high on the dunes and relatively small scattered shrubs in the interdunes. *Triodia* grasses (spinifex), dominate the vegetation in both habitats but different species occur in each; *T. schinzii* is restricted entirely to the dunes, and *T. basedowii* occurs only in the interdunes. It was hypothesised that the deep sandy dunes afford greater water availability but lower nutrient supply to plants in this habitat compared with those occurring in the lower landscape position of the interdunes. Water-relations parameters (leaf water potentials, stomatal conductance,  $\delta^{13}\text{C}$ ) revealed that dune plants, particularly woody species, displayed higher water status and water use than closely related and often congeneric plants in the interdunes. Nutrient concentrations in soils were significantly higher in the interdunes, but concentrations in foliage were similar for related species between habitats. It is concluded that the dunes provide a greater store of accessible water than the soil profile in the interdunes. The greater buffering capacity of dunes reduce seasonal fluctuations in water use for deep-rooted species, particularly the large *Corymbia chippendalei* trees. The more mesic conditions on dunes may also facilitate the occurrence of species adapted to subtropical areas with higher rainfall, such as *Triodia schinzii*.

Plant cover at a nearby mine-rehabilitation site (12%) was much lower than that found in the natural habitat (49%). Furthermore, species richness was very low at the rehabilitation site with only three *Acacia* shrubs and two *Triodia* grasses occurring; this was in marked contrast to 165 species in the natural habitat. At the rehabilitation site, plants occurred only where the mine-waste material was covered with at least 0.2 m of soil from the natural site, and away from erosion lines running down the sloping sides

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(18° angle). It was suspected that the mine-waste material, a compacted silty shale, is chemically and/or physically hostile to root growth and that the limited cover soil layer is insufficient to support plant water requirements. The waste material was considerably alkaline (pH 8.7) compared with the natural soil (pH 6.5) and this is likely to reduce the availability of some macro- and micro-nutrients. This was evidently offset by higher availability of many nutrients, including P, N and K in the waste material as foliar concentrations were generally similar at both sites. Al concentrations in foliage were significantly higher at the rehabilitation site, but there were no signs of toxicity for the five species present. Physical properties of the compacted, silty mine-waste material were evidently causing mechanical difficulties for root penetration. All species displayed roots confined to shallower layers than found at the natural site, and the sinker roots of the *Acacia* shrubs were particularly stunted. In general, plant water relations were adversely affected during the dry season for *Acacia* species but not for the *Triodia* grasses. At the rehabilitation site, acacias displayed higher foliar  $\delta^{13}\text{C}$  values, lower stomatal conductance and lower stem sap velocity during dry periods.

Following an experimental wetting pulse equivalent to a summer cyclone event, *A. ancistrocarpa* plants displayed significant increases in stomatal conductance, leaf water potential and sap velocity in lateral roots within three days of irrigation at the natural site and two days at the rehabilitation site. Secondary sinker roots originating from distal sections of lateral roots were evidently supplying water to maintain hydraulic function in laterals, thus enabling a fast pulse response. This was accentuated at the rehabilitation site where roots were confined closer to the surface. These results indicate that plants at the rehabilitation site are more dependent on small pulses of water and have less access to deep reserves than plants at the natural site. It is concluded that high runoff losses and insufficient soil depth are major factors contributing to plant water stress, and combined with the direct impacts of erosion, are largely responsible for plant death and ultimately poor plant cover. These issues can be alleviated if cover soil depth is increased to more than 0.5 m and slope angles are reduced to <12°.

This study demonstrates the value of an ecophysiological approach for diagnosing problems affecting plant establishment at mine-rehabilitation sites. Furthermore, it has provided recommendations that will improve the rehabilitation strategy and lead to the development of a well vegetated, resilient ecosystem on a stable and non-polluting land form.

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"Science cannot solve the ultimate mystery of Nature- and that is because, in the last analysis, we ourselves are part of the mystery that we are trying to solve"

Max Planck (1858-1947) Physicist

I acknowledge, with deepest respect, the traditional owners of the land studied in this thesis; particularly the Martu, Wanman, Kartudjara, Potidjara and Yulparitja peoples of the Great Sandy Desert.

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### **Published works from this thesis:**

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### **Declaration**

I declare that the work presented in this thesis is entirely my own and that any contributions made by others are acknowledged accordingly. The thesis has been completed during the course of enrolment in a PhD degree at the University of Western Australia and has not been used previously for a degree or diploma at any other institution

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# Chapter 1

## General Introduction

### *The desert environment: interactions between climate and soils*

Water availability is the primary factor limiting photosynthesis, reproduction, microbial activity and nutrient cycling in desert ecosystems, and strongly influences vegetation type and density (Noy-Meir 1973; Smith *et al.* 1995; Xu and Li 2006). Deserts cover approximately one third of the Earth's land surface and are characterised by limited rainfall, extremes in temperature and typically sparse vegetation cover (Hadley and Szarek 1981; Polis 1991). The word desert is derived from the Latin *desertum*, meaning abandoned or uninhabited place, and does not itself refer to aridity (Oxford English Dictionary 2002). True to the meaning of the word, many of the hot sub-tropical deserts (e.g., the Sahara and Namib of Africa, the Empty Quarter of the Middle East, the Gobi and Taklamakan of central Asia, and the Atacama of South America), and the polar icesheet deserts (Antarctica and Greenland) are largely devoid of plant life. However, many other deserts display considerable vegetation cover, such as those in Australia (e.g., the Great Sandy, Gibson and Great Victoria Deserts), parts of North America (e.g., the Sonoran) and southern Africa (e.g. the Kalahari). Taking into consideration physical and biological aspects of these environments, Noy-Meir (1973) defined desert ecosystems as “water-controlled ecosystems with infrequent, discrete and largely unpredictable water inputs”.

The availability of water to vegetation in desert ecosystems is influenced by a myriad of interacting factors including rainfall amount, seasonality, intensity and duration, as well as evaporation, soil type, landscape topography, geology, hydrology, and also by vegetation itself (Knoop and Walker 1985; Bowman and Minchin 1987; Sala *et al.* 1988; Lee and Lauenroth 1994; Wondzell *et al.* 1996). Compounding the effect of limited water inputs, evaporation losses are extreme in sub-tropical deserts because of high temperatures, high solar irradiance levels, wind and low relative air humidity. For example, deserts in Australia typically receive 200-350 mm rainfall per year and display annual potential evaporation rates up to 4000 mm in places (Appendix I, Figure I.1 and I.2 respectively - Bureau of Meteorology 2009a,b). These values for mean annual rainfall and potential evaporation are high compared with deserts elsewhere; e.g.,

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Sahara desert, eastern Mauritania: 100 mm and 2500 mm, respectively (Hayward and Oguntinyinbo 1987); Thar desert, northern Pakistan: 200 mm and 2700 mm, respectively (Geyh and Ploethner 2008); Gurbantonggut desert, northwest China: 160 mm and 2000 mm, respectively (Xu and Li 2006).

Rainfall in desert ecosystems is typically unpredictable in its timing, intensity and volume, although seasonal trends are common (Noy-Meir 1973). Extreme fluctuations in the water content of shallow soil layers can occur over hours or days, whilst relatively more moderate changes occur at greater depths over the course of seasons and years (Sala *et al.* 1981; Sala and Lauenroth 1982; Ehleringer and Dawson 1992; Schwinning and Ehleringer 2001). The seasonality of rainfall and evaporative conditions immediately following a rain event interact strongly with soil type to influence the proportion of water that penetrates in to the profile. Monsoonal summer rainfall, usually in the form of short, intense showers, is typically followed by hot, dry conditions and relatively high losses to the atmosphere compared with winter rains (Ehleringer *et al.* 1991; Lin *et al.* 1996). As a result, a smaller proportion of rainfall penetrates and to a shallower depth compared with an equivalent volume of winter rainfall (Williams and Ehleringer 1996, 2000; Golluscio *et al.* 1998; Schwinning and Sala 2004).

Soil type interacts strongly with rainfall seasonality and soil moisture varies spatially and temporally as a result (Noy-Meir 1973). Sandy soils display large particle sizes, large pore spaces, weak matrix potentials and a high saturated hydraulic conductivity ( $K_s$ ) so water infiltrates quickly to deeper soil layers and limited capillary rise reduces evaporation from the soil surface (Pavlik 1980; Knoop and Walker 1985; Sperry and Hacke 2002). By contrast, finer-textured soils have low  $K_s$  values, so moisture is held in shallow soil layers and high capillary forces allow water to diffuse back to the surface from which it is readily evaporated (Seely and Louw 1980; Orshan 1986; Brown and Archer 1990). For these reasons a higher proportion of rainfall is captured and available at depth by sandy soils than by clay soils in hot arid environments; a phenomenon known as the inverse texture effect (Noy-Meir 1973; Sala *et al.* 1988; English *et al.* 2005). However, the lower water-holding capacity of sandy soils means a greater depth is needed to store an equivalent amount of water than in finer soils. These factors greatly influence plant water relations, morphology, anatomy and physiology. For example, sandy soils should be associated with less negative soil and plant water potentials and deeper root systems (Sperry *et al.* 1998; Jackson *et al.* 2000; Schenk and

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Jackson 2002; Sperry and Hacke 2002; Seyfried *et al.* 2005). Interactions between soils, plant adaptations and spatial and temporal fluctuations in water availability will be discussed in later sections of this Chapter.

*Water availability and biological processes in deserts*

The concept of ‘effective’ precipitation is central to hypotheses explaining ecosystem processes in water-limited systems (Thornthwaite 1933; Noy-Meir 1973; Ogle and Reynolds 2004; Schwinning and Sala 2004; Fernandez 2007). Inherent in this concept is the notion that the size of the rain event dictates the type and size of the biological response. For example, small precipitation events (~2 mm) that barely penetrate the soil surface may have important implications for cryptogamic crust organisms (Cable and Huxman 2004) and soil microbes (Cui and Caldwell 1997; Austin *et al.* 2004), but not affect water uptake of any plant life-forms (Schwinning *et al.* 2003). Moderate rainfall events (5-15 mm) are likely to improve water status of shallow-rooted species such as grasses (Sala and Lauenroth 1982), but not cause any increase in water use for trees (Zeppel *et al.* 2008). Relatively large showers (>20 mm) are needed to trigger germination in many desert plants (Beatley 1974) or for water uptake in many woody shrubs and trees (Schwinning *et al.* 2003). These processes were recognised by Westoby and Bridges in unpublished works and formalised by Noy-Meir (1973) as the ‘pulse-reserve’ paradigm. In this concept, the ‘pulse’ refers to the surge in biological activity, primary production and reproduction after a ‘trigger’ event of effective rainfall; the ‘reserve’ refers to the converted products such as carbohydrates, biomass and propagules that allow the biota to persist through times without precipitation inputs (Noy-Meir 1973). In more recent years, the meaning of the term ‘pulse’ has been expanded and used to refer to ‘pulses’ of rainfall and soil moisture availability, as well as ‘pulses’ of biological activity (Reynolds *et al.* 2004; Schwinning and Sala 2004; Fernandez 2007; Zeppel *et al.* 2008).

Delays in biological activity after rainfall are common; certain woody plants with predominantly deep root systems will not display any changes in water uptake and photosynthesis until deeper soil layers are recharged; a process that may take weeks, months, years or even longer (Williams and Ehleringer 2000; Schwinning and Ehleringer 2001; Burgess 2006). Alternatively, co-existing plants can be physiologically active and use water at different times of year (Shreve 1942; Fowler 1986; Weltzin and McPherson 1997; Reynolds *et al.* 2000). The interrelationship between the spatial and

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temporal availability of water and its effect on vegetation was first addressed for a semi-arid savanna system by Walter (1971). He recognised that roots of grasses were confined to upper soil layers, while roots of trees accessed deep layers, and proposed that separation of niches for water uptake reduced competition and permitted their co-existence; a model he termed the ‘two-layer’ hypothesis (Walter 1971). Walter (1971) also suggested that in wetter areas, woody plants should dominate due to a higher proportion of rainfall infiltrating to deeper soil layers, whilst for drier areas grasses should dominate due to shallow penetration of wetting fronts. Although this model is considered appropriate for explaining the long-term effects of precipitation in shaping the vegetation in many semi-arid savannas (e.g., Soriano and Sala 1984; Knoop and Walker 1985; Brown and Archer 1990; Dodd *et al.* 1998; Schenk and Jackson 2002), many have found this hypothesis too simplistic for other systems (Sala *et al.* 1989; Le Roux *et al.* 1995; Scholes and Archer 1997; Ludwig *et al.* 2004; Burgess *et al.* 2006).

The fundamental principles of the ‘pulse-reserve’ paradigm (Noy-Meir 1973) and the ‘two-layer’ hypothesis (Walter 1971) are elaborated upon in more recent models to define interactions between water availability and biological processes. Newer and more comprehensive models include the ‘hierarchy of pulse responses’ concept by Schwinning and Sala (2004), and the ‘threshold-delay’ model by Ogle and Reynolds (2004). These consider additional attributes and feedbacks between physical aspects such as antecedent soil moisture, infiltration depth and pulse duration, as well as ecophysiological aspects such as carbon gain, plasticity in rooting habits, various plant phenologies and the potential for delayed responses of plants to rainfall.

#### *Plant water-use strategies in desert ecosystems*

Plant water-use patterns and responses to rainfall in water-limited systems depend on a suite of parameters including rooting depth, root morphology, stomatal behaviour, leaf anatomy and physiology, phenology, hydraulic architecture and soil physical properties (Ogle and Reynolds 2004; Xu and Li 2006; Mitchell *et al.* 2008). In desert environments, a broad variety of plant life-forms and root functional types exist, indicating a complex array of trade-offs among these parameters (Ehleringer *et al.* 1991; Flanagan *et al.* 1992; Golluscio and Sala 1993; Lin *et al.* 1996; Breshears and Barnes 1999). As a consequence, there is not one ideal set of traits that can exploit water wherever and whenever it becomes available (Schwinning and Ehleringer 2001; Xu *et al.* 2007; Mitchell *et al.* 2008). Life-forms include all components of the vegetation



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assemblage and are adapted specifically to a particular niche in order to reduce competition for resources (Fowler 1986). Annual grasses and herbaceous species employ a 'drought-escape' strategy adapted for fast growth and early reproduction when resources are available, then subsist in the form of seeds during unfavourable times (Rice and Mack 1991; Aronson *et al.* 1993; Ludwig *et al.* 2004). Perennial species generally display more conservative resource use, slower growth, greater allocation of biomass to root systems to attain greater penetration into the soil profile, and other physiological and morphological strategies for avoiding dehydration stress (Ludlow 1989; Stanton *et al.* 2000). For example, perennial evergreen woody species and succulents tightly control stomatal conductance of water vapour according to soil moisture, atmospheric demand and tissue reserves of water (Nilsen *et al.* 1983; Duff *et al.* 1997; Eamus 1999; Ogle and Reynolds 2002; Graham and Nobel 2005); drought-deciduous shrubs and trees lose foliage to avoid excess water loss (Smith *et al.* 1995; Schwinning and Ehleringer 2001; Sperry and Hacke 2002); and perennial grasses can reduce transpiration by morphological alterations such as leaf rolling (McWilliam and Milson 1974; Jacobs 1984; Mant 1998; Clary *et al.* 2004).

Plant life-form and root functional type are often interrelated and, combined with phenology, define plant water-use strategies; a concept developed in the two-layer hypothesis (Walter 1971) and the threshold-delay model (Ogle and Reynolds 2004). Rooting depth and morphology are the main factors determining plant functional type, because patterns of water uptake depend largely on where roots are in the soil profile (Schwinning and Ehleringer 2001; Sperry and Hacke 2002; Xu and Li 2006). Desert plants display a variety of root system functional types, with examples at both ends of the root depth spectrum (Schenk and Jackson 2002). Plants with shallow roots only (<0.3 m) include many grasses (Scholes and Archer 1997; Weltzin and McPherson 1997), herbaceous species (Cowling *et al.* 1999; Li *et al.* 2004) and CAM succulents (Fowler 1986; Esler and Rundel 1999). Plants with predominantly deep roots (> 3 m) include certain trees and shrubs in desert areas with access to a water table (phreatophytes e.g., *Tamarix ramosissima* and *Populus euphratica*; Greis *et al.* 2003; Xu *et al.* 2007). Shallow roots facilitate rapid uptake of water and nutrients that become available following rain, but are more prone to desiccation, xylem cavitation (Tyree and Sperry 1989), and higher respiration costs because of higher surface soil temperatures than deep roots (Schwinning and Ehleringer 2001; Schenk and Jackson 2002). Deep roots are present where moisture at depth is more reliable than for surface layers, and

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are particularly important for sustaining transpiration and photosynthesis during rainless periods (Oliveira *et al.* 2005). In strongly seasonal environments with a sufficiently predictable (often summer) rainy season and pronounced dry season, woody species often exhibit both shallow lateral roots and deep tap roots (a dimorphic root system) to take advantage of moisture pulses near the surface and reliable stores at depth (Ehleringer and Dawson 1992; Pate *et al.* 1995; Dawson and Pate 1996; Burgess *et al.* 1998; Williams and Ehleringer 2000; Hultine *et al.* 2003, 2004). The diversity of root functional types facilitates spatial and temporal separation of niches for water uptake, promotes species co-existence and therefore shapes vegetation community structure (Caldwell and Richards 1986; Casper and Jackson 1997; Williams and Ehleringer 2000; Lavorel and Garnier 2002).

A diverse assemblage of plant life-forms and root functional types promotes maximum utilisation of rainfall in water-limited environments (Lefroy *et al.* 1999; Pate and Bell 1999). Indeed, natural vegetation in such environments is likely to use all available rain-derived soil moisture, preventing deep drainage in all but the wettest years if the soil is of sufficient depth and favourable texture to allow unhindered development of plant roots (Phillips 1994; Smettem 1998; Van de Water *et al.* 2002; Schwinning and Sala 2004; Seyfried *et al.* 2005; Mitchell *et al.* 2009). Determination of plant water-use patterns and the dynamics between vegetation, soil and climate are important for understanding the ecohydrology of an area and for making informed decisions regarding water management (Zalewski 2000; Eamus *et al.* 2006). These issues will be returned to later and discussed with respect to mine-site rehabilitation.

#### *Nutrient availability in desert systems*

Nutrient availability is tightly coupled with water availability in water-limited ecosystems (Noy-Meir 1973). This is because microbial activity, organic matter breakdown and mineralisation of nitrogen and phosphorus are restricted largely to wet periods following rain events (Skopp *et al.* 1990; Austin *et al.* 2004; Ford *et al.* 2007).

Soils, particularly in sandy deserts, are typically low in nutrients, especially phosphorus (P) and nitrogen (N) (Hadley and Szarek 1981; Rice *et al.* 1994; Smith *et al.* 1997; Bennet and Adams 2001). Coarse soils have a relatively small surface area compared with clay soils, poor nutrient-retention properties (few P-binding sites) and are strongly leached (Tan 1993). The spatial distribution of nutrients is patchy because of physical

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and biological heterogeneity affecting the movement and interception of nutrient-rich particles primarily associated with wind and water flows (Burke *et al.* 1998; Aguiar and Sala 1999). Leaf litter and organic matter collects in soil depressions or is trapped beneath plants whilst topsoil dust deposited on leaves is washed-off during rainfall and concentrated towards the base of the plant due to stem-flow or through-fall (Hook *et al.* 1991; Ludwig and Tongway 1995; Bennett and Adams 1999; Li *et al.* 2007). These enrichment zones or ‘islands of fertility’ are perpetuated by the trapping of propagules amongst the leaf litter and germination of seedlings close to the original ‘nurse plant’ (Scholes and Archer 1997; Tielborger and Kadmon 1997; Schlesinger and Pilmanis 1998; Ludwig *et al.* 1999). Biological crust organisms, including mosses, lichens and cyanobacteria are also associated in and around these islands of fertility. These crusts are often composed of cyanobacteria, bryophytes and lichens and play an important role in trapping fine soil particles (Stoneburner *et al.* 1993; Hodgins and Rogers 1997; Eldridge 2001). Cyanobacteria (e.g., *Nostoc*) in crusts and N<sub>2</sub>-fixing bacteria in the digestive tract of termites (e.g., *Klebsiella* and *Azobacter*) fix atmospheric dinitrogen and are major contributors to the nitrogen economy of many desert ecosystems (Tongway and Smith 1989; Pate *et al.* 1998; Harper and Belnap 2001; Gomathi *et al.* 2005).

A number of adaptations have evolved in plants to improve nutrient uptake, including symbioses with nodulating bacteria (e.g., rhizobia) that fix dinitrogen (e.g., in Fabaceae- Long 1996) or mycorrhizal fungi that enhance the supply of phosphorus (P) (e.g., in Myrtaceae- Brundrett 2002) or morphological/physiological adaptations such as cluster roots (e.g., in Proteaceae- Lambers *et al.* 2006). Cluster or ‘proteoid’ roots mobilise organic and inorganic P by releasing root exudates such as phosphatases and carboxylates (Shane and Lambers 2005). Many grass species (Poaceae) release phytosiderophores that mobilise iron (Fe) or zinc (Zn) (Römheld and Marschner 1986; Cakmak *et al.* 1996).

*Study site information: The Great Sandy Desert and Nifty Copper Mine*

The Great Sandy Desert is located in north-western Australia and covers an area of 360,000 km<sup>2</sup>. It overlies the Canning Basin and is bordered by rocky ranges in the Kimberley to the north and in the Pilbara to the west and south-west. The Gibson Desert and Little Sandy Desert lie to the south, and to the east is the Tanami Desert. The Great Sandy is characterised by Quaternary red aeolian sand dunes organised into linear and

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braided dunes oriented roughly south-east – north-west. The dunes were formed during the peak aridity of the last glacial maximum 20 thousand years ago and have been largely stationary for the last 13,000 years due to moister conditions and substantial vegetation cover (Bowler 1976; Nanson *et al.* 1992; Rhodes *et al.* 2004). Dune height averages 10-12 m, but some dunes can be up to 20 m. Aside from the dune ridges, the overall landscape is very flat, and there are no drainage channels or creek lines over hundreds of square kilometres. Elevation above sea level for interdune floors is 300 m. Rocky outcrops are not common, although the Throssel Range to the south and Paterson Range to the south-east are notable intrusions into the vast dune fields of the Great and Little Sandy Deserts.

The vegetation of the area is classified as semi-arid shrub steppe, with plant cover dominated by spinifex grasses, including *Triodia schinzii* (previously known as *Plechtrachne schinzii*) in the dunes and *Triodia basedowii* in the interdunes (Beard 1970, 1974; Beadle 1981; Griffin 1990). Spinifex grass communities cover 25% of Australia, making this vegetation type the most extensive on the continent. The two species studied here represent both spinifex groups; the ‘soft’ spinifex group predominantly occurs in the moister, sub-tropical regions of northern Australia and includes *T. schinzii*; the ‘hard’ spinifex group is dominant throughout the central and southern parts of arid Australia and includes *T. basedowii*. The distributions of these ‘soft’ and ‘hard’ spinifex species overlap around 22° S and it was in this transition zone that the present study took place.

Perhaps one of the most striking features of the vegetation is the presence of relatively large trees (*Corymbia chippendalei*) high on the slopes of the sandy dune ridges while absent elsewhere. Many of these bloodwood eucalypts display trunk diameters at breast height in excess of 1 m and are likely more than 200 years old. The fact that these trees have remained on the tops of the dunes for this period of time supports the statement that the dunes are stable and stationary. Sand movement on the dunes is largely restricted to periods following fire once groundcover has been combusted.

Fires in the region are usually the result of lightning strikes during the summer months prior to the onset of monsoonal rains. Given the areas’ remoteness and lack of infrastructure or property, fires may burn for several weeks without human intervention and cover tens of thousands of hectares. Prior to European settlement the fire regime

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was influenced greatly by the burning practices of Aboriginal peoples who created a fine-grain mosaic of frequently burnt small patches (Burrows et al. 1991). A decline in such traditional practices over the past two hundred years has led to a fire regime now dominated by natural ignition processes, primarily lightning, and less frequent but larger wildfires (Burrows et al. 1991). Fire scars typically run south-east with the prevailing north-westerly winds, but variable wind patterns lead to fire paths in all directions. Fires often cross from one dune/interdune system to the next without disruption, although open sections on the tops of the dunes can restrict fires from crossing over if winds are in line with the dune ridges. Vegetation cover on dune slopes and interdunes is similar and both landscape elements are equally exposed to fire.

The study sites where this research was conducted are all within a 10 km radius of Nifty Copper Operation (NCO) located in the south-western part of the Great Sandy Desert. The mine was started in 1993 as an open-pit operation predominantly extracting oxidised copper ores (malachite -  $\text{Cu}_2\text{CO}_3(\text{OH})_2$ , azurite -  $\text{Cu}_3(\text{CO}_3)_2(\text{OH})_2$ ), but since 2004 has developed underground tunnel mining for unoxidised sulfide ore (chalcopyrite -  $\text{CuFeS}_2$ ). These ores are associated with shales and silicified dolomitic rock known as the Nifty Carbonate Member, part of the neo-Proterozoic Broadhurst Formation. Rocks are removed by explosive blasting and excavation, and then trucked out of the pit to either the processing facility if the copper concentration is of an economically viable grade, or to the waste-rock dump (WRD) if it is not. Oxide ores are processed on-site by leaching with sulfuric acid, solvent extraction and electro-winning to produce raw copper plates; sulfide ores are roasted with sulfuric acid and the copper concentrate is removed from site for metal extraction elsewhere. The tailings dam for processed sulfide sludge covers approximately 85 ha, the heap-leach pads for oxide treatment occupy about 95 ha, and the WRD covers around 170 ha. All require rehabilitation at mine closure, although the WRD was focus for this investigation. It is an elevated landform 30 m high with sloping sides ( $\sim 18^\circ$ ), and the majority of it the area on top has been levelled flat with heavy machinery.

The WRD contains inert overburden material, low-grade oxide and chalcopyrite rock. Some of the pyritic rocks react with water and oxygen to form sulfuric acid, which has the potential to leach Cu and contaminating metals such as lead (Pb), cadmium (Cd) and arsenic (As) into solution. Elsewhere throughout the world, poor environmental practices by mining operations have resulted in the escape of such toxic leachates into

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the environment, a process termed ‘acid mine drainage’, and caused the pollution of rivers, lakes and groundwater sources (Lottermoser 1999; Achterberg *et al.* 2003; Johnson and Hallberg 2005). At Nifty copper operation, potentially acid-forming pyritic rocks are encapsulated beneath a clay layer (> 3 m) and native soil cover (~0.2 m) at the surface to act as a growth medium for plants. In theory, water run-off and evapotranspiration by plants and soil should prevent the ingress of moisture into encapsulated pyrite rock, assuming the landform structure is not compromised by erosion and that plant cover is sufficient to utilise all water available and prevent deep drainage. Preliminary observations found that the WRD displayed severe erosion on rehabilitated and non-rehabilitated areas. Large gullies, some over 10 m wide, 4 m deep and running the entire length of the slope, occurred where rain had pooled on the relatively flat-top section and overflowed, washing away the slope beneath. In other places on the flat-top section where pooled water had not breached the edge, vertical tunnel erosion was also of major concern as preferential flow paths could facilitate direct channelling of water into encapsulated pyrite bodies and cause acid mine drainage. In addition to these large-scale, flat-top catchment erosion issues, relatively smaller-scale slope erosion (sheet and rill) was also occurring as a result of localised rainfall impact directly on the slopes.

Only one section of the waste-rock dump approximately 500 m wide and 90 m long had been rehabilitated at the time this investigation took place. This rehabilitation site was located on the southern slopes (18°) of the waste-rock dump. Topsoil had been applied in 1995, and seedling emergence from this soil seed-bank had been successful and uniform across the area (pers. comm. Phil Davidson- NCO Environmental Manager). High mortality rates occurred in the first years after establishment and many dead stems were evident throughout the rehabilitation site when it was first visited in 2001. Plant cover at the rehabilitation site was low compared with the natural vegetation, and not meeting standards by environmental managers and government regulators (pers. comm. Phil Davidson- NCO Environmental Manager).

#### *Challenges and requirements of mine-site rehabilitation*

The rehabilitation of heavily disturbed lands in arid and semiarid regions is often challenging due to environmental extremes, particularly in relation to water availability. Successful revegetation in these environments often depends on the vagaries of precipitation and the overriding effect this has on propagule establishment. Indeed,

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emerging and juvenile plants are typically more vulnerable to biotic and abiotic stressors than mature plants (Orcutt and Nilsen 2000). Despite the adversities, particularly in the early stages of plant establishment, restoration of key ecological values can be attained if favourable conditions for plant growth are created at the outset (Aronson *et al.* 1993).

The ultimate goal of ecological restoration is to reinstate natural processes, biodiversity and ecosystem functioning similar to that of the original, native ecosystem prior to disturbance. However, limited resources and understanding of complex interactions within natural ecosystems mean the effective re-establishment of native communities is rarely achieved, particularly when soils are very degraded and/or different from the original site (Aronson *et al.* 1993). An alternative aim then, is to best repair the impacts brought about by human disturbance, establish suitable conditions for plant growth, and ultimately develop a safe, stable, non-polluting and self-sustaining ecosystem (Environmental Protection Authority 1995).

Legislation in Australia demands that environmental rehabilitation is carried out by mining companies and progress monitored by government regulatory bodies both during operation and for many years after. These regulatory bodies also determine and withhold environmental bond monies that are supposed to reflect the costs of earthworks and rehabilitation should the mining company collapse. They are also legislated to penalise environmentally negligent or non-compliant companies with substantial fines or withdrawal of operating permits. If appropriate measures are taken to restore ecological integrity, bond monies may be relinquished in portions based on the success of the rehabilitation in the years following mine closure. For this reason, it is in the best interests of companies, the government and all other stakeholders to achieve best-possible environmental outcomes. Fundamental to this goal is the necessity to define the progress of rehabilitation. This requires appropriate monitoring of key criteria such as erosion, physical and chemical properties of soils and water in and around the mine as well as indicators for ecosystem function and biological health such as biodiversity, soil micro-organism activity, vegetation cover, and plant health (Jasper *et al.* 1998; Lubke and Avis 1998). An important part of this process involves understanding the local natural vegetation and its interaction with environmental conditions.

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### *Scope of thesis*

This thesis presents new information on the ecophysiology of native plants in an Australian desert environment. Water and nutrient relations are defined for dominant woody and non-woody plants in their natural habitat and in an artificially created habitat on a mine rehabilitation site. Comparisons of these parameters, and others relating to soil physical and chemical properties, were made to gain an understanding of the reasons behind poor plant cover on the mine rehabilitation. The following chapters begin by defining edaphic conditions, plant water relations, and mineral nutrient status for closely related species on dunes and interdunes in the natural vegetation. The key objectives were to define plant functioning and adaptations at dune and interdune sites and explain why the largest trees existed only in highly elevated positions in the landscape (Chapter 2), and why there are two distinct plant communities, highlighted by two different species of *Triodia* grasses, on dunes and interdunes (Chapter 3). With an understanding of the ecophysiology of plants in their natural habitat, conditions on the mine-rehabilitation site are then investigated with the aim to determine how plants were affected by shallow soil depths and waste-rock material (Chapter 4). The impacts of altered edaphic conditions on the rehabilitation site are further assessed in terms of the effects on water uptake patterns following a wetting pulse for one particular species, *Acacia ancistrocarpa* (Chapter 5). The thesis concludes with a general discussion of the findings and the implications for mine-site rehabilitation in the Australian arid zone. Suggestions are made to improve conditions for plant survival, generate higher projected cover and species richness. It is anticipated that the outcomes from this research will assist in improving rehabilitation design and lead to the development of vegetated, stable, non-polluting landforms at this and other mine sites throughout arid Australia and arid regions worldwide.



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## Chapter 2

### Water relations and mineral nutrition of closely related woody plant species on desert dunes and interdunes

#### Abstract

Vegetation on dunes and interdunes in hot, sub-tropical deserts is profoundly influenced by the temporal and spatial variation in availability of water and nutrients in the landscape. I hypothesised that water is more available to plants occurring on dunes habitat but that nutrients are in greater concentrations in the interdunes. Over the course of two years, I examined water relations and photosynthesis of six dominant woody species throughout each season, in addition to foliar  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  and nutrient composition. In general, stomatal conductance ( $g_s$ ) was greater and leaf water potential ( $\Psi$ ) less negative for dune species than for closely related species in the interdunes. The largest tree species in the landscape, *Corymbia chippendalei* ((D.J.Carr & S.G.M.Carr) K.D.Hill & L.A.S.Johnson), occurred only in the dune habitat, and maintained moderate  $g_s$  values year round, ranging between  $240 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$  in the wet season to  $160 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$  in the middle of the dry season. It also displayed a relatively stable  $\Psi$ , between  $-0.3$  and  $-0.5$  MPa at predawn, and between  $-1.3$  and  $-1.6$  MPa at midday throughout the year, unlike the closely related species in the interdunes, *Eucalyptus victrix* (L.A.S.Johnson & K.D.Hill), which always displayed significantly lower  $\Psi$  values ( $0.2$  to  $1.1$  MPa more negative). The two *Grevillea* species displayed  $\Psi$  values within a similar range as *C. chippendalei*, whilst the *Acacia* species exhibited consistently more negative values, especially late in the dry season. Considerable reductions in  $g_s$  occurred at this time for all species, except *C. chippendalei*. Rates of photosynthesis ( $A$ ) followed the trends in  $g_s$ , yet  $\delta^{13}\text{C}$  values varied little between related species in the dune and interdune habitats. Mineral nutrient concentrations in soil and foliage tended to be greater in the interdunes. Average N:P ratio in foliage was 28:1, indicating P was more limiting than N. Soil depth and texture, in conjunction with their effects on water availability and root growth, were considered to be the most influential factors affecting plant distribution in the Great Sandy Desert. It is concluded that dunes hold relatively more water than adjacent interdunes, sustaining more

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favourable water status in deep-rooted species from this habitat, further into the dry season. Conversely, species in the interdunes must be more desiccation tolerant and develop root systems with greater ability to penetrate conglomerated lateritic gravel layers in order to access water where and when it is available.

## **Introduction**

In desert environments, water is the principal factor limiting productivity, plant recruitment, microbial activity and nutrient cycling (Noy-Meir 1973; Hadley and Szarek 1981; Ehleringer and Cooper 1988; Smith *et al.* 1995; Reynolds *et al.* 1999). Almost one third of Earth's land surface is classified as desert, the hottest and driest of these occurring mostly between 5° and 30° N and S of the equator (Hadley and Szarek 1981; Polis 1991). Of these subtropical arid regions, about 20% are covered by aeolian sand (Seely 1991; Thomas 1992). With little rainfall, wind is the primary vector that shapes these landscapes causing erosion in some areas and deposition in others (Pye and Tsoar 1990).

Dunes are formed where sand accumulates, whilst interdunes, which provide the material for their formation, become eroded and deflated (Danin 1996). Edaphic properties of sand dunes contrast sharply with interdunes, resulting in different moisture and nutrient dynamics and discrete plant communities on each [see Pavlik 1980 (Eureka Dunes California), Buckley 1981 (Simpson Desert Australia), Walter and Box 1983 (Karakum Desert Central Asia), Moreno-Casasola 1988 (coastal dunes in Mexico), Yeaton 1988 (Namib Desert, Namibia), Danin 1996 (Haluza Dunes of the Negev Desert, Israel), Dech and Maun 2005 (Lake Huron sand dunes, Canada)]. Soil depth and texture are considered the most important edaphic properties that influence the moisture regime in arid environments with episodic rainfall (Noy-Meir 1973; Pavlik 1980).

In sandy soils, the relatively coarse particle size and larger pore spaces permit rapid hydraulic conductivity and infiltration to deeper layers (Chadwick and Dalke 1965; Sperry and Hacke 2002). Furthermore, weak capillary forces limit upward transport of moisture; hence evaporative extraction is greatly reduced once the wetting zone descends below 50 mm of the surface (Alizai and Hubert 1970; Pavlik 1980). In heavier-textured soils, the wetting front is arrested in shallow surface layers, and because of greater capillary rise, proportionally more water is lost to evaporation when hot dry conditions return (Seely and Louw 1980; Orshan 1986). The efficient capture of

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water by sandy soils in arid environments with episodic rainfall is known as the ‘inverse texture effect’ and is most pronounced when short pulses of rainfall are followed by hot, dry conditions (Noy-Meir 1973). However, the inherently low water-holding capacity of sandy soils means a large volume (depth) is required to store this resource. The deep sands of the dunes serve this purpose; thus relatively more precipitation may be stored within them than in the shallower interdunes (Prill 1968; Noy-Meir 1973).

Differences in resource availability and their impact upon water and nutrient relations of plants on desert dunes and interdunes has received little attention in the literature and is poorly understood (Rosenthal *et al.* 2005). Contrasting patterns have been reported, with some authors finding more favourable plant water status on dune ridges (Pavlik 1980; Rosenthal *et al.* 2005), whilst others identified no significant differences (Forseth *et al.* 1984), or even improved growth and water status in plants occurring off the dune in lower parts of the desert landscape (Gries 2003; Niu *et al.* 2005). However, each of the aforementioned investigations were unique in terms of their climatic, physical and hydrological settings, as their study sites displayed varying degrees of aridity (35-312 mm annual rainfall), extreme differences in temperature (-24°C to +35°C), precipitation type and seasonality (snow and/or rain, winter or summer), a range of soil textures (fine silt to coarse sand) and varying access to a water table (from near surface to none at all). The current investigation in the Great Sandy Desert, Australia, adds to this body of knowledge with data from an environment that differs again from those previously studied and benefits from being able to compare closely related species in dune and interdune habitats.

The Great Sandy Desert accounts for almost 10% of the 5 million square kilometres that makes up Australia’s arid and semi-arid zone (Australian Bureau of Statistics, 2006). Sand dunes throughout the desert were aligned by the dominant wind patterns of the last glacial maximum about 20,000 years ago (Hesse *et al.* 2004). Underlying the desert surface is the Canning sedimentary basin, which exhibits a fresh to saline regional water table and numerous confined and unconfined aquifers in fractured rock provinces and palaeodrainage deposits (Halse *et al.* 1990, Waters and Rivers Commission 2003). Like most of Australia’s interior, the Great Sandy Desert receives on average, relatively high annual rainfall (250-350 mm) compared with many other sub-tropical deserts (Australian Bureau of Statistics 2006) (Appendix I, Figure I.1). However, the apparent sufficiency of water is more than offset by extreme evaporation rates, over 4000 mm per

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annum in places, and summer temperatures approaching 50° C (Bureau of Meteorology 2006) (Appendix I, Figure I.2).

Lack of water is also coupled with poor nutrient availability throughout the sand desert regions of Australia as soils have been strongly leached since their origin during the Quaternary (Mabbutt 1962; Winkworth 1967). These soils are especially low in total phosphorus and nitrogen (Islam *et al.* 2000, Bennett and Adams 2001). The distribution of these and other nutrients is typically heterogenous due to the development of 'islands of fertility' and tight nutrient cycling beneath plant crowns (Tongway and Ludwig 1994). Nutrient cycling and decomposition of leaf litter is largely restricted to periods after rain when microbial activity (Skopp *et al.* 1990; Ford *et al.* 2007) and cryptogamic crust formation is possible (Austin *et al.* 2004). Termites also play a major role in nutrient cycling, and combined with crust organisms (e.g. cyanobacteria) are likely major contributors of N to this system (Tongway *et al.* 1989; Metting 1991). However, termite nests and subterranean galleries were common in the interdunes but non-existent in the dunes. Similarly, cryptogamic soil crusts typically formed after rains in large patches in the interdunes but were very infrequent and always much smaller in the dune habitat. I expected, therefore, that the availability of nitrogen and other nutrients would be greater in the interdunes than the dunes.

Throughout the Great Sandy Desert, dunes and interdunes are characterised by distinctly different plant communities. The largest trees in the landscape, *Corymbia chippendalei* (Myrtaceae), are only ever found on the upper slopes of the sand dunes. I aimed to establish an understanding of why a different suite of plant species occur in each of the two habitats, and explain how it was possible for the largest trees to exist in an elevated position beyond reach of the water table. Aspects of water and nutrient availability were considered as two alternative reasons influencing species distribution in this environment. My primary hypothesis states that water is more available to plant species on the sandy dune ridges than on the shallower interdunal flats in this system. It is therefore expected that water stored within the dunes remains accessible for a longer period, and thus delays the effects of plant water stress further into the dry season. A second hypothesis proposes that plants growing in the interdunes, would exhibit foliage with higher concentrations of nutrients than closely related species in the dune habitat, because of the increased likelihood of organic matter build-up lower in the landscape, greater nutrient cycling and inputs possibly from termites and cryptogamic soil crusts.

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To test these hypotheses, I carried out comparative measurements on plant water relations and nutrition of three congeneric or closely related dune-interdune species pairs, representing three different functional groups.

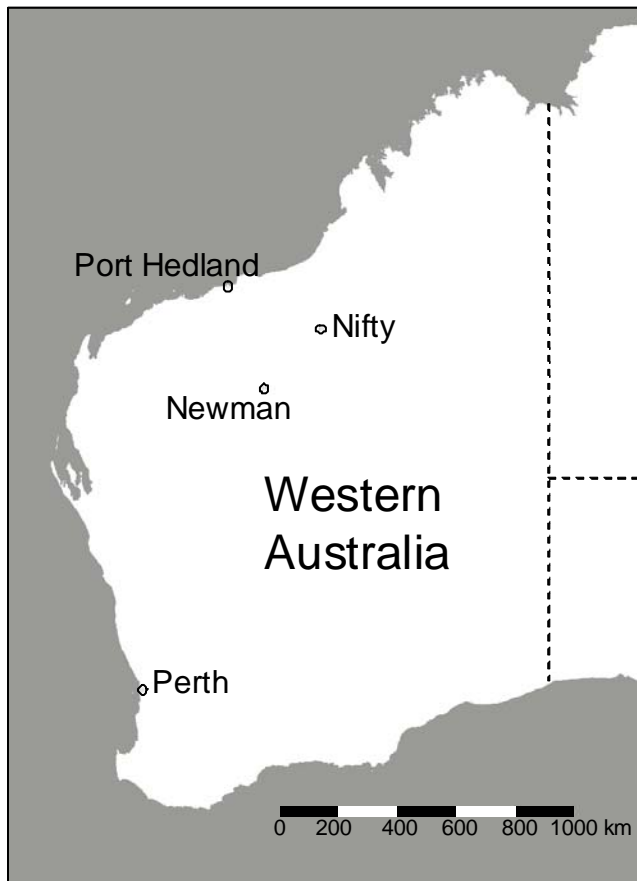
## Materials and Methods

### *Study site and species*

The study area was located 350 km inland of Port Hedland near Nifty Copper Operation (21°40'S, 121° 35'E) in the Great Sandy Desert of northern Western Australia (See Map, Figure 2.1). The landscape as a whole is remarkably flat with an average elevation above sea level of about 300 m (Rockwater Hydrology Report 2003). Without any surface drainage channels in the area, rainwater typically soaks in directly where it falls; even on the dune slopes. Long, linear sand dunes and braided dunes characterise the landscape (Figure 2.2a), ranging in height from 3 to 37 m with an average height of 12 m and a base of 100 m (Beard 1969). These dunes generally are aligned west-north-west to east-south-east (Beard 1969). The sand grains of the dune are slightly coarser than, but generally similar to, the dune sands of other desert areas of the world, but have an iron oxide patina giving them a rusty red colour (Brown 1959). Interdunes range in width from less than 50 m for braided dunes to over 1500 m for linear dunes. Below the surface of the interdunes, a lateritic gravel layer generally begins at 50 cm, eventually forming a conglomerated ironstone hardpan by 2-3 m. This hardpan underlies the landscape as a flat pavement and continues beneath the dunes without conforming to their shape. A white kaolinite/muscovite clay horizon is found typically between 8-20 m below this hardpan layer and supports a perched water table (Nifty Copper Mine Drill Log 2003). Average depth to water beneath most interdunes throughout the area is around 10-12 m, but in some low-lying depressions maybe within 5 m of the surface (Rockwater Hydrology Report 2003; Nifty Copper Mine Drill Log 2003).

Adjacent dunes and interdunes were selected as study sites where flat sections across the interdune exceeded 300 m and remained unburnt for at least 10 years. Vegetation was very similar on all dunes throughout the area, with the most prominent species being the eucalypt, *C. chippendalei* (Myrtaceae) (Figure 2.2a). These trees, some of which exhibited basal stem diameters of up to 40 cm, were only ever found on the uppermost sections of the sandy ridges. Other common dune species included *Grevillea stenobotrya* (Proteaceae), *Acacia jensenii* (Fabaceae) and *Triodia schinzii* (Poaceae)

(Figure 2.2a-b). Most interdunes were characterised by scattered shrubs such as *Grevillea wickhamii* (Proteaceae), *Acacia ancistrocarpa* (Fabaceae) and cover was dominated by *Triodia basedowii* (Figure 2.2c). In lower-lying areas of some interdunal flats, small-statured *Eucalyptus victrix* and *Melaleuca* species (Myrtaceae) co-occurred (Figure 2.2d) on gravelly patches with a brackish water table often within 5 m of the surface. Information on water and nutrient relations are presented here for woody species of three functional types including (1) the non-leguminous, mycorrhizal, relatively large eucalypt trees (*C. chippendalei* and *E. victrix*), (2) the smaller, non-mycorrhizal, cluster-bearing proteaceous tree-shrubs (*G. stenobotrya* and *G. wickhamii*), and (3) the leguminous, mycorrhizal, multi-stemmed shrubs (*A. jensenii* and *A. ancistrocarpa*). The two spinifex grass species, *T. schinzii* and *T. basedowii*, are discussed in Chapter 3.



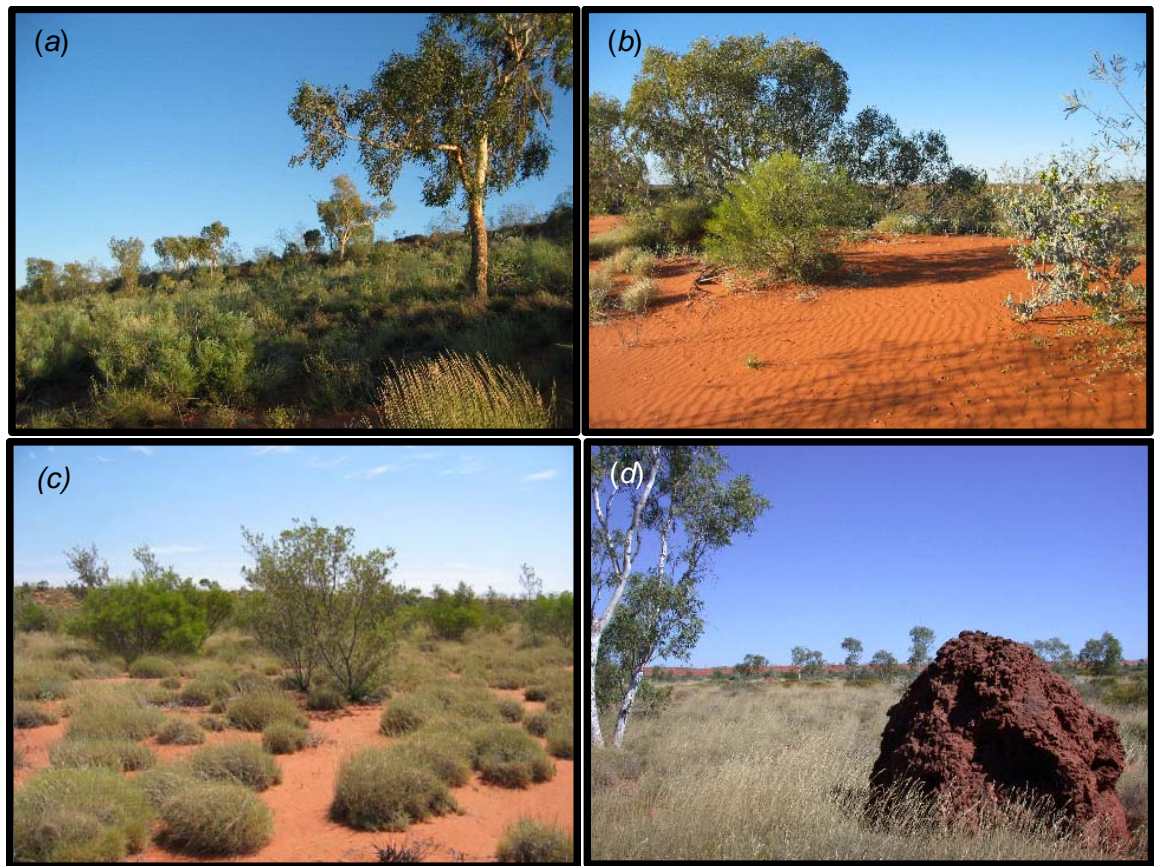
**Figure 2.1** The location of the study site at Nifty Copper Operation in the Great Sandy Desert, north Western Australia.

#### *Soil physical and chemical properties*

Soil samples were taken in the middle of the dry season (July 2002) from nine locations, three from the dune crest, three from the slope and three from the interdunal flats. At each location, about 2 kg of dry soil was collected from 0-10 cm depth in open ground and placed inside a paper-lined calico bag.

Soil pH was measured on a 1:5 extract of soil and 0.01 M CaCl<sub>2</sub> in deionised water following the method of Rayment and Higginson (1992). Electrical conductivity (EC) was measured at 25°C on a





**Figure 2.2** Photographs of the study area depicting (a) vegetation of the dune slope including the largest tree species in the landscape, *Corymbia chippendalei* (right and top), (b) bare ground on the dune crest with *Grevillea stenobotrya* (centre left), (c) typical interdune dominated by *Triodia basedowii* associated with *Grevillea wickhamii* (centre) and *Acacia ancistrocarpa* (left), (d) low-lying interdune characterised by *Eucalyptus victrix* (left and background), scattered *Melaleuca* shrubs, *Triodia basedowii* and termite mounds.

1:5 extract of soil and deionised water (Rayment and Higginson 1992). Particle sizing was carried out on soil dispersed with a solution of Calgon (hexasodium metaphosphate) and sodium hydroxide. Silt (0.002 - 0.020 mm) and clay (<0.002 mm) were measured by density after standard settling time based on the plummet procedure by Loveday (1974). Another separate subsample of soil was ground to less than 0.15 mm and the following analyses conducted. Organic carbon was determined by dichromate oxidation in the presence of sulfuric acid followed by colourimetry to determine the amount of  $\text{Cr}^{3+}$  produced according to the Rayment and Higginson (1992) method. Total soil nitrogen was measured after Kjeldahl digestion using a copper sulfate-potassium sulfate catalyst, then as ammonium-N measured by automated colourimetry by the nitroprusside dichloro-*S*-triazine modification (Blakemore *et al.* 1987) of the Berthelot indophenol reaction reviewed by Searle (1984). Total phosphorus was also measured by colourimetry on the Kjeldahl digest, following the Murphy and Riley (1962) molybdenum blue procedure. Extractable P, K, Na, Ca, S, Mg, B, Cu, Fe,

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Mn, Zn and Co were determined by inductively coupled plasma atomic emission spectroscopy (ICP-AES Fisons ARL Instrument Model 3580B, Beverly, MA) after extracting soils using a Mehlich 3 solution (2.5 g + 25 mL) for 5 minutes.

### *Climate*

Long-term average annual rainfall for this part of the Great Sandy Desert is around 330 mm (Bureau of Meteorology 2006). Most of this precipitation is high intensity rainfall brought in by occasional tropical thunderstorms and cyclones between January and March. Outside this brief wet season, there may be little or no rain for months at a time. The timing and volume of rain events is very unpredictable, with some years receiving less than 120 mm (e.g., 1991) and others over 1000 mm (e.g., 2004). The year leading up to this investigation was one of the wettest on record (2000: 849 mm), and the first year of measurements (2001) was also extremely wet (2001: 523 mm) relative to the long term average (Bureau of Meteorology 2006 – Figure 2.3a). The second year of measurements was a time when rainfall was just below average (2002: 274 mm) (Bureau of Meteorology 2006 - Figure 2.3a). In all three years, rainfall in February was above average making it the wettest month, whilst August, September and October were almost completely dry. Evaporation (class A pan) averages around 4100 mm per year, and on a monthly basis, is three times average monthly rainfall in February and over 200 times in October (Bureau of Meteorology 2006 - Figure 2.3a). Mean monthly maximum vapour pressure deficit (VPD) follows a similar pattern: highest between October and January, with peaks exceeding 6 kPa, a trough during winter and a marked depression during the wettest summer month, February. Mean monthly minimum values did not decrease below 0.4 kPa, except in March 2000 as a result of heavy wet-season rains (Figure 2.3b). Average maximum temperatures were typically around 40°C in December and January, but only around 26°C in June and July (Figure 2.3c). Mean minima ranged between 25°C in summer to 10°C in winter, although extremes of 7°C above average maxima and below average minima were recorded throughout this time.

### *Weather data*

Daily temperature, relative humidity, rainfall and evaporation were recorded at Telfer Gold Mine, 67 km east of the study site. From 2003 to the present day, a fully automated, Campbell Scientific data-logging weather station has been in operation at Nifty Copper Mine and provided similar readings to that collected by the Bureau of Meteorology station at Telfer over the same period. For the purposes of this

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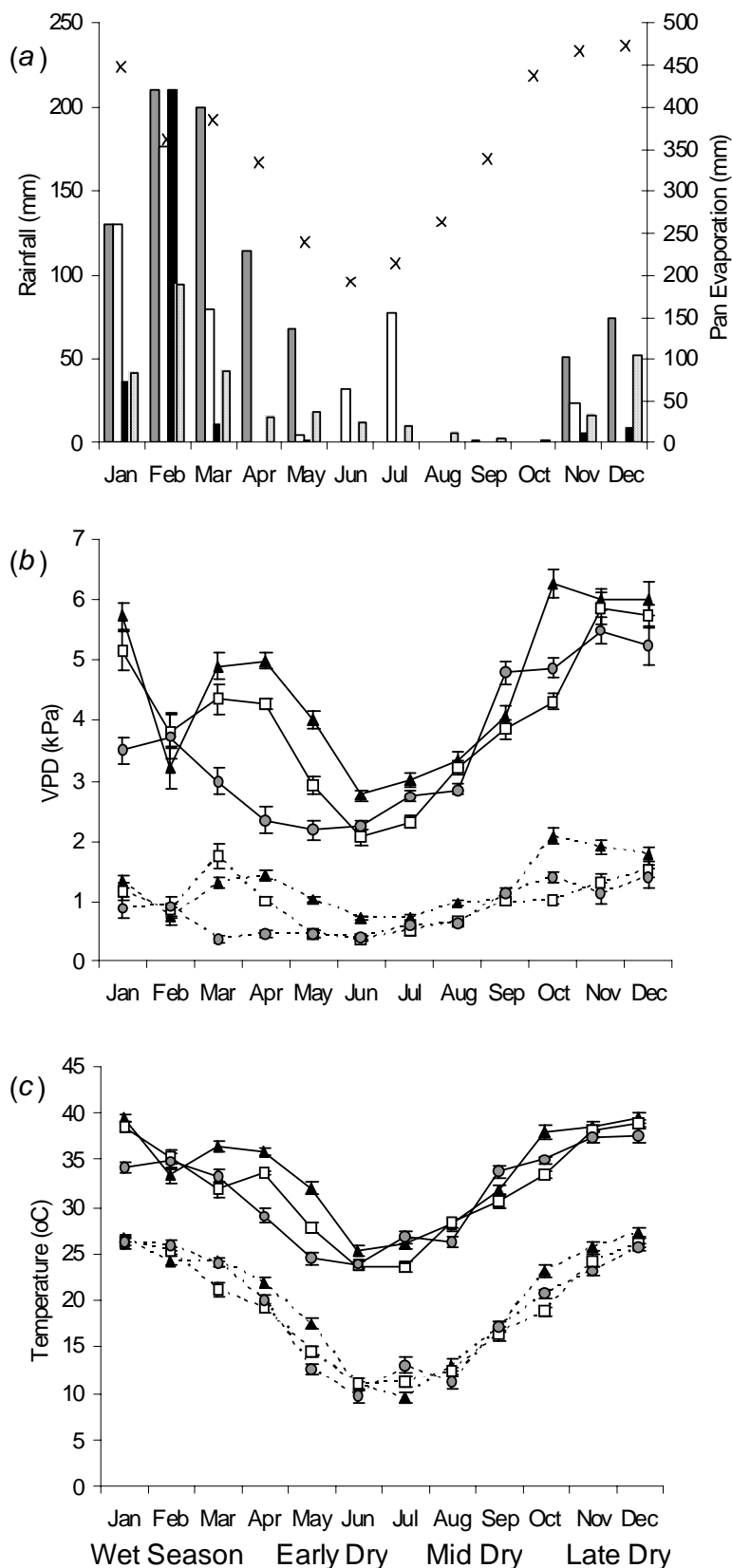
investigation, I am confident that weather data recorded at Telfer approximated those at Nifty during the current study (2001-2002). Similar weather at the two sites can be attributed to the fact that both sites are the same elevation above sea level (300 m ASL) and the landscape in between is, overall, very flat with no prominent features other than sand dunes.

#### *Root morphology*

Excavations were carried out on at least nine individuals of each of the six woody species to identify root-distribution patterns. In the interdunes, excavations were made around individuals to a depth of 1-2 m by hand or, in dense gravelly areas, with a backhoe (Caterpillar 428B). On the dune, most digging was done manually to a depth of 1-2 m. Of the nine *C. chippendalei* trees, the root systems of six were exposed manually to a depth of 1.5 m; the other three were exposed to a depth of 8 m by a large excavator (Hitachi EX1800) to make way for mining activities.

#### *Water potential*

Leaf water potential was measured using a Scholander-type pressure chamber (PMS Instruments, Corvallis, Oregon, USA). Over the course of two consecutive years, eight sampling periods, each of ten days, were carried out so as to capture each season twice. The seasons were named according to time since summer rains; hence, the 'wet' season typically occurred from January to March, 'early' in the dry season is from April to June, 'middle' of the dry season is from July to September and 'late' in the dry season is from October to December. During the course of this study, wet-season rains began in January of each year. Leaf water potential measurements were taken at predawn (03.00-05.00) and midday (12.00-14.00) on randomly selected individuals from different locations within each plant community. Three twig/shoot sections, approximately 10 cm long displaying two to nine leaves (depending on species) were cut from three to five individuals. Upon being cut, leaves were sealed in zip-lock plastic bags with only the petiole protruding and placed inside the pressure bomb to begin measurements within one minute of being excised from the plant.



**Figure 2.3** Climatic information including (a) monthly rainfall for 2000 (grey bars), 2001 (open bars), 2002 (black bars), and long-term mean monthly rainfall (dotted bars) for Telfer, 67 km from the study site. Crosses (x) indicate long-term mean monthly pan evaporation at Telfer. (b) Mean monthly maximum (solid line) and minimum (dashed line) vapour pressure deficit (kPa) for 2000 (o), 2001 (□) and 2002 (▲). (c) Mean monthly maximum (solid line) and minimum (dashed line) temperatures (°C) for 2000 (o), 2001 (□) and 2002 (▲). Original data courtesy of the Bureau of Meteorology.

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### *Gas exchange*

Gas exchange was measured on intact leaves in the field using a Li-Cor 6400 portable infra-red gas analyser (LI-COR Inc. Lincoln, NE, USA). Measurements of  $A$  and  $g_s$  started in January 2001 and finished in January 2003, were spaced roughly three months apart and always carried out between 10.00 and 14.00 hours on predominantly sunny days. An artificial light source of red and blue LEDs was used to administer a photosynthetic photon flux density (PPFD) of  $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$  at all times and in all seasons. Light-saturation curves determined prior to this investigation identified  $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$  was an appropriate PPFD ensuring optimal illumination for these species (unpublished data). Leaf chamber carbon dioxide concentration was between 360 and  $375 \mu\text{mol CO}_2 \text{mol}^{-1}$  with reference gas maintained at  $380 \mu\text{mol CO}_2 \text{mol}^{-1}$ . Vapour pressure and temperature in the chamber were maintained as close as possible to those of ambient air. Leaf temperatures were calculated using an energy balance equation (Licor 6400 Manual 2000).

Measurements were done on the youngest fully expanded mature leaves. Only those that were healthy, without notable insect damage and located on the north side of the crown were selected for measurement. Species assessed for leaf gas exchange included *C. chippendalei*, *E. victrix* (both Myrtaceae), *A. jensenii*, *A. ancistrocarpa* (Fabaceae), *G. stenobotrya* and *G. wickhamii* (Proteaceae). At least three measurements were taken on leaves of each plant and between three and seven individuals were assessed for every species at all sampling times. Measured leaf sections were sealed in zip-lock plastic bags, chilled and taken to the laboratory where their leaf areas were measured on a back-lit flatbed scanner at a scanning resolution of  $0.2 \mu\text{m}$  (WinRhizo V3.0.3 1995, Regent Instruments Quebec, Canada). Once areas were determined, leaves were oven dried at  $70^\circ \text{C}$  for one week then dry weights recorded.

### *Isotope composition*

Healthy leaves, free from insect attack, from at least five individuals, were collected for carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotope composition from each of the six species during the dry season (July) 2002. From each individual, 20-50 leaves were cut from three branches on the northern side of the crown, air dried in the field, oven dried at  $70^\circ\text{C}$  in the laboratory, then ground using a ball mill. A special collection of *G. stenobotrya* leaves were also obtained from individuals at three locations in the interdunes for direct comparison with plants of this species growing in its preferred

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habitat on the dunes.  $\delta^{13}\text{C}$  analysis was performed using continuous flow mass spectrometry (Roboprep + Tracermass Ion Ratio Mass Spectrometer - Europa Scientific, Crewe, UK).  $^{13}\text{C}:^{12}\text{C}$  ratios of the  $\text{CO}_2$  produced by combustion at  $1000^\circ\text{C}$  in an oxygen atmosphere were then compared against those obtained by combustion of a cornflour standard (ANCA 53), calibrated in turn against the international standard NBS-22.  $^{15}\text{N}:^{14}\text{N}$  ratios were compared against a radish standard (ANCA 54) calibrated against known international standards (IAEA-N1, IAEA-N2, IAEA NO3). Analytical precision based on multiple replicate analyses for  $\delta^{13}\text{C} = \pm 0.2\text{‰}$  relative to the PeeDee Belemnite standard; for  $\delta^{15}\text{N} = \pm 0.3\text{‰}$  relative to air. Carbon isotope composition was used to estimate the ratio between leaf internal and ambient  $\text{CO}_2$  concentration when that carbon was being fixed, using the equations for  $\text{C}_3$  plants outlined in Farquhar *et al.* (1982).

#### *Foliage mineral composition*

The same leaf material collected for isotope composition was sub-sampled for nutrient analysis. Nitrogen concentration was determined colourimetrically (indophenol blue method) using an Autoanalyser system after digestion with sulfuric acid and hydrogen peroxide (Yuen and Pollard 1954). Another subsample of leaf material was digested with a mixture of nitric and perchloric acids (McQuaker *et al.* 1979), and then analysed by ICP-AES (Varian Vista axial spectrometer, Palo Alto, CA, USA) to determine concentrations of phosphorus, potassium, calcium, magnesium, sulfur, boron, copper, iron, manganese and zinc.

#### *Statistics*

Data were analysed using JPM V4 (SAS Institute Inc). General linear models (GLM) were used to compare measurement means of related species between habitats; measurements analysed in this way included leaf water potential, stomatal conductance, photosynthesis,  $C_i/C_a$ ,  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  and mineral nutrient concentrations. Homogeneity of variances were assessed using Cochran's test and data transformed (square root or log) if group variances were heterogenous or not normally distributed. Pairwise comparisons were carried out using Tukey's *post-hoc* test when the GLM indicated significant treatment effects (Quinn and Keough 2002). Results are reported as significant where  $p < 0.05$ .

## Results

### *Soil characteristics*

Surface soils (0 to 0.1 m) on dunes and interdunes were extremely sandy, composed of between 1 and 5.5% silt and clay, and displayed very low water holding capacity (8 to 11%) (Table 2.1). Soil depth varied greatly between habitats; dunes were on average 12 m deep, whilst interdunes were typically less than 2 m deep. Soils were slightly acidic (pH 5.8 to 6) and had very low electrical conductivity (Table 2.1). Organic matter and macro- and micro-nutrients were typically in higher concentrations in interdune soils, by sometimes as much as ten-fold (Table 2.1).

**Table 2.1** Physical and chemical soil properties of dune crest, dune slope and interdune.

Attribute	Dune Crest	Dune Slope	Interdune
Depth to gravel layer or laterite from soil surface	10-15m	2-9m	0.5-2m
Soil pH (0-10 cm)	5.8 ± 0.12	6.0 ± 0.12	5.9 ± 0.07
Soil EC 1:5 w/v (0-10 cm) mS/m	1 ± 0	1 ± 0	1 ± 0
Sand Content (0-10 cm)	99.0%	99.0%	94.5%
Silt Content (0-10 cm)	0.5%	0.5%	0.5%
Clay Content (0-10 cm)	0.5%	0.5%	5.0%
Textural class	Sand	Sand	Sand
Bulk Density (g.cm <sup>-3</sup> )	1.58	1.57	1.53
Water Holding Capacity (v/v)	9%	8%	11%
Cation Exchange Capacity (NH <sub>4</sub> Cl m.eq%)	1%	1%	1%
Organic Carbon (0-10 cm) mg.g <sup>-1</sup>	0.4 ± 0.03	0.4 ± 0.03	1.1 ± 0.06
Soil (0-10 cm) N - µg.g <sup>-1</sup>	50 ± 5	50 ± 5	90 ± 5
Soil (0-10 cm) P - µg.g <sup>-1</sup>	1 ± 0.01	1 ± 0.01	2 ± 0.01
Soil (0-10 cm) K - µg.g <sup>-1</sup>	6.0 ± 0.3	5.7 ± 0.3	14.0 ± 0.6
Soil (0-10 cm) Na - µg.g <sup>-1</sup>	1.0 ± 0.1	1.3 ± 0.3	2.3 ± 0.9
Soil (0-10 cm) Ca - µg.g <sup>-1</sup>	10 ± 2.6	9.3 ± 1.5	41.7 ± 6.7
Soil (0-10 cm) S - µg.g <sup>-1</sup>	1.6 ± 0.3	1.3 ± 0.3	1.3 ± 0.3
Soil (0-10 cm) Mg - µg.g <sup>-1</sup>	3.0 ± 0.6	2.3 ± 0.3	11.7 ± 1.2
Soil (0-10 cm) B - µg.g <sup>-1</sup>	0.1 ± 0.01	0.13 ± 0.03	0.13 ± 0.03
Soil (0-10 cm) Cu - µg.g <sup>-1</sup>	0.1 ± 0.01	0.1 ± 0.01	0.3 ± 0.07
Soil (0-10 cm) Fe - µg.g <sup>-1</sup>	5.0 ± 0.3	5.7 ± 0.3	17.7 ± 0.9
Soil (0-10 cm) Mn - µg.g <sup>-1</sup>	2.3 ± 0.3	4.0 ± 1.0	39.7 ± 4.9
Soil (0-10 cm) Zn - µg.g <sup>-1</sup>	<0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0
Soil (0-10 cm) Co - µg.g <sup>-1</sup>	0.05 ± 0.001	0.05 ± 0.003	0.31 ± 0.05

### *Root morphology and excavations*

Excavations of nine *C. chippendalei* trees on the dune revealed that the trunk of this species often continued 1-2 m below ground before giving rise to the root crown. Near-surface lateral roots were never encountered on large individuals, but dozens of substantially sized roots (30-100 mm diameter) were found heading diagonally down from this deep common root junction giving a tentacular appearance. Many roots were still greater than 10 mm in diameter, 8 m from their point of origin at the root crown. In the closely related interdune species, *E. victrix* displayed a spreading, heavily lateralised root system. At the base of these trees, most major roots extended horizontally at first, but within 2 m often began to grow downwards, sometimes almost vertically. Such

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roots were assumed to be acting as tap roots. In addition, small secondary laterals and secondary sinker roots were also common for *E. victrix*. The lower-lying areas inhabited by *E. victrix* typically displayed an extremely dense gravel layer within 10 cm of the surface, which became heavily conglomerated and cemented by 50 cm depth, greatly impeding manual digging efforts. Large termite mounds over 1.5 m tall were common in this area (see Figure 2.2d) and subterranean galleries were occasionally encountered during the digging process.

Excavations of dune and interdune *Grevillea* species revealed that both species displayed dimorphic root systems, with a large number of laterals in the top 30 cm, and typically one main tap root. After substantial wet season rains in February 2002 (over 200 mm- Figure 2.3a), freshly formed proteoid roots were observed in the top 15 cm on lateral roots of both species. Small secondary sinker roots were occasionally found originating from major laterals of both *Grevillea* species. *A. ancistrocarpa*, which co-occurred in the interdunes with *G. wickhamii*, also displayed this strongly dimorphic rooting pattern. These interdunes displayed deeper soil than the *E. victrix* interdunes, with significant gravel accumulation starting below 50 cm depth, becoming conglomerated into a hardpan by 2 m. Termite galleries were far more abundant below ground in these interdunes compared with those observed in the *E. victrix* community. However, large above ground structures did not occur in these sandy interdunes; only small mounds, less than 20 cm tall, were occasionally found.

On the dune, *A. jensenii* showed a modified dimorphic root system with even greater development of near-surface lateral roots as rhizomes just below the surface of the loose sand. These shallow, laterally spreading rhizomes often gave rise to numerous (5-7) above-ground shoots or clones, the oldest of which developed their own tap roots. Once new clones were fully established, the rhizomes connecting them to the parent plant died off, leaving the parent free-standing as an individual. Termites were occasionally found in dead wood on the dune crest but below ground termite galleries were never encountered; only in a few places were galleries found below ground at the foot of the dune slopes where it meets with the flat interdune.

#### *Leaf water status and gas exchange*

Consistent with my prediction, seasonal average  $\Psi$  values were generally less negative for dune species than for those in the interdunes. In cases where there was a significant



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difference between habitats, the dune species showed less negative values in five out of six instances at predawn, and also at midday (Figure 1.4). The dune tree species, *C. chippendalei* displayed significantly higher predawn and midday  $\Psi$  values in all seasons than the related eucalypt in the interdunes, *E. victrix* (Tukey HSD,  $p < 0.05$ ).  $\Psi$  across seasons fluctuated considerably more in *E. victrix* (difference from wet to dry seasons of 0.7 MPa predawn and 1.1 MPa at midday) compared with *C. chippendalei*, which maintained relatively stable  $\Psi$  values throughout the year (difference of 0.2 MPa predawn and 0.4 MPa)(Figure 2.4). Such different patterns, particularly during dry season, contributed to a significant interaction term between habitat and season ( $p < 0.0001$ ).

Significant interaction effects between habitat and season were also detected for *Acacia* species at predawn ( $p < 0.0001$ ) and midday ( $p < 0.0001$ ). Nonetheless, there were no significant differences between habitats except late during the dry season when *A. jensenii* displayed significantly more negative predawn ( $\Psi_{pd}$ ) and midday ( $\Psi_{md}$ ) water potentials (Tukey HSD,  $p < 0.05$ ) than its congeneric species in the interdunes, *A. ancistrocarpa*. Significant interaction effects between habitat and season also dominated the general linear model for  $\Psi_{pd}$  ( $p < 0.0001$ ) and  $\Psi_{md}$  ( $p < 0.0001$ ) of *Grevillea* species. The only significant differences determined by Tukey's test showed the dune species, *G. stenobotrya* displayed higher predawn  $\Psi$  values early during the dry season, and higher midday  $\Psi$  values during the middle of the dry season, compared with its congeneric species in the interdune, *G. wickhamii*. Both *Grevillea* species displayed leaf water potentials in a similar range to those of the dune tree, *C. chippendalei*, with  $\Psi_{pd}$  values consistently less negative than -0.5 MPa and  $\Psi_{md}$  values of -1.9 MPa. *Acacia* species typically displayed more negative  $\Psi$  values, approaching -3.0 MPa for *A. jensenii* late in the dry season.

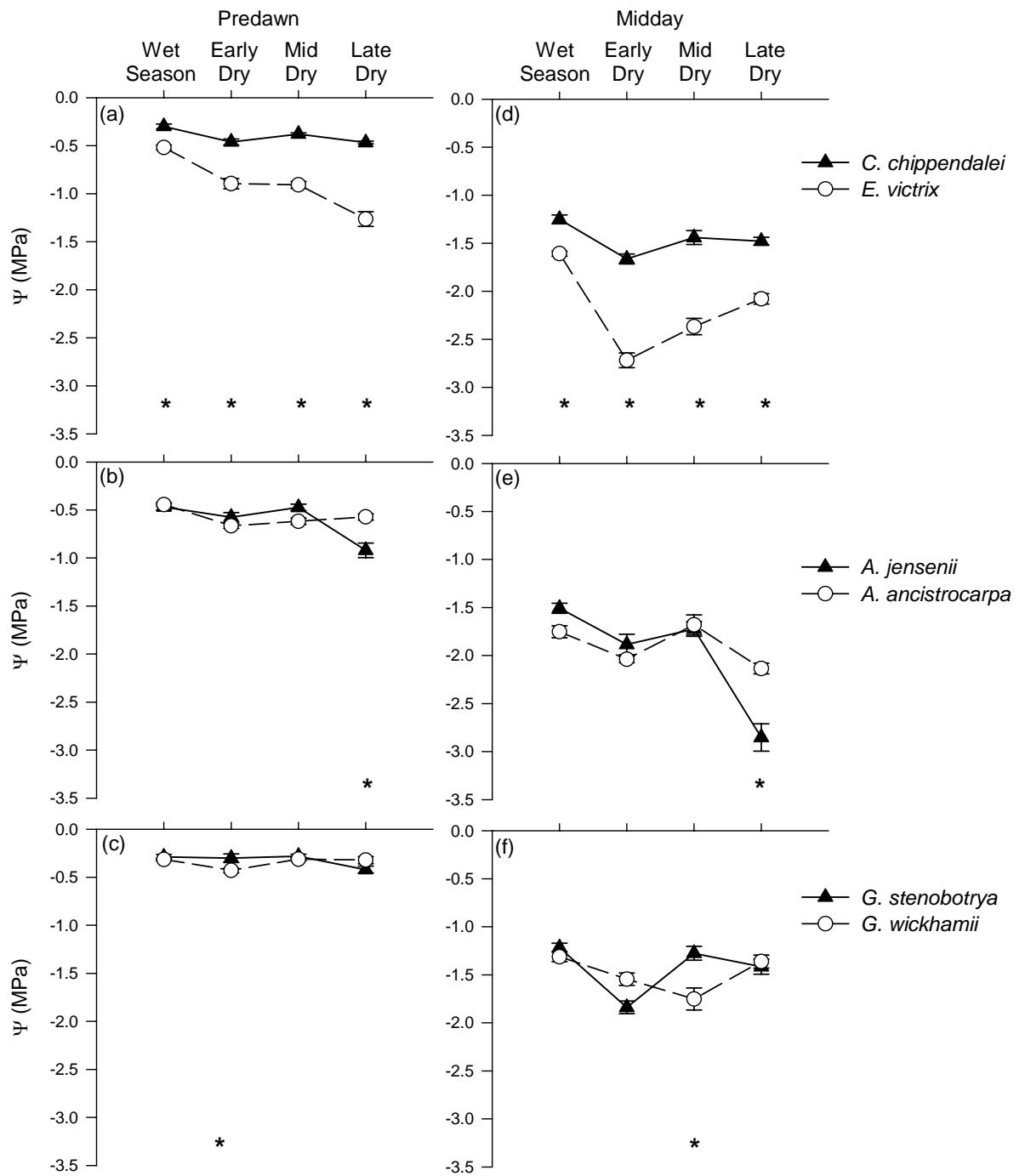
As expected, maximum rates of  $A$  and  $g_s$  typically occurred in the wet season (January to March) in both years of the study, and were at their lowest during the middle to late part of the dry season (July- December) (Figure 2.5). Within species pairs, plants on the dune displayed significantly higher  $A$  and  $g_s$  values than their counterparts in the interdune late during the dry season in two out of three cases. The eucalypt in the dune habitat, *C. chippendalei*, experienced the least variation in  $A$  and  $g_s$  throughout the year of all six species. Seasonal average  $A$  values ranged between 11  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  late in the dry season, to 16  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  early in the dry season;  $g_s$  ranged between 240

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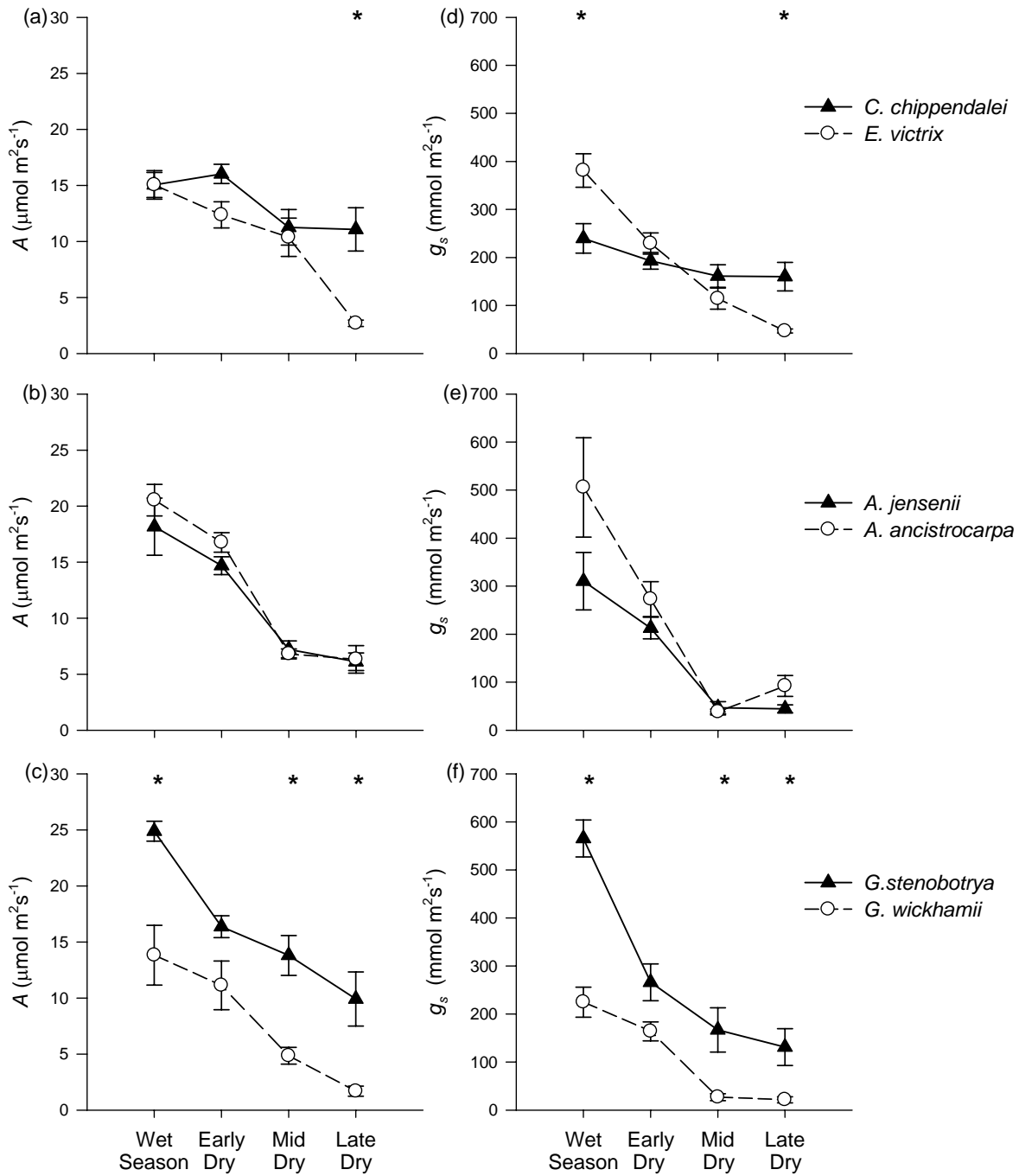
mmol H<sub>2</sub>O m<sup>-2</sup> s<sup>-1</sup> in the wet season, to 160 mmol H<sub>2</sub>O m<sup>-2</sup> s<sup>-1</sup> late in the dry (Figure 2.5d). Just prior to the break of the wet season in 2002, less than 1 mm of rain had been recorded for the area in 256 days (eight months). At this particular time, average  $g_s$  for *C. chippendalei* trees was 84 mmol H<sub>2</sub>O m<sup>-2</sup> s<sup>-1</sup>; considerably greater than for any other species including the closely related eucalypt in the interdunes, *E. victrix*, which decreased below 50 mmol H<sub>2</sub>O m<sup>-2</sup> s<sup>-1</sup>. As was the case with predawn and midday leaf water potentials, the GLM revealed a significant interaction effect between habitat and season for  $A$  ( $p=0.0028$ ) and  $g_s$  ( $p=0.0001$ ) in the eucalypts. Nonetheless, *post-hoc* tests revealed that *E. victrix* displayed significantly lower  $A$  and  $g_s$  late during the dry season but significantly higher rates of  $g_s$  during the wet season (Tukey HSD,  $p<0.05$ ).

Photosynthesis was not significantly different between *A. jensenii* from the dunes and *A. ancistrocarpa* from the interdunes ( $p=0.8776$ ), and there was no interaction effect between habitat and season ( $p=0.2255$ ). Conversely,  $g_s$  was significantly lower in *A. jensenii* than *A. ancistrocarpa* ( $p=0.0160$ ). The interaction term between habitat and season was not significant for  $g_s$  in *Acacia* species ( $p=0.2134$ ), and also for  $g_s$  and  $A$  in *Grevillea* species ( $p=0.0671$  and  $p=0.0905$  respectively). Consistent with my hypothesis, the dune species, *G. stenobotrya*, displayed significantly greater  $A$  ( $p<0.0001$ ) and  $g_s$  ( $p<0.0001$ ) values than its congeneric relative in the interdune, *G. wickhamii*, particularly during the wet season, middle and late parts of the dry season (Tukey HSD,  $p<0.05$ ) (Figure 2.5c and f).

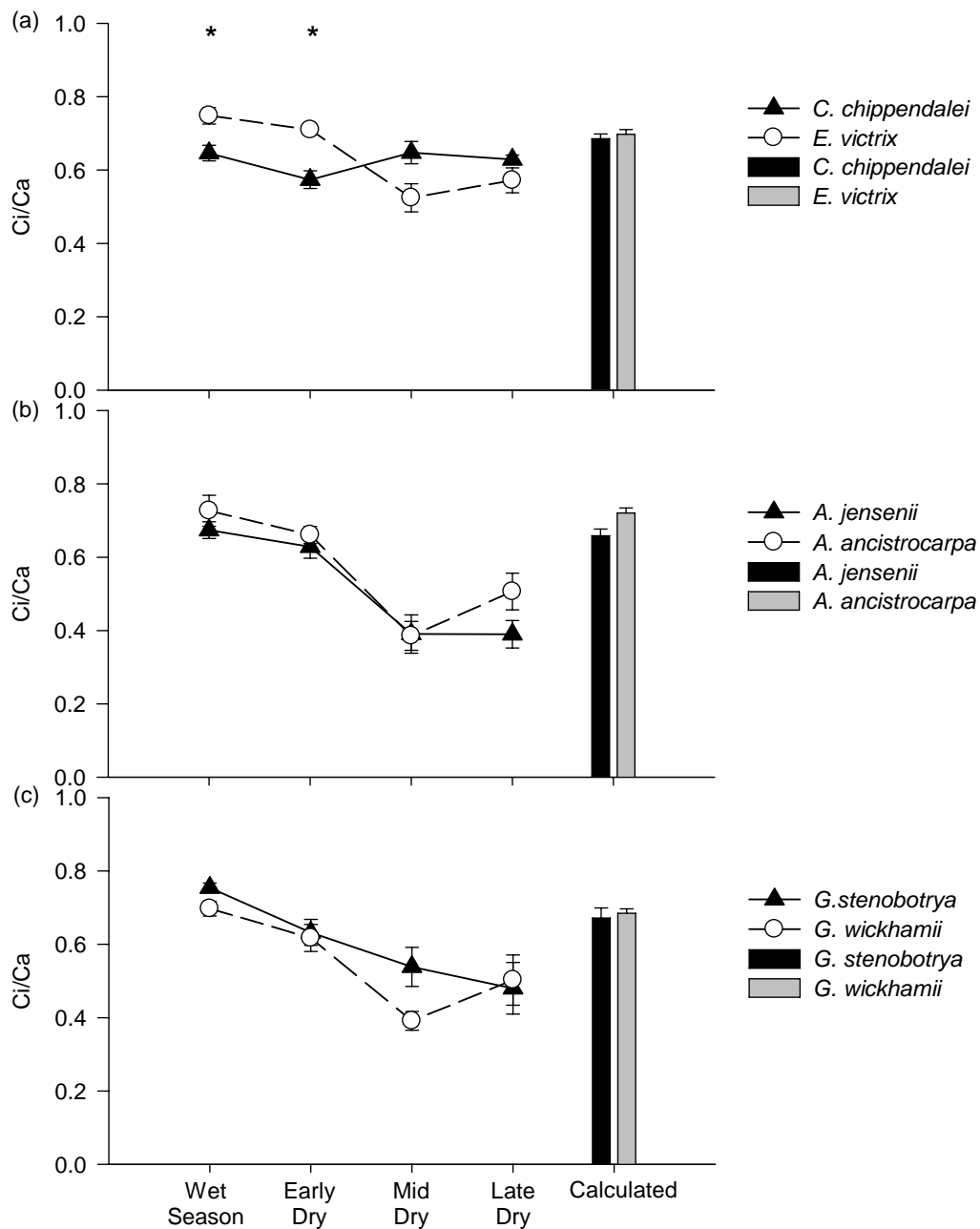
Instantaneous  $C_i/C_a$  measured by gas exchange followed a distinct seasonal trend, with highest values typically occurring in the wet season and early part of the dry season. These high wet-season values corresponded well with calculated  $C_i/C_a$  values (~0.65-0.8), based on  $\delta^{13}C$  analyses of leaf tissue (Figure 2.6). There were very few differences in measured  $C_i/C_a$  between dune and interdune relatives; the only departure from this was for the eucalypt trees, where *C. chippendalei* displayed significantly greater values than *E. victrix* for the wet and early during the dry season. At the lower end of the spectrum, both *Acacia* species displayed  $C_i/C_a$  values down to 0.39, as did *G. wickhamii* in the interdune. The lowest  $C_i/C_a$  exhibited by *G. stenobotrya* was 0.48 during the late dry season. The only species that did not show a marked decline in  $C_i/C_a$  from the wet season into the dry was *C. chippendalei*, which maintained a value of around 0.6 in all seasons.



**Figure 2.4** Mean leaf water potentials at predawn (a-c) and midday (d-f) throughout the wet season (wet), early part of the dry season (early dry), the middle of the dry season (mid dry), and late in the dry season (late dry) comparing plants growing on dunes (black triangles with solid line) with closely related species in the interdunes (open circles with dashed line). Error bars are standard errors of the mean. Symbols marked with an asterisk (\*) denote significant differences ( $p < 0.05$ ).



**Figure 2.5** Mean net photosynthetic rate (a-c) and mean stomatal conductance (d-f) throughout the wet season (wet), early part of the dry season (early dry), the middle of the dry season (mid dry), and late in the dry season (late dry) comparing species growing on dunes (black triangles with solid line) with their closely related species in the interdunes (open circles with dashed line). Error bars are standard errors of the mean. Symbols marked with an asterisk (\*) denote significant differences ( $p < 0.05$ ).



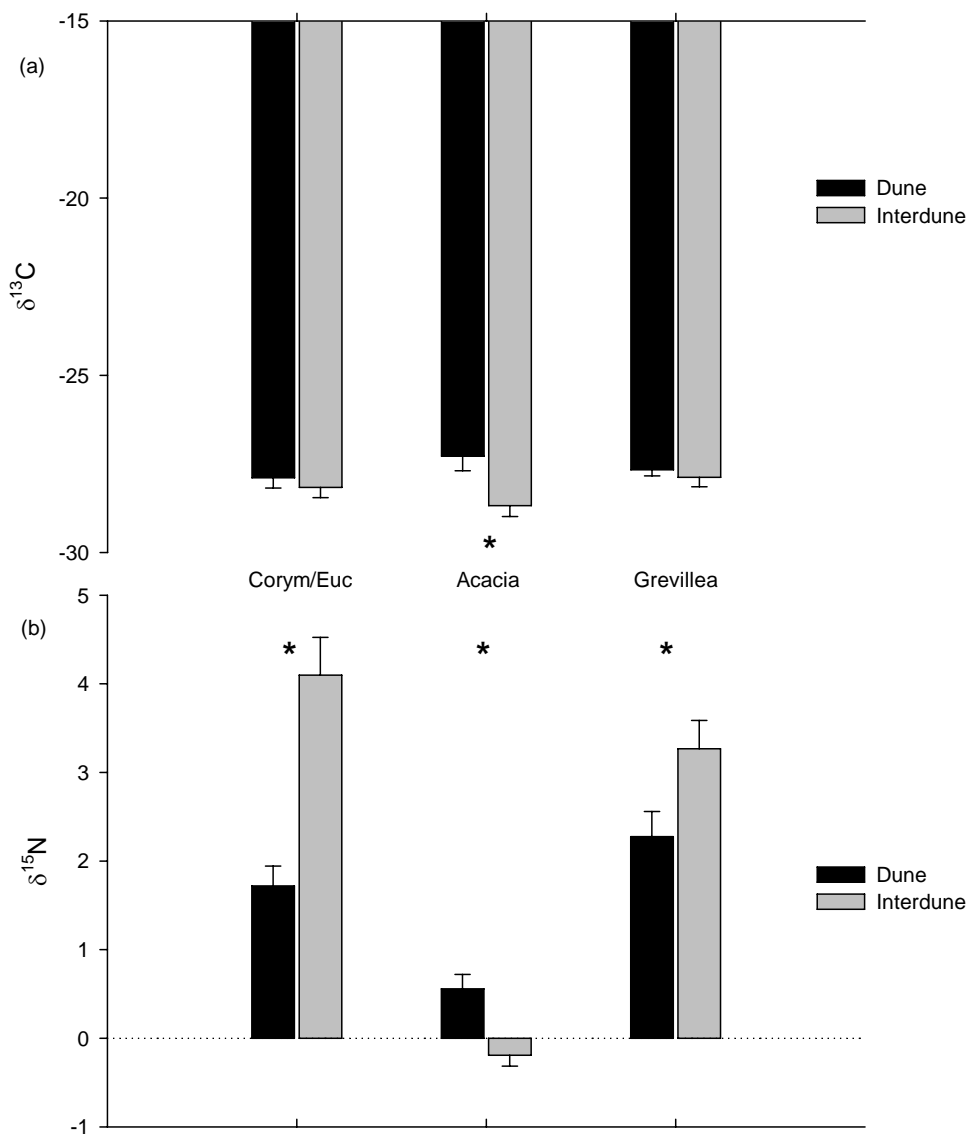
**Figure 2.6** Measured Ci/Ca from gas exchange throughout the wet season (wet) the early part of the dry season (early dry), the middle of the dry season (mid dry), and late in the dry season (late dry) for plants growing in the dune habitat (black triangles with solid line) and closely related species in the interdunes (open circles with dashed line), compared with calculated Ci/Ca from  $\delta^{13}\text{C}$  isotope signature (columns: dune-black fill; interdune-grey fill) (a-c). Error bars are standard errors of the mean. Symbols marked with an asterisk (\*) denote significant differences ( $\alpha=0.05$ ).

#### Leaf Stable Isotope Content: $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$

Carbon-isotope analysis ( $\delta^{13}\text{C}$ ) of foliage was not significantly different between plants in the dune habitat and their close relatives in the interdunes, except in the case of the *Acacia* species (Figure 2.7a). Interestingly, the value for *A. jensenii* was significantly less negative than that for *A. ancistrocarpa*, indicating higher water-use efficiency. A special collection of leaves from *G. stenobotrya* plants in the interdune displayed a  $\delta^{13}\text{C}$

value of  $-26.5\text{‰}$  (s.e.=0.36, n=3), whilst leaf material from this species growing in its usual location on the dune displayed a value of  $-27.7\text{‰}$  (s.e.=0.17, n=8), which was significantly different at  $\alpha=0.05$ .

Foliar  $\delta^{15}\text{N}$  values depicted large differences between the *Acacia* and non-leguminous species, within and also between habitats (Figure 2.7b). Within habitats the *Acacia* species displayed values that were less than half those of their non-fixing neighbours, and very close to zero, providing evidence for symbiotic  $\text{N}_2$  fixation. Woody non-fixing species from the interdune had significantly higher  $\delta^{15}\text{N}$  values than woody non-fixing species in the dune habitat (Figure 2.7b).



**Figure 2.7** Stable isotope composition for the six related species growing on dunes and interdunes including (a)  $\delta^{13}\text{C}$  ‰ and (b)  $\delta^{15}\text{N}$  ‰. Error bars are standard errors of the mean. Symbols marked with an asterisk (\*) denote significant differences ( $p < 0.05$ ).

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### *Leaf Nutrient Analysis*

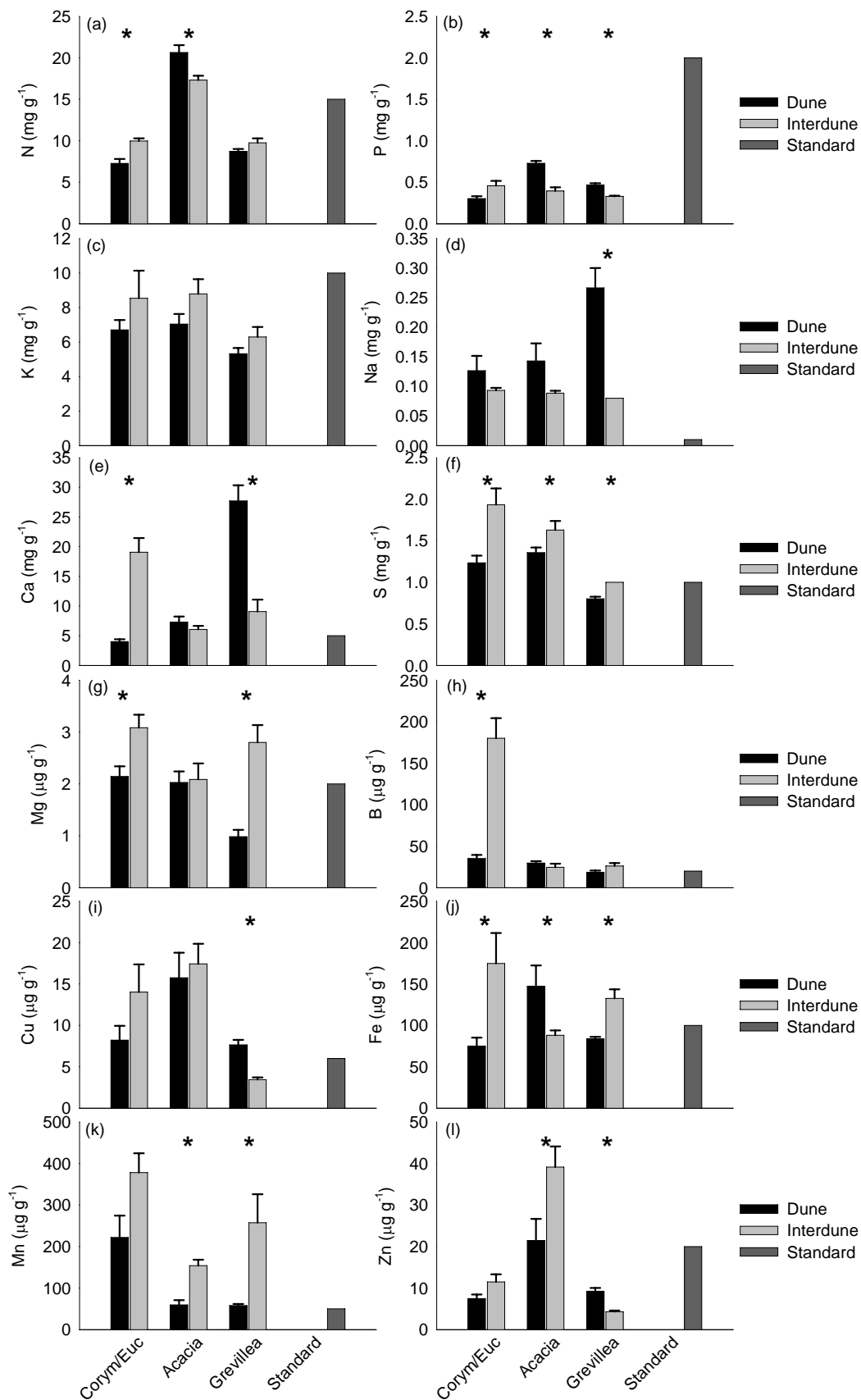
Foliar nutrient concentrations varied among the six species and there were few consistent trends across genera for specific elements. Overall, there was a prevalence of significantly higher nutrient concentrations in foliage for species from the interdune; a pattern that occurred in 39% of all species-pair comparisons across all nutrients (Figure 2.8). Dune plants showed significantly higher values in 22% of comparisons, whilst there were no significant differences between habitats in the remainder (Figure 2.8).

Foliage of the interdune species, *E. victrix* displayed significantly higher concentrations for most nutrients analysed, including N and P, compared with its dune relative, *C. chippendalei*. Conversely, the dune species *A. jensenii* showed higher N and P concentrations than the interdune species *A. ancistrocarpa*. *Acacia* species exhibited considerably higher concentrations of N and Zn than the *Grevilleas* and eucalypts. *G. stenobotrya* on the dune displayed significantly higher concentrations of P, Na, Ca, Cu and Zn than *G. wickhamii* in the interdune. Concentrations of S were consistently greater in foliage for interdune plants.

Using Epstein and Bloom's (2005) standard for 'adequate nutrition' as a benchmark, all species showed extremely low concentrations for P, and to a lesser extent N (with the exception of the *Acacia* species) and K. In most other cases, nutrient concentrations in leaves showed values in the range of 'adequate nutrition'. The two *Grevillea* species, *C. chippendalei* and *E. victrix* showed particularly low values for Zn. At the opposite extreme, *E. victrix* accumulated B to a value ( $180 \mu\text{g g}^{-1}$ ) nine times greater than the standard given by Epstein and Bloom (2005) (Figure 2.8h). This species also accumulated over 10 times more Mn ( $545 \mu\text{g g}^{-1}$ ) than that specified by Epstein and Bloom (Figure 2.8k).

## **Discussion**

It was hypothesised that plants in the dune habitat would display more favourable water relations (higher stomatal conductance and less negative leaf water potentials) than closely related plant species in the interdunes because of the greater soil depth and associated water storage capacity within the sandy dune ridges. A second hypothesis proposed that plants in the interdunes would exhibit greater nutrient concentrations in their foliage than relatives in the dune habitat, because of greater organic matter



**Figure 2.8.** Macro- and micronutrient concentrations (a-l) for *Acacia jensenii*, *A. ancistrocarpa*, *Corymbia chippendalei*, *Eucalyptus victrix*, *Grevillea stenobotrya* and *G. wickhamii* on dunes and interdunes compared with the standard considered adequate for nutrition presented by Epstein and Bloom (2005). Error bars are standard errors of the mean. Symbols marked with an asterisk (\*) denote significant differences ( $p < 0.05$ ).



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accumulation, termite activity and cryptogamic soil crust development in lower parts of the landscape.

*Soil characteristics and root morphology on dunes and interdunes*

Soil depth was considered the main edaphic property influencing the moisture regime in this study, with the 10-12 m high dunes providing a large volume to store rainfall compared with the relatively shallow (1-2 m deep), gravelly interdunes. Soil texture was similar and extremely sandy on dunes and interdunes, although the slightly greater proportion of clay and silt in the interdune (5.5%) compared with the dune (1%) may have some effect on water movement and retention within the soil. The finer material in the interdune is likely to permit greater capillary rise of moisture and evaporative loss than soils of the dune when rainfall events are followed by hot, dry or windy conditions. In this way, small pulses of rainfall are better captured and stored by the dune than the interdune. Large rainfall events associated with tropical thunderstorms and cyclones will penetrate deep into the soils of both habitats, largely eliminating any inverse texture effect differences.

The loose, uniform sands of the dunes also permitted extensive, uninhibited root proliferation to depth, allowing plants the opportunity to pursue rain wetting fronts deep into the dune. In the interdunes, the dense gravel layers and ironstone hardpans were observed to impede root growth. Rooting patterns are likely to be determined by a combination of the phenotypic response of root growth to environmental conditions and each species' inherent predisposition to attain a certain maximum rooting depth. Very different rooting patterns were found for the eucalypt species, with *C. chippendalei* on the dunes possessing typically no surface laterals, but numerous, very long, straight roots penetrating deep within the dune to utilise stored moisture. By contrast, *E. victrix* trees on the lower-lying interdunes displayed many near-surface sprawling roots in the top 20 cm, apparently unable to penetrate the dense, conglomerated gravel hardpan until finding a low resistance pathway to greater depths. The particular location at which they turn downwards is likely be a result of locally improved moisture availability in the soil or a biopore, such as an old root channel, allowing deeper penetration towards the water table. Old root channels and animal burrowings, especially those of ants and termites reduce soil bulk density and improve infiltration of water (Elkins *et al.* 1986; De Bruyn and Conacher 1990; Whitford *et al.* 1992). It is also possible there could be cracks or crevices in the conglomerated ironstone gravel that either lead down to the water table

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or hold a water reservoir. The ability of plants to exploit cracks on shallow soils over ironstone has been highlighted as a principal factor accounting for the distribution of particular *Hakea* species in south-western Australia (Poot and Lambers 2003).

The dimorphic rooting pattern was common on dunes (e.g., *G. stenobotrya*) and interdunes (e.g., *A. ancistrocarpa*, *G. wickhamii*) where dense gravels were at least 1-2 m below ground. The observation that *G. stenobotrya* is occasionally found on sandy interdunes, but never in shallow gravelly areas, suggests that dimorphic root systems are well suited to deep sandy soils (Pate and Dixon 1996). The dune species *A. jensenii* displayed a modified dimorphic root system with shoot-bearing rhizomes spreading across the most exposed sections of dune crests. Sinker roots were not well developed in young clones indicating they were relying upon the parent tree for water. This species was never found in the interdune, possibly due to difficulties establishing rhizomes and sinker roots in soils with gravel not far from the surface. Rhizomatous growth and other forms of vegetative reproduction, including the ability to resprout, are favoured on dunes because establishment from seed is very difficult due to wind movements causing sand accumulation and seedling burial or sand deflation and exposure of root systems (Danin 1996). These forces are particularly accentuated after fire, when vegetation cover is depleted and soils are exposed. Many dune species, including *C. chippendalei*, *A. jensenii* and even the grass species *T. schnizii* were observed resprouting from basal or epicormic buds after fire. The seeder strategy was more common for species in the interdunes (e.g., *A. ancistrocarpa* and *T. basedowii*).

#### *Water relations interactions- leaf water potential, gas exchange and $\delta^{13}C$*

Dune eucalypt and *Grevillea* species typically displayed more favourable plant water status and gas exchange than closely related species in the interdunes. There were few differences between *Acacia* species in each habitat for these same parameters. Fluctuations in predawn leaf water potential ( $\Psi_{pd}$ ), midday leaf water potential ( $\Psi_{md}$ ),  $g_s$  and  $A$  throughout the seasons were greatest in *Acacia* species and least for the dune eucalypt, *C. chippendalei*. The fact that this species maintained a relatively constant water status and gas exchange throughout the year indicates it has access to a reliable store of water deep within the dune and, with the absence of near surface roots, is unable to utilise pulses of rain in the short term. Indeed, it is well established in the literature that not all species respond immediately to additional water as uptake is dependent upon root architecture, plant growth phenology, timing of rainfall and plant

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functional type (Flanagan *et al.* 1992; Lin *et al.* 1996; Schwinning *et al.* 2002; Gillespie and Loik 2004).

The other five species studied here all exhibited substantial investment in lateral roots which facilitated water uptake soon after wet season rains and concomitant improvements in leaf water potential and gas exchange. Despite possessing a heavily lateralised root system, *G. stenobotrya* on the dunes displayed similar  $\Psi_{pd}$  to that of *C. chippendalei* throughout all seasons -0.3 and -0.5 MPa (Figure 2.3), indicating the tap root of this species was also accessing this deep store of water. Both *Grevillea* species demonstrated a very narrow and similar range of  $\Psi_{pd}$  (-0.3 MPa to -0.4 MPa) and  $\Psi_{md}$  (-1.3 MPa to -1.8 MPa). This result is in stark contrast to that for stomatal conductance and photosynthesis, where *G. stenobotrya* showed significantly higher  $g_s$  and  $A$  values than *G. wickhamii* throughout every season. *G. wickhamii* evidently limited  $g_s$  in order to maintain a moderate  $\Psi_{md}$ .

The finding in this study that most species on dunes and interdunes typically maintained relatively moderate leaf water potentials, compared with species in other equally arid or even more mesic habitats, is largely due to their occurrence on sandy soils. In soils with such a high sand content (95-99% sand; Table 2.1), decreasing  $\Psi$  below 3 MPa would confer little advantage in attaining more water (Lambers *et al.* 1998). The large interstitial air spaces in sandy soils, compared with clay soils, lead to a rapid decline in hydraulic conductivity and soil water content with more negative soil water potentials (Sperry *et al.* 1998; Hacke *et al.* 2000; Hultine *et al.* 2005). Data presented here are closely aligned with those in Sperry and Hacke (2002), with similar  $\Psi$  values for desert plants inhabiting sandy soils and less negative than  $\Psi$  values for the same species on loamy soils.  $\Psi$  values are also correlated with the cavitation resistance of xylem and reflect plant hydraulic traits (Bhaskar and Ackerly 2006). It is concluded the present species display stomata that are sensitive to hydraulic signals, and regulate leaf water potential within a relatively narrow range to avoid risks of leaf damage due to desiccation.

Late in the dry season, when temperatures and VPDs were extreme (>38 °C and >6 kPa, respectively; Figure 2.3), most species demonstrated a strong decline in  $g_s$ , except *C. chippendalei* (which displayed the highest stomatal conductance of all species at this time) and *G. stenobotrya* on the dunes (Figure 2.5). These species maintained  $g_s$  values

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over three times greater than that for related species in the interdunes, despite the presence of a water table within 5 m of the surface for *E. victrix* and 10 m of the surface for *G. wickhamii*. This finding supports the suggestion that water is more readily available in the deep soil layers of the dune than in the interdune during the dry months of the year. Furthermore, it is evident that the dense gravel layers inhibit root access to the water table, thus limiting water uptake of *E. victrix* and *G. wickhamii*.

Considering *G. stenobotrya* displayed the highest  $g_s$  values of all species in the wet season ( $565 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ ) and maintained moderate values ( $>130 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ ) late into the dry season, these plants must have ready access to water all year round. Possessing a dimorphic root system, hydraulic redistribution of water from the tap root to the lateral roots may allow continued hydration and maintenance of root primordia in dry soil, so that rapid growth is possible soon after rains moisten the topsoil (Burgess *et al.* 1998; 2000).

Photosynthesis and stomatal conductance of the two *Acacia* species did not significantly differ at any time of year. Leaf water potentials were also similar between species, except in the late part of the dry season when *A. jensenii* became more desiccated. *A. ancistrocarpa* displayed a similar range in  $\Psi$  values as a related species in the wet-dry tropics of northern Australia (*A. auriculiformis* Eamus and Cole 1997). The dune species *A. jensenii* displayed vegetative offshoots with underdeveloped root systems that likely placed demands on water supply from the parent plant. In this sense, offspring would be 'parasitising' on the parent, especially during the driest times of year when available water can be found only deeper in the soil profile, beyond the reach of young roots. As a result, any advantage of improved water availability in the dune habitat may be negated by the extra burden placed on parent plants by dependent juveniles. This may explain the finding that  $\Psi_{pd}$  and  $\Psi_{md}$  values were significantly more negative in *A. jensenii* than the non-clonal relative *A. ancistrocarpa* late during the dry season. Supporting evidence that juvenile shoots are 'parasitic' on parent plants is provided by Callaghan (1984) who found young vegetative offspring of the clonal sedge *Uncinia meridensis* were in receipt of photosynthate from parent tillers.

With respect to  $A$ , patterns were very similar to those for  $g_s$  for dune plants, particularly in *Grevillea* species, showing significantly greater  $A$  than congeneric species in the interdunes (Figure 2.5). The ratio between intracellular and ambient  $\text{CO}_2$  concentrations

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showed the highest values in the wet season, and lowest during the middle or late parts of the dry season (Figure 2.6).  $C_i/C_a$  values calculated from  $\delta^{13}\text{C}$ -isotope data strongly agreed with  $C_i/C_a$  values derived from gas-exchange measurements during the wet season; hence, it is concluded that the majority of structural carbon in leaf tissue for all these species was derived from photosynthate produced between January to March, immediately following rains.

$\delta^{13}\text{C}$  analyses did not reveal significant differences between the six related species discussed above, except in the case of the *Acacia* species where  $\delta^{13}\text{C}$  of *A. jensenii* was less negative than  $\delta^{13}\text{C}$  of *A. ancistrocarpa* (Figure 2.7a). Whilst some studies have described a decrease in  $\delta$  with decreasing rainfall (Stewart *et al.* 1995), others have demonstrated little change in community-averaged  $\delta^{13}\text{C}$  values along rainfall gradients (Schulze *et al.* 1991, 1996a, 1996b, 1998). Maintenance of high  $\delta^{13}\text{C}$  in drier habitats is presumably due to a shift in species composition towards species with greater biomass allocation to roots and greater rooting depth. Within the same species, however, carbon-isotope discrimination does reflect differences in water availability (Schulze *et al.* 2006). Leaf material from the one species that did occur in both habitats in this study area, *G. stenobotrya*, displayed a significantly more negative  $\delta^{13}\text{C}$  value when collected from plants in the dune habitat than from those in the interdunes, indicating greater water availability on the dune.

#### *Mineral nutrition- soil and plant relationships*

These red sands have been heavily leached since the Quaternary and exhibit extremely low phosphorus content much like the oligotrophic sandplain soils of south-western Australia (Dodd *et al.* 1984; Lambers *et al.* 2006). Nutrient concentrations were greater in soils of the interdunes than the dunes in nearly all cases, sometimes as much as tenfold (Table 2.1). In addition, organic matter content was nearly three times higher in the interdunes than the dunes (Table 2.1). The greater clay and silt content in the interdunes (5.5%) compared with the dunes (1%) is likely to partly account for these findings, directly and/or indirectly (Table 2.1). Fine-textured soils tend to have more labile C and N pools than coarse-textured soils, and often show a much greater flush of N mineralization after rains (Austin *et al.* 2004). With higher proportions of organic matter and fine clay, microbial activity and N mineralisation could be greater in the interdunes than dunes when rainfall occurs, commensurate with current knowledge on

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the microbial activity and nutrient cycling in arid and semi-arid ecosystems (Charley and West 1977; Foster 1988; Austin *et al.* 2004; Ford *et al.* 2007).

The presence of a cryptogamic crust and greater termite abundance in the interdunes is likely to have also have contributed to elevated soil nutrient concentrations. A cryptogamic crust was observed following rains in the interdunes, but only in occasional small patches on the dunes around where litter had accumulated. Cyanobacteria (e.g., *Nostoc* spp) in the crust fix atmospheric N<sub>2</sub> (Eskew and Ting 1978; Evans and Ehleringer 1993; Belnap *et al.* 2004) and can be the largest source of N in arid and semi-arid systems (Evans and Belnap 1999). They may also increase P, K and organic matter content (Kleiner and Harper 1977; Anderson *et al.* 1982), and enhance the availability of Ca, Mg and Mn (Harper and Belnap 2001). Termite mound soils also contain significantly larger quantities of total N than soils away from such mounds (Tongway *et al.* 1989). Termite nests, although largely subterranean in this part of the Great Sandy Desert, were very common in the interdunes, but rarely found in the dunes, probably because they require greater proportions of clay and silt to build (Hesse 1955; Pomeroy 1978; De Bruyn and Conacher 1990).

Potentially N<sub>2</sub>-fixing *Acacia* species displayed foliar N concentrations that were two- to three-fold greater than those of their non-fixing neighbours (Figure 2.8).  $\delta^{15}\text{N}$  values of these legumes were much lower than those of non-fixing species, and close to zero, indicating dinitrogen fixation may be occurring (if mineral N source is the same) for these plants both in the interdunes and even more so in the dune habitat (Figure 2.8). Similarly, a study by Pate *et al.* (1998), in the Murchison area of Western Australia (~28°S 117°E; 262 mm annual rainfall) also found that leguminous species on a dune demonstrated  $\delta^{15}\text{N}$  values indicative of dinitrogen fixation, yet several *Acacia* species in an adjacent mulga (*A. aneura*) community did not. Low soil N availability on the dune relative to the mulga was proposed as a factor responsible for N<sub>2</sub> fixation at the Murchison site (Pate *et al.* 1998). In light of the finding that soil N concentrations at the Murchison mulga site and in the interdune in the current investigation were very similar (around 9-10  $\mu\text{g g}^{-1}$ ), there appear to be additional factors, e.g., soil texture, P availability, water availability or time since fire, that may influence nodulation and N<sub>2</sub> fixation patterns in these species.

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Foliar nutrient concentrations compared between related species were not consistently greater in one habitat, however there was a trend for higher values in plants in the interdunes. Only one nutrient showed consistently higher concentrations for all species in one habitat, and that was S, which was significantly higher in foliage of plants in the interdunes. Less pronounced differences in foliar mineral concentrations between habitats than difference in soils may be attributed to the enhancement of 'islands of fertility' (Schlesinger *et al.* 1996) by longer-lived resprouter species in the dune habitat than seeder species in the interdunes; this will be discussed further in Chapter 3.

Compared with the standards for 'adequate nutrition' presented in Epstein and Bloom (2005), the nutrient that would appear to be the most severely limiting in all cases was P, with species generally displaying values between 10 and 30% of that considered 'adequate' (Figure 2.8). After P, N was the next element in lowest concentration relative to the Epstein and Bloom (2005) standard, then K and Zn. At the other end of the spectrum to nutrient deficiency, hyperaccumulation of boron was displayed by *E. victrix*, with a concentration nine times that of the Epstein and Bloom (2005) standard, and at least six times more than shown by any other species listed, including its relative *C. chippendalei* (Figure 2.8). High concentrations of boron are often associated with shallow saline water tables in semi-arid and arid climates with little drainage (Gupta *et al.* 1985), because borates are soluble and accumulate with sodium chloride salts (Hutchinson and Veits 1969; Marcar *et al.* 1999). With a B concentration of 175  $\mu\text{g g}^{-1}$ , this places *E. victrix* well into the 'high range' compared with other field-grown *Eucalyptus* species (Boardman *et al.* 1997; Marcar *et al.* 1999). Such high B concentrations in *E. victrix* suggest this species is accessing the water table some 5 m below the surface. *E. victrix* also displayed relatively high concentrations of Mn compared with all other species and the Epstein and Bloom (2005) standard for 'adequate nutrition'.

Comparing total concentrations of nutrients with the Epstein and Bloom (2005) standards is a good first step to understanding absolute values in the broader context, but defining which of these elements is primarily limiting plant growth in this particular ecosystem is a more involved question. Marschner (1995) states that where two or more nutrients are limiting growth, their relative concentrations may be more important than their absolute concentrations, as increasing one may promote growth and result in the deficiency of another. It has since been found that in temperate ecosystems, community

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average N:P ratios greater than 16:1 are indicative of P limitation, while an N:P ratio less than 14:1 are indicative of N limitation; between these ratios, singular or co-limitation of N and/or P is likely (Koerselman and Meuleman 1996; Verhoeven *et al.* 1996). In savannah grasses from the tropics of East Africa, Ludwig *et al.* (2001) found N:P ratios as low as 12 were indicative of P limitation as N requirements of these species were relatively lower than those of herbaceous species studied in temperate systems mentioned above; values less than 10 were still deemed indicative of N limitation. Bennett and Adams (2001) found N:P ratios around 7 in semi-arid, north-west Australia for above-ground biomass of perennial grasses growing on red swelling clays. A fertiliser application trial at this site resulted in significant increases in biomass resulted after additions of N, as well as after additions of N and P combined, but not after additions of P alone (Bennett and Adams 2001). They concluded that N, and not P was limiting growth in that particular ecosystem (Bennett and Adams 2001). The current investigation in the Great Sandy Desert found the average N:P ratio in foliage of the six woody species was 28:1, suggesting that P was most limiting growth. This finding is in agreement with at least four other studies conducted in semi-arid Australia, each reporting N:P ratios greater than 18 (Christie 1979; Silcock *et al.* 1985; Holm & Allen 1988; Rice *et al.* 1994). Further research into N:P ratios, combined with fertiliser application trials are needed to better define nutrient limitations for a range of different soil types in arid and semi-arid environments.

### *Synthesis*

Nutrient concentrations in soils were greater in the interdunes than in the dunes, as hypothesised, but differences in foliar nutrient concentration were less pronounced between sites. Water status and stomatal conductance tended to be higher for plants in the dune habitat, particularly in the dry season. The finding that dune species were generally better supplied with water supports the hypothesis that the deep sands of the dunes store water and provide more mesic conditions than in the interdunes.



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## Chapter 3

### Water relations and mineral nutrition of *Triodia* grasses on desert dunes and interdunes

#### Abstract

Desert dunes and interdunes provide habitat heterogeneity and profoundly influence the spatial and temporal distribution of water and nutrients throughout the landscape. These underlying physical processes shape the plant species composition and their ecophysiology. Spinifex grasses dominate the vegetation throughout much of Australia and are categorised into two groups; ‘soft’ species occur mostly in northern, subtropical to semi-arid regions, whilst ‘hard’ species occur mostly throughout the dry centre and southern interior. This study examined the water and nutrient relations and leaf anatomy of dominant soft and hard spinifex in the Great Sandy Desert where their distributions overlap. The ‘soft’ species, *Triodia schinzii* (Henrard) Lazarides, occurs only on sand dunes, whilst the ‘hard’ species, *T. basedowii* E.Pritz., is restricted to the flat interdunes. I proposed two hypotheses: 1) that the dune species, *T. schinzii* would display more favourable water status and 2) the interdune species, *T. basedowii* would display higher leaf nutrient concentrations. *T. schinzii* displayed significantly less negative leaf water potentials at predawn and at midday (-0.4 and -2.0 MPa respectively) than *T. basedowii* (-0.9 and -3.0 MPa respectively) throughout the middle of the dry season. Photosynthesis rates were also significantly higher in *T. schinzii* than *T. basedowii* in the wet season (140 versus 84 nmol g<sup>-1</sup>s<sup>-1</sup>), but there were no significant differences between species in leaf conductance. Leaf δ<sup>13</sup>C composition confirmed anatomical observations that both species were C<sub>4</sub> and were in line with the finding that *T. schinzii* displayed significantly greater photosynthetic water-use efficiency during the wet season than *T. basedowii*. In general, foliar nutrient concentrations were not significantly different between species; however, both species exhibited especially low leaf [P] and to a lesser extent [N]. I conclude that water is more readily available in the dune than the interdune as a result of greater soil depth and associated water storage capacity. These properties are considered the main factors influencing plant species distribution. Given the climatic and geographic distribution of these two *Triodia* species, it is suggested that sand dunes provide a mesic corridor for *T. schinzii* to extend its range from higher-rainfall areas into the arid interior.

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## Introduction

Water and nutrient availability are closely coupled in desert and semi-desert regions (Noy-Meir 1973, Hadley and Szarek 1981). In sandy deserts, adjacent dunes and interdunes generate topographic and edaphic heterogeneity (Danin 1996; Rosenthal *et al.* 2005) with distinct plant communities reflecting differing moisture and nutrient regimes (Pavlik 1980; Walter and Box 1983; Yeaton 1988). Sandy soils in arid environments with episodic rainfall store water more efficiently than heavier-textured soils due to the ‘inverse texture effect’ (Chadwick and Dalke 1965; Noy-Meir 1973; Pavlik 1980). Their relatively coarse particle size and larger pore spaces allow rapid hydraulic conductivity, so pulses of rainfall penetrate quickly to deeper soil layers (Hennessy *et al.* 1985; Sperry and Hacke 2002). Furthermore, capillary forces are very weak in sandy soils, limiting upward transport and evaporative loss from the soil surface once the wetting front descends below 50-100 mm (Alizai and Hulbert 1970; Seely and Louw 1980; Orshan 1986). Sufficient soil depth is required to store this moisture since the water-holding capacity of sands is relatively low compared with that of heavier-textured soils (Prill 1968).

Sand dunes, with their large soil volume, are ideally structured to maximise water storage in arid environments with episodic rainfall (Prill 1968; Fet *et al.* 1998). The effect on water and nutrient relations of plants occupying dunes and interdunes has been reported in a small number of publications, from locations with widely differing climatic, physical and hydrological conditions. Based on measurements of plant water status ( $\Psi$ ), plant cover and primary productivity, various and contrasting patterns have been reported. Some studies have found more favourable conditions in dune habitats (Pavlik 1980; Rosenthal *et al.* 2005), others in interdune habitats (Gries *et al.* 2003; Niu *et al.* 2005), whilst others have reported no significant differences between habitats (Forseth *et al.* 1984). One intention of the present study was to contribute to this body of knowledge with information from an Australian desert system and offer some explanation of what is driving reported differences in the aforementioned studies.

The vegetation of Australia’s arid and semi-arid regions is reasonably diverse and dominated by hummock grasslands, principally composed of *Triodia* species (Griffin 1990). Commonly referred to as ‘spinifex’, these grasslands cover approximately 1.8 million square kilometres and form the single most extensive vegetation type on the

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continent (Burbidge 1953; Griffin 1990). Spinifex are strongly xerophytic, long-lived perennials and have needle-like leaf blades (McWilliam and Mison 1974; Jacobs 1984). Due to their ability to tightly roll leaf margins and protect stomata inside longitudinal grooves, such specialised anatomy helps them reduce transpiration and tolerate long periods without rain. Anatomy and the relationship with gas exchange will be considered further in this study. The *Triodia* group is divided into two major categories: ‘soft’ spinifex and ‘hard’ spinifex (Mant 1998). ‘Soft’ taxa lack stomata and associated photosynthetic tissues on the outer, abaxial leaf side, and are typically associated with the subtropical monsoonal region of the semi-arid north where rainfall is more predictable. ‘Hard’ taxa have stomata on both adaxial and abaxial surfaces of the leaf, and are found throughout Australia's arid interior, with representatives in all mainland states of the country (Lazarides 1997).

Two widespread species, the ‘soft’ type *T. schinzii* and the ‘hard’ species *T. basedowii*, overlap in distribution by hundreds of kilometres around 22° S across much of the Australian continent (Winkworth 1967; Lazarides 1997). In the Great Sandy Desert, where the current study took place, they segregate into discrete communities according to habitat: *T. schinzii* only occurs on dunes, most of which are well vegetated and stable, whereas *T. basedowii* is restricted to the flat, equally well vegetated interdunes. This habitat preference is not maintained throughout their range. Further north and into the tropics, *T. schinzii* dominates undulating and flat sand-plains, whilst further south *T. basedowii* prevails on dunes and interdunes throughout the Simpson and Gibson Deserts (Winkworth 1967; Dickman *et al.* 1999).

The soils of these arid and semi-arid regions are typically low in P and N (Rice *et al.* 1994; Bennett and Adams 2001). Nutrients are often distributed unevenly across the landscape and confined to patches beneath plant crowns, fallen vegetation or in soil depressions (Bennett and Adams 1999; Ludwig *et al.* 1999). Their availability is also restricted largely to wet periods when microbial activity is stimulated (Skopp *et al.* 1990; Ford *et al.* 2007). Termites and cryptogamic crust organisms also contribute greatly to the nutrient dynamics of many arid zone systems (Tongway and Smith 1989; De Bruyn and Conacher 1990; Harper and Belnap 2001). Throughout dry areas of Australia, cryptogamic crusts predominantly composed of Cyanobacteria and Bryophytes, play an important role binding and stabilising soil particles (Stoneburner *et al.* 1993; Hodgins and Rogers 1997; Eldridge 2001). Such crusts were occasionally

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observed in patches following wet-season rains in the interdune but not on the dune. Similarly, active termite galleries were frequently encountered in the interdunes, but never in the sandy dune crests.

The aim of this investigation was to develop an understanding of the water and nutrient relations of two contrasting spinifex species and explore causes why they form different plant communities in each habitat. Knowing there are only slight differences in soil texture between dunes and interdunes (Grigg *et al.* 2008 - Chapter 2), it is proposed that soil depth and water availability are the main factors determining species distribution. My primary hypothesis, therefore, is that *T. schinzii* from the dune should display better water status throughout the year than *T. basedowii* from the interdune, because the larger soil volume within the dune stores rain from the previous wet season. However, nutrient distribution throughout the landscape was also considered a factor that may influence plant community composition in each habitat. Taking into account the greater abundance of termites, occasional presence of a cryptogamic crust and the potential for greater accumulation of organic matter lower in the landscape, my second hypothesis proposes that foliage of *T. basedowii* in the interdune should display greater leaf nutrient concentrations than *T. schinzii* from the dune.

## **Materials and Methods**

### *Location and general information on the study site*

This study was conducted in the Great Sandy Desert of North Western Australia near Nifty Copper Operation (21°40'S 121° 35'E), approximately 350 km inland from the coastal town Port Hedland. The terrain is dominated by sand dunes with an average height of 12 m and there are no significant surface-drainage channels in the area. Dunes were formed during the last glacial maximum 16-20,000 years BP and stabilised in their current positions 10-13,000 years BP (Bowler 1976; Nanson *et al.* 1992; Rhodes *et al.* 2004). The well vegetated nature of dunes and interdunes throughout this time has prevented mass sand movement and dune encroachment. Dune sands are homogeneous to depth. Interdunes typically display lateritic gravels within half a meter of the surface which become increasingly conglomerated with depth and form a hardpan by 2-3 m (Beard 1969). This hardpan underlies the landscape as a more or less flat pavement and continues beneath the deep sandy dunes without conforming to their shape. Average depth to a perched water table beneath most interdunes throughout the area is around 10-12 m (Rockwater Hydrology Report 2003; Nifty Copper Mine Drill Log 2003).

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Study sites were selected on adjacent dunes and interdunes where flat sections between dunes exceed 300 m in width and were unburnt for at least 10 years.

### *Climate*

The study area is semi-arid, with warm dry winters and long hot summers characterised by occasional yet intense rainfall from tropical cyclones and thunderstorms. Rainfall is extremely unpredictable and there is a large degree of variability between years (Beard 1969). The long-term average annual rainfall is around 330 mm. In the twelve months prior to the commencement of this investigation, 849 mm of rain fell in the area, making 2000 one of the wettest years on record. Ecophysiological measurements began at the start of 2001, which was also a wetter than average year (2001=523 mm), and continued until the end of 2002 (274 mm) (Bureau of Meteorology 2008). February was consistently the wettest month in all three years, whilst August, September and October were without measurable rainfall. Total potential evaporation (Class A pan) for this part of the Great Sandy Desert averages 4100 mm per year (Bureau of Meteorology 2008), and far exceeds rainfall in every month. Vapour pressure deficit (VPD) typically exceeds 6 kPa between October and January; a time when daily maximum temperatures are often greater than 40°C (see Grigg *et al.* 2008 - Chapter 2). During winter (June and July), temperatures typically range between 26°C in the day and below 10°C at night.

### *Soils*

Soils of the area are predominantly red sands of Quaternary origin; dunes contain only 0.5% silt (0.002 - 0.020 mm) and 0.5% clay (<0.002 mm) and are homogeneous throughout, whilst the interdunes contain 0.5% silt and 5% clay (see Grigg *et al.* 2008 - Chapter 2). Water-holding capacity of these soils ranges between 8-11% and bulk density between 1.5 and 1.6 kg l<sup>-1</sup>. Soil from the top 10 cm displays a pH of 5.8-6.0 and EC is extremely low at around 0.1 μS m<sup>-1</sup>. Organic carbon concentration was considerably lower in soils of the dune (0.4 ± 0.03 mg g<sup>-1</sup>) than the interdune (1.1 ± 0.06 mg g<sup>-1</sup>). Also, nutrient status is lower in dune soil than interdune soil for the elements N, P, K, Ca, Mg, Cu, Fe, Mn and Co. Soil samples were collected in bare patches away from plant crowns. For details on methods and results for soil physical and chemical analyses see Grigg *et al.* (2008) (Chapter 2).

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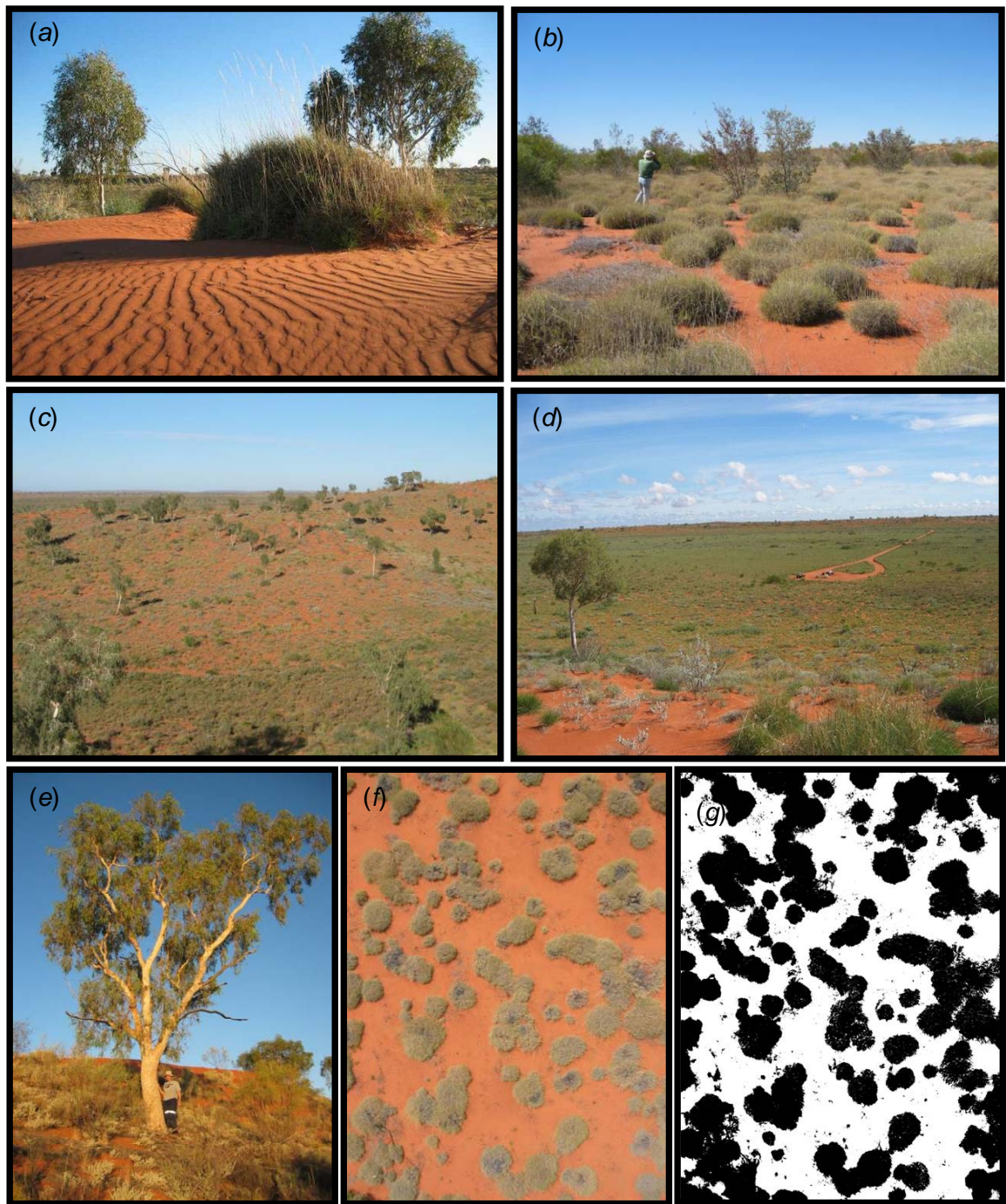
### *Vegetation species composition, density and cover*

Vegetation throughout the area is dominated by spinifex grasses, with *T. schinzii* inhabiting the dune (Figure 3.1a) and *T. basedowii* the flat interdunes (Figure 3.1b, d, f). *T. schinzii* forms accretion mounds of soil up to 0.5 m high, whilst *T. basedowii* does not. The most prominent tree species on the dune is the eucalypt *Corymbia chippendalei* (Myrtaceae) (Figure 3.1a, c, e); other common dune species include *Grevillea stenobotrya* (Proteaceae), *Acacia jensenii* (Fabaceae) and *Crotalaria cunninghamii* (Fabaceae) (Table 3.1). Species composition on dunes varies little from one dune to the next as the homogeneous, similar edaphic conditions occur on each. In most interdunes, common woody shrub species include *Grevillea wickhamii* (Proteaceae) and *Acacia ancistrocarpa* (Fabaceae) (Figure 3.1b). Thin patches of cryptogamic crust, thought to be composed of bryophytes and cyanobacteria, became discernible on the soil surface following significant rains only in the interdunes, not the dunes.

Plant species richness and density of individuals were recorded for six, 150-m long transects, each divided into 15, 10 m x 10 m quadrats. Two transects were laid out at each of three sites, orientated in a north-south direction so as to start in the interdune, go over the dune and onto the flat interdune on the other side. Digital photographs were taken vertically at various altitudes between 10 m and 250 m above the ground (see Figure 3.1f) with a radio-controlled digital camera suspended from weather balloons filled with helium gas. So as to avoid shadows, photographs were taken when overcast conditions prevailed throughout the middle of the day in summer. Total projected plant cover (living and non-living standing biomass) values were calculated by image analysis following principles outlined in Bennett *et al.* (2003). ImageJ (Version 1.32- National Institute of Health USA) software was used for image analysis (see Figure 1g).

### *Anatomy of spinifex leaves*

Fresh leaf material of both species was hand sectioned and examined under a light microscope with visible light and also with ultraviolet light to elicit autofluorescence. Sections were examined when untreated and after staining with one, or a combination of stains including Toluidine Blue, Aniline Blue, Basic Fuchsin, Rhodamine B and Iodine. Specimens were examined at a range of magnifications from 100 x to 400 x and photographs taken.



**Figure 3.1** Photographs of the study area depicting (a) *Triodia schinzii* on a dune crest with *Corymbia chippendalei* trees in the background (b) *Triodia basedowii* hummocks in the interdune with scattered *Grevillea wickhamii* and *Acacia ancistrocarpa* shrubs in the background (c) a large, 20 m high sand dune adjacent to a narrow interdune (d) a broad, flat interdune highlighting the absence of surface drainage channels (e) a well vegetated dune slope characterised by a large *C. chippendalei* tree (f) low-level aerial photograph above an interdune dominated by *T. basedowii* (g) black and white threshold image of *T. basedowii* used for area analysis (47% total projected cover).

### *Gas exchange of spinifex leaves*

Leaf gas exchange was measured *in situ* using a Li-Cor 6400 portable infra-red gas analyser (LI-COR Inc. Lincoln, NE, USA). These measurements were conducted on eight occasions over a two-year period starting in January 2001. Field site visits were

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generally three months apart in order to capture each season twice over this two-year period. The seasons were named according to time since summer rains; hence, the ‘wet’ season included January, February and March. The following three months, April to June, were considered the ‘early’ part of the dry season, and July to September the ‘middle’ part of the dry season. The last three months, October to December, were referred to as the ‘late’ part of the dry season. During the course of this study, wet-season rains began in January of each year.

Sampling was carried out between 10.00 and 14.00 hours. An artificial light source of red and blue LEDs was used to administer a light-saturating photosynthetic photon flux density (PPFD) of  $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$  at all times and in all seasons. Vapour pressure and temperature in the chamber were maintained as close as possible to those of ambient air. Leaf chamber carbon dioxide concentration was between 360 and  $375 \mu\text{mol mol}^{-1}$ . Leaf temperatures were calculated using an energy balance equation (Licor 6400 Manual 2000).

Measurements were made on the youngest, fully matured, healthy leaves on the north side of each plant. At least three measurements were taken on each plant and between three and five individuals were assessed for each species at all sampling times. Measured leaf sections were sealed in zip-lock plastic bags, chilled and taken to the laboratory where their leaf areas were measured on a back-lit flatbed scanner at a scanning resolution of  $0.2 \mu\text{m}$  (WinRhizo V3.0.3 1995, Regent Instruments Quebec, Canada). Once areas were determined, leaves were oven dried at  $70^\circ\text{C}$  for one week, then dry weights recorded. Due to changing degrees of leaf rolling between seasons, it was decided to express photosynthesis and leaf conductance on a dry mass basis. In light of such leaf rolling, the boundary layer was considered a major factor determining gas exchange so the term leaf conductance was considered more appropriate than stomatal conductance in this case.

#### *Water potentials of spinifex leaves*

Leaf water potentials of *T. schinzii* and *T. basedowii* were measured at predawn (03.00-05.00 h) and midday (12.00-14.00 h) using a Scholander-type pressure chamber (PMS Instruments, Corvallis, Oregon, USA) on the same eight field site visits outlined above for leaf gas exchange. At each measurement time, predawn or midday, leaf water potentials were recorded for three shoot sections exhibiting at least four leaves from



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three to five randomly selected individuals. Immediately after being excised from the parent plant, shoot/leaf samples were sealed inside zip-lock plastic bags with only the cut end protruding and placed inside the pressure bomb to begin measurements within one minute of cutting.

#### *Spinifex foliar nutrient composition*

Healthy, mature leaves, free from insect attack were collected from six individuals of each *Triodia* species during the dry season (July) 2002. From each individual plant, approximately 20 leaves were cut from three sections on the northern side of the crown, air dried in the field, oven dried at 70°C in the laboratory, then ground using a ball mill.

Nitrogen concentration was determined colourimetrically (indophenol blue method) using an Autoanalyser system after digestion with sulfuric acid and hydrogen peroxide (Yuen and Pollard, 1954). Another subsample of leaf material was digested with a mixture of nitric and perchloric acids (McQuaker *et al.* 1979), and then analysed by ICP-AES (Varian Vista axial spectrometer, Palo Alto, CA, USA) to determine concentrations of phosphorus, potassium, sodium, calcium, magnesium, sulfur, boron, copper, iron, manganese, molybdenum, zinc, aluminium and silicon. Analyses were performed at the West Australian Chemistry Centre.

#### *Carbon metabolism and Nitrogen source: C and N isotope composition*

The same leaf material collected for nutrient analyses was sub-sampled for carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotope composition.  $\delta^{13}\text{C}$  analysis was performed using continuous flow mass spectrometry (Roboprep + Tracermass Ion Ratio Mass Spectrometer - Europa Scientific, Crewe, UK).  $^{13}\text{C}:^{12}\text{C}$  ratios of the  $\text{CO}_2$  produced by combustion at 1000°C in an oxygen atmosphere were then compared with those obtained by combustion of a cornflour standard (ANCA 53), calibrated in turn against the international standard NBS-22.  $^{15}\text{N}:^{14}\text{N}$  ratios were compared against a radish standard (ANCA 54) calibrated against known international standards (IAEA-N1, IAEA-N2, IAEA NO3). Analytical precision based on multiple replicate analyses for  $\delta^{13}\text{C} = \pm 0.2\%$  relative to the PeeDee Belemnite standard; for  $\delta^{15}\text{N} = \pm 0.3\%$  relative to air.

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### *Statistics*

Data were analysed using JMP V4 (SAS Institute Inc). General linear models (GLM) were used to compare measurement means of related species between habitats; measurements analysed in this way included leaf water potential, leaf conductance, photosynthesis,  $C_i/C_a$ ,  $\delta^{13}C$ ,  $\delta^{15}N$  and mineral nutrient concentrations. Homogeneity of variances was assessed using Cochran's test and data transformed (square root or log) if group variances were heterogenous or not normally distributed. Pairwise comparisons were carried out using Tukey's *post-hoc* test when the GLM indicated significant treatment effects (Quinn and Keough 2002). Results are reported as significant where  $p < 0.05$ .

## **Results**

### *Landscape, plant communities and distribution of spinifex species*

Species composition of the dunes was distinctly different from that of the interdunes, with virtually all species restricted to one habitat or the other (Table 3.1). Of the 165 species identified at the study site, Table 3.1 lists 30 commonly occurring taxa, illustrating strong representation of the Myrtaceae, Fabaceae, Proteaceae, Chloanthaceae and Poaceae in both systems.

Total projected plant cover was roughly equal on interdunes and dune slopes in this part of the Great Sandy Desert, but the percentage of bare ground was higher on the tops of the dunes (Table 3.1). It should be noted, however, that the relatively flattened crest occupied less than one quarter of the dune surface area, so projected plant cover over the dune as a whole was around 42%. Spinifex hummocks, made up of living green leaves and dead material in the centre of mature plants, constituted around 90% of the total projected plant cover and were considered the largest component of the standing biomass in this system. *T. basedowii* dominated all interdunes, but never occurred on dune slopes or crests (Table 3.1). The rooting depth of this species was typically less than 1 m but may be restricted to shallower depths where lateritic gravel density impedes root growth. *T. schinzii* occupied most of the dune slope and parts of the dune crest (Table 3.1), and displayed root systems which extended 2 m below the surface.

**Table 3.1** Vegetated versus bare soil projected area, species composition, plant abundance and cover on dunes and interdunes in the study area. The dunes have been further classified into dune crests and dune slopes, to highlight differences in plant density, but they are collectively referred to as ‘dune’. *Abundance* refers to the number of individual stems per hectare [None (0 stems ha<sup>-1</sup>), Sparse (1-10 stems ha<sup>-1</sup>), Occasional (11-20 stems ha<sup>-1</sup>), Common (21-100 stems ha<sup>-1</sup>), Abundant (>100 stems ha<sup>-1</sup>)] whilst *cover* refers to the percentage projected area of crowns for that species [None (0%), Very Low (0-1%), Low (1-3%), Moderate (3-15%), High (>15%)].

<b>Habitat Information</b>		<b>Dune Crest</b>	<b>Dune Slope</b>	<b>Interdune Flat</b>
Total projected area that is exposed, bare soil		79% ± 2%	52% ± 3%	51% ± 3%
Total projected area vegetated (plant matter-living parts and litter)		21% ± 2%	48% ± 3%	49% ± 3%
<b>Species</b>	<b>Family</b>			
<i>Newcastelia spodiotricha</i> -F. Muell.	Chloanthaceae	Sparce - Very Low	Occasional - Low	None
<i>Dicrasyllis doranii</i> -F. Muell.	Chloanthaceae	Common - Low	Common - Moderate	None
<i>Dampiera aff. cinerea</i> -Ewart & O.B. Davies	Goodeniaceae	Common - Very Low	Common - Moderate	None
<i>Acacia jensenii</i> -Maiden	Mimosaceae	Common - Low	Common - Low	None
<i>Calytrix carinata</i> -R. Br.	Myrtaceae	Sparce - Very Low	Common - Low	None
<i>Corymbia chippendalei</i> -(Carr & Carr) Hill & Johnson	Myrtaceae	Occasional - Moderate	Occasional - Moderate	None
<i>Eucalyptus pachyphylla</i> -F. Muell.	Myrtaceae	Sparce - Very Low	Sparce - Low	None
<i>Aluta maisoneuvii</i> -(F. Muell.) Rye & Trudgen	Myrtaceae	Sparce - Very Low	Occasional - Low	None
<i>Aotus aff. phylloides</i> -(F. Muell.) Benth.	Fabaceae	Common - Very Low	Common - Very Low	None
<i>Crotalaria cunninghamii</i> -R. Br.	Fabaceae	Common - Very Low	Common - Very Low	None
<i>Triodia schinzii</i> -(Henrard) Lazarides	Poaceae	Common - Moderate	Abundant - High	None
<i>Eriachne aristidea</i> -F. Muell.	Poaceae	Sparce - Very Low	Occasional - Very Low	Sparce - Very Low
<i>Grevillea stenobotrya</i> -F. Muell.	Proteaceae	Common - Low	Abundant - Moderate	Sparce - Very Low
<i>Gompholobium polyzygum</i> -F. Muell.	Fabaceae	None	Sparce - Very Low	Occasional - Low
<i>Scaevola parvifolia</i> -Carolin	Goodeniaceae	None	Occasional - Very Low	Common - Low
<i>Ptilotus calostachys</i> -F. Muell.	Amaranthaceae	None	None	Sparce - Low
<i>Dicrasyllis cordifolia</i> -Munir	Chloanthaceae	None	None	Sparce - Low
<i>Newcastelia cladotricha</i> -F. Muell.	Chloanthaceae	None	None	Common - Low
<i>Acacia ancistrocarpa</i> -Maiden & Blakely	Mimosaceae	None	None	Common - Moderate
<i>Acacia hilliana</i> -Maiden	Mimosaceae	None	None	Occasional - Low
<i>Acacia translucens</i> -Cunn. Ex Hook	Mimosaceae	None	None	Common - Moderate
<i>Eucalyptus victrix</i> -L.A.S. Johnson & K.D. Hill	Myrtaceae	None	None	Occasional - Moderate
<i>Melaleuca glomerata</i> -F. Muell.	Myrtaceae	None	None	Occasional - Low
<i>Melaleuca lasiandra</i> -F. Muell.	Myrtaceae	None	None	Occasional - Low
<i>Jacksonia aculeata</i> -W. Fitz.	Fabaceae	None	None	Common - Low
<i>Triodia basedowii</i> -E. Pritzel	Poaceae	None	None	Abundant - High
<i>Triodia aff. wiseana</i> -E. Pritzel	Poaceae	None	None	Sparce - Low
<i>Grevillea eriostachya</i> -Lindley	Proteaceae	None	None	Sparce - Low
<i>Grevillea wickhamii</i> -Meisn. McGill	Proteaceae	None	None	Common - Moderate
<i>Hakea lorea</i> -R. Br.	Proteaceae	None	None	Sparce - Low

### *Spinifex leaf anatomy*

As is characteristic of *Triodia* species, both usually exhibited leaf lamina tightly rolled into a needle-like form with the adaxial surface forming the major groove. Papillae, or trichomes, project from the epidermal cells lining this groove which interdigitate and occlude much of the groove volume (Craig and Goodchild 1977). *T. schinzii* displayed sunken stomatal grooves and mesophyll tissue only on the adaxial (inner) side of the leaf (Figure 3.2a, c, e), whilst *T. basedowii* displayed such structures on both the adaxial and

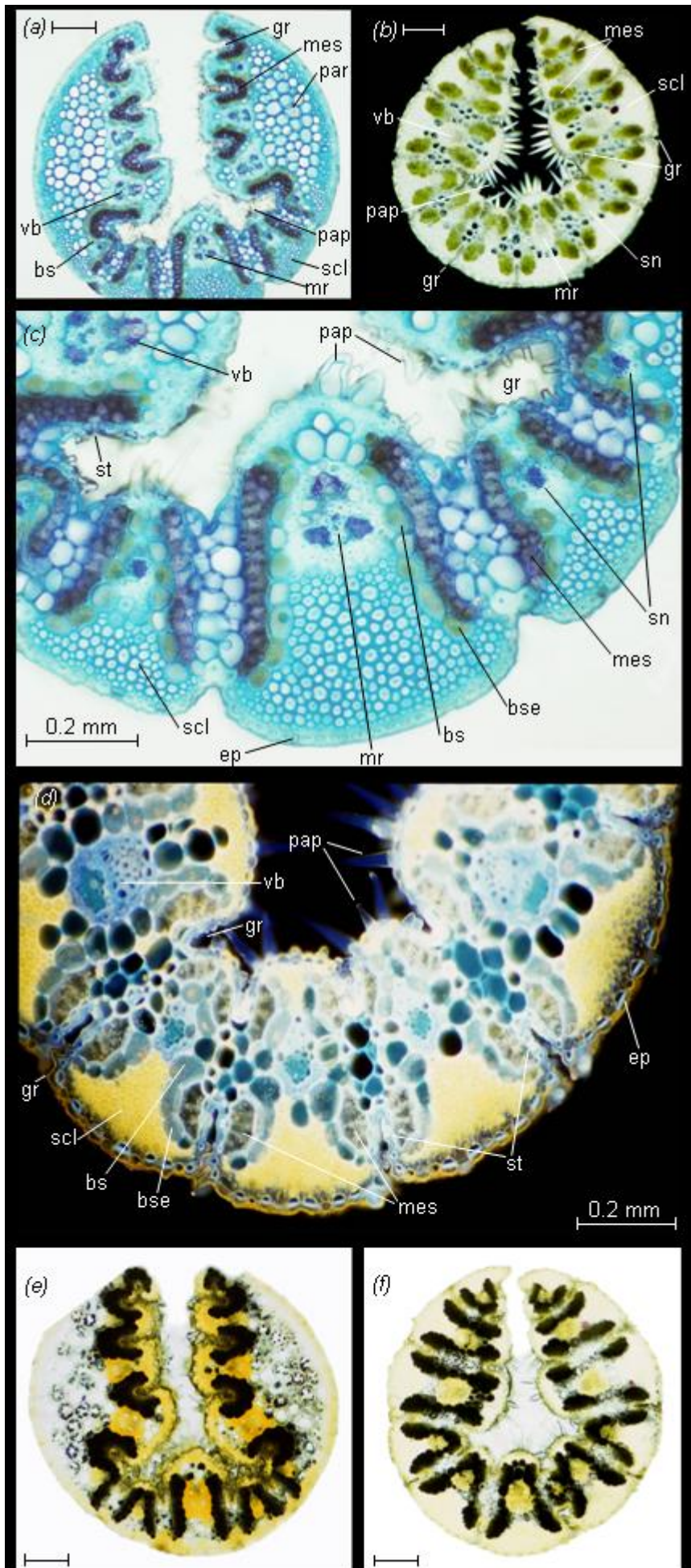
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abaxial (outer) sides (Figure 3.2b, d, f). Both species demonstrated a modified Kranz leaf anatomy, as the thick-walled bundle sheath cells were accompanied by bundle sheath extension cells, which wrap around the mesophyll (Figure 3.2c, d). Iodine staining identified very high concentrations of starch granules in bundle-sheath cells, mesophyll cells and low concentrations in parenchyma cells of both species (Figure 3.2e and 2f).

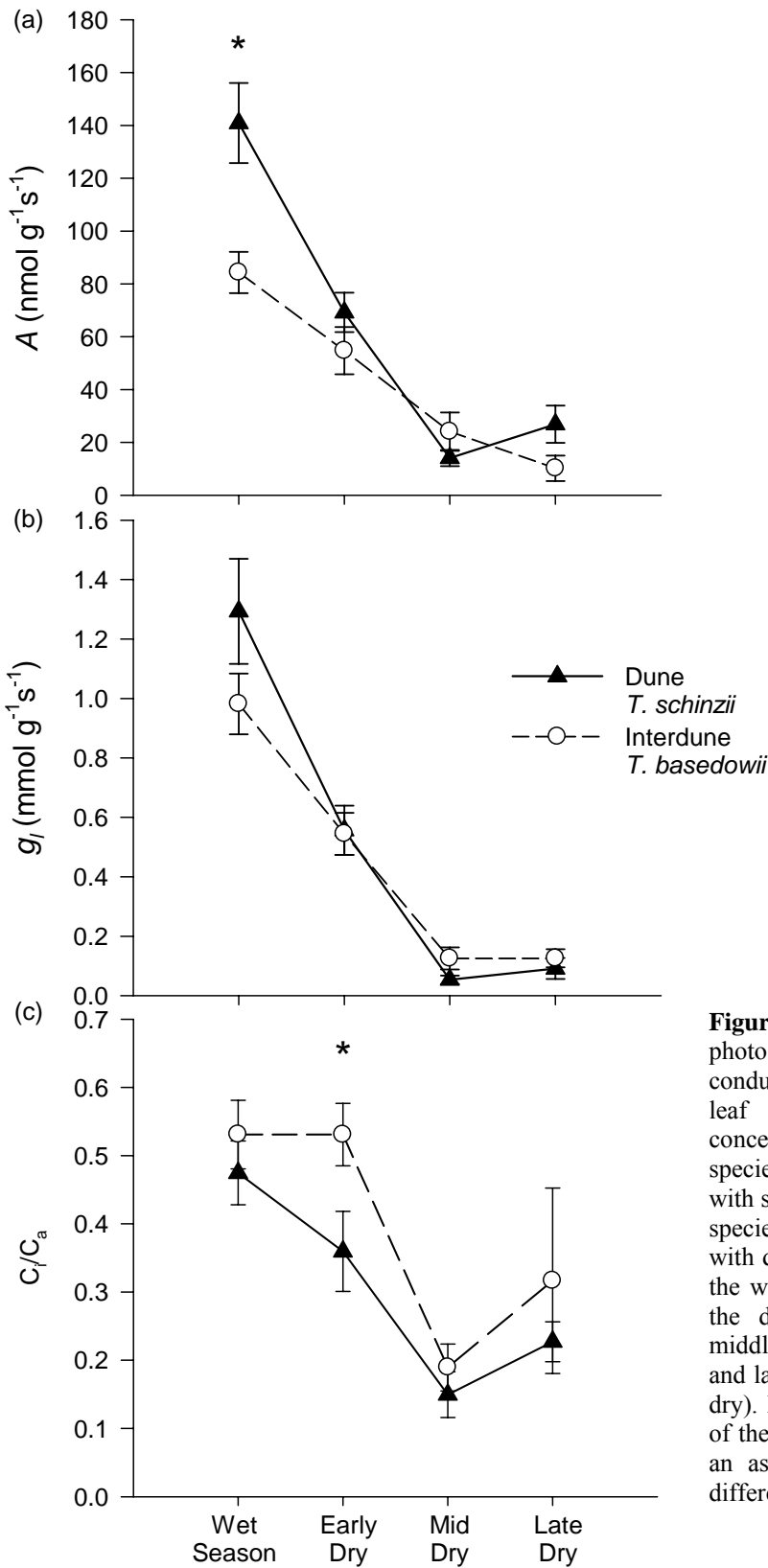
#### *Photosynthesis and water relations*

Maximum rates of photosynthesis ( $A$ ) occurred in the wet season in both years of the study, and were at their lowest during the middle of the dry season for *T. schinzii* and late in the dry season for *T. basedowii* (Figure 3.3a). These slightly different seasonal patterns resulted in a significant interaction term between species and season ( $df= 70$ ,  $p= 0.0077$ ), although a significant difference between species was indicated ( $p=0.0091$ ). During the wet season, when leaves were in their least rolled state, *T. schinzii* plants in the dune habitat displayed an average net  $\text{CO}_2$  assimilation rate of  $140 \text{ nmol g}^{-1} \text{ s}^{-1}$ , whilst *T. basedowii* in the interdunes displayed  $85 \text{ nmol g}^{-1} \text{ s}^{-1}$ . A *post-hoc* test revealed this difference was significant. Late during the dry season, *T. schinzii* displayed average  $A$  values of  $26 \text{ nmol g}^{-1} \text{ s}^{-1}$  compared with  $10 \text{ nmol g}^{-1} \text{ s}^{-1}$  for *T. basedowii*. During one sampling time when there had been less than 1 mm of rain recorded in 256 days, *T. schinzii* individuals averaged  $A$  values of  $9.4 \text{ nmol g}^{-1} \text{ s}^{-1}$  whilst *T. basedowii* individuals exhibited values of  $2.7 \text{ nmol g}^{-1} \text{ s}^{-1}$ . In March 2002, three days after a tropical cyclone brought 89 mm of rain to the site, with temperatures around  $36^\circ\text{C}$ , *T. schinzii* displayed a net rate of photosynthesis averaging  $180 \text{ nmol g}^{-1} \text{ s}^{-1}$ . However, by July 2002, this had decreased to  $13 \text{ nmol g}^{-1} \text{ s}^{-1}$ .

Seasonal patterns of leaf conductance followed a similar trend to photosynthesis, however, there were no significant differences between species at any time of year ( $df= 70$ ,  $p= 0.1505$ ). Maximum leaf conductance values in the wet season were around  $1.2 \text{ mmol g}^{-1} \text{ s}^{-1}$  for *T. schinzii* (Figure 3.3b). Although considered less appropriate because of leaf-rolling issues, this figure equates to approximately  $350 \text{ mmol m}^{-2} \text{ s}^{-1}$  when expressed on a leaf area basis. The lowest  $g_l$  values during the middle of the dry season were below  $0.1 \text{ mmol g}^{-1} \text{ s}^{-1}$  for both species- or about  $25 \text{ mmol m}^{-2} \text{ s}^{-1}$  when considered on an area basis. Both species displayed similar area/mass relationships as there was no significant difference ( $df= 140$ ,  $p= 0.1639$ ) in mean specific leaf area (SLA) between *T. schinzii* ( $27.9 \pm 0.9 \text{ s.e.}$ ) and *T. basedowii* ( $29.4 \pm 0.7 \text{ s.e.}$ ).



**Figure 3.2** Photographs of leaf transverse sections depicting (a) *T. schinzii* whole leaf section stained with toluidine blue viewed under a light microscope; note the photosynthetic mesophyll tissues (mes) are associated with the adaxial (inner) surface or main groove (b) *T. basedowii* whole leaf section unstained and viewed using a Nomarski differential interference contrast microscope; note the spine-like papillae (pap) in the main groove and photosynthetic tissues present on both adaxial and abaxial sides (c) *T. schinzii* leaf section stained with toluidine blue showing stomata (st) inside the main groove (gr) and bundle sheath extension (bse) cells very distant from vascular tissue (d) *T. basedowii* leaf section stained with Rhodamine B and Aniline Blue; note the stomatal grooves sunken inwards from the abaxial (outer) and adaxial surfaces (e) and (f) iodine staining of *T. schinzii* and *T. basedowii* respectively showing presence of starch mainly in bundle sheath and mesophyll cells, with some starch grains in parenchyma cells. Scale bars in all images equate to 0.2 mm. Abbreviations: vb- vascular bundles, gr- stomatal groove, mes- mesophyll, bs- bundle sheath, bse- bundle sheath extension cells, pap- papillae, scl- sclerenchyma, par- parenchyma, mr- mid-rib, sn- subsidiary nerve, st- stomata, ep- epidermis.

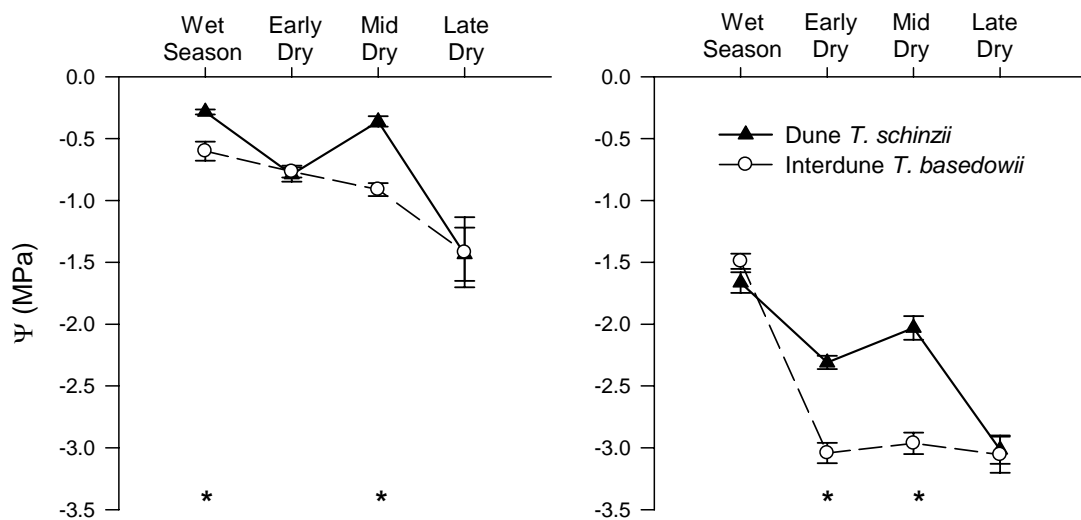


**Figure 3.3** Mean net photosynthetic rate (a), mean leaf conductance (b) and mean ratio of leaf internal to external CO<sub>2</sub> concentrations (c) for the dune species *T. schinzii* (black triangles with solid line, n=32) and interdune species *T. basedowii* (open circles with dashed line, n=39) throughout the wet season (wet), early part of the dry season (early dry), the middle of the dry season (mid dry), and late during the dry season (late dry). Error bars are standard errors of the mean. Symbols marked with an asterisk (\*) denote significant differences (α=0.05).

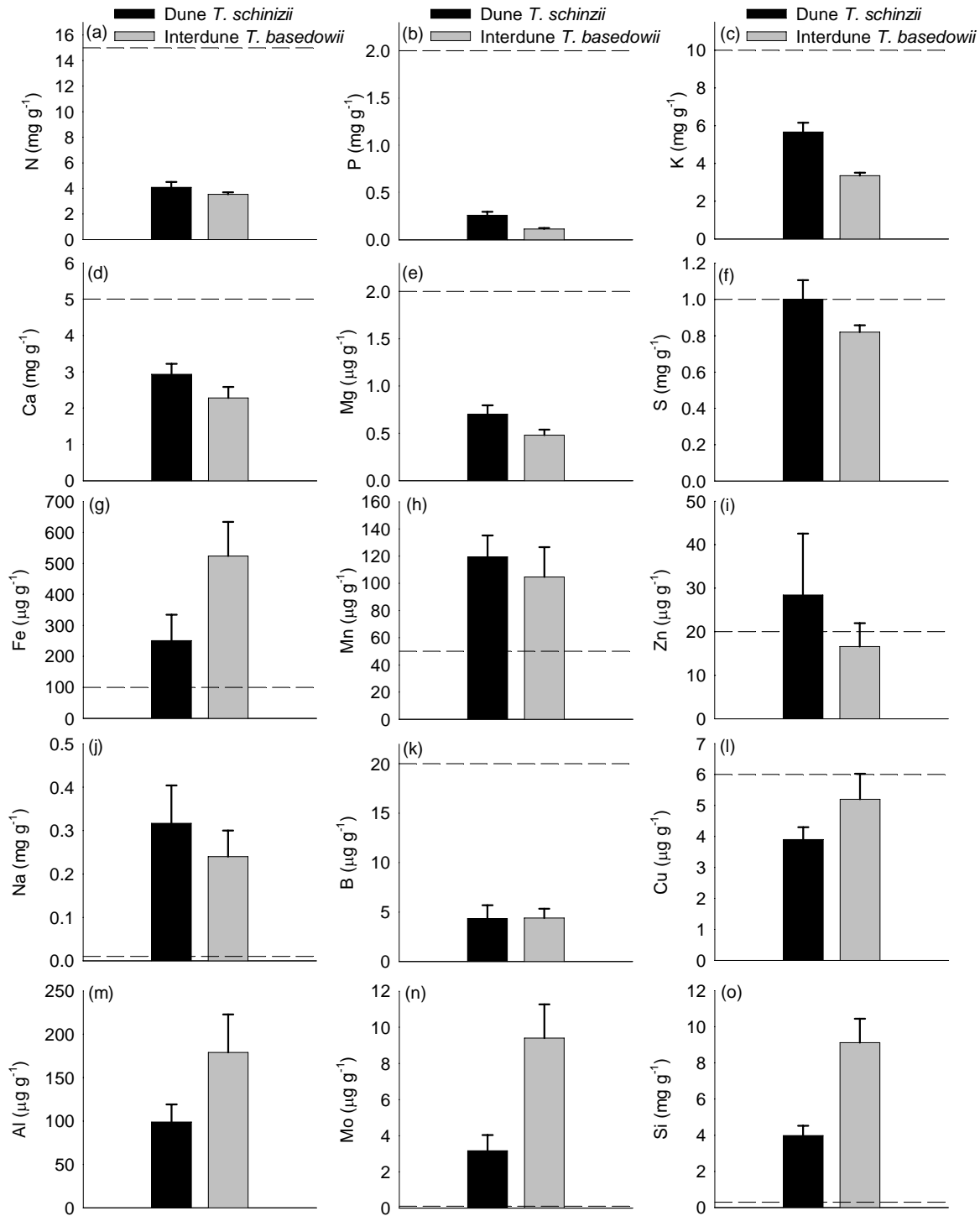
With higher rates of photosynthesis in *T. schinzii* than in *T. basedowii*, but similar leaf conductance in each,  $C_i/C_a$  values were significantly lower in the dune species (df=70, p= 0.0374) (Figure 3.3c). Foliar  $\delta^{13}C$  concentrations were also significantly different

between species ( $df= 11$ ,  $p=0.0406$ ), with *T. schinzii* displaying a less negative value ( $-13.9 \text{ ‰} \pm 0.13 \text{ s.e.}$ ) than *T. basedowii* ( $-14.3 \text{ ‰} \pm 0.11 \text{ s.e.}$ ).

Leaf water potentials were highest during the wet season and lowest at the end of the dry season for both species (Figure 3.4). However, the two species displayed different seasonal patterns in  $\Psi$ , which were highlighted by significant species x season interaction terms for predawn ( $df= 162$ ,  $p= 0.0329$ ) and midday ( $df= 157$ ,  $p= 0.0001$ ) leaf water potential. The interaction may be due to the fact that *T. schinzii* maintained less negative  $\Psi$  values further into the dry season than *T. basedowii*. Midday  $\Psi$  values in *T. basedowii* dropped sharply from  $-1.5 \text{ MPa}$  in the wet season to  $-3.0 \text{ MPa}$  in the early part of the dry season, then persisted at  $-3.0 \text{ MPa}$  for the remainder of the dry (Figure 3.4). Conversely, *T. schinzii* displayed  $\Psi$  midday values around  $-2.0 \text{ MPa}$  during the early and middle of the dry season. *Post-hoc* tests indicated significant differences in  $\Psi$  midday values between species during these seasons; and indicated predawn  $\Psi$  values were less negative in *T. schinzii* than *T. basedowii* during the wet season and middle part of the dry season. There was no difference in  $\Psi$  values between species late in the dry season with predawn values  $\sim -1.5 \text{ MPa}$  and midday values  $\sim -3.0 \text{ MPa}$  (Figure 3.4).



**Figure 3.4** Mean leaf water potentials at (a) predawn and (b) midday for the dune species *T. schinzii* (black triangles with solid line,  $n=75$ ) and interdune species *T. basedowii* (open circles with dashed line,  $n=88$ ) throughout the wet season (wet), early part of the dry season (early dry), the middle of the dry season (mid dry), and late during the dry season (late dry). Error bars are standard errors of the mean. Symbols marked with an asterisk (\*) denote significant differences ( $\alpha=0.05$ ).



**Figure 3.5** Macro- and micronutrient concentrations (a-o) for the dune species *T. schinzii* (black filled bars,  $n=6$ ) and the interdune species *T. basedowii* (grey filled bars,  $n=6$ ) compared with values for 'adequate' nutrition (dashed horizontal line) defined by Epstein and Bloom (2005). Error bars are standard errors of the mean. Symbols marked with an asterisk (\*) denote significant differences ( $\alpha=0.05$ ).



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### *Nutrient relations*

Foliar nutrient concentrations of the two *Triodia* species were compared with reference values considered to be adequate for plant nutrition (Epstein and Bloom 2005). Relative to these standard values, P was lowest (10-15% of the reference value), followed by N (~25% of the reference value) (Figure 3.5). In terms of site-related differences, *T. schinzii* on the dune displayed a significantly higher P concentration than *T. basedowii* in the interdune. There were no significant differences in N concentration between these species. There was also no difference in  $\delta^{15}\text{N}$  concentration in foliage; *T. schinzii* mean =  $1.40 \pm 0.35$  ‰ (s.e.) and *T. basedowii* mean =  $1.39 \pm 0.60$  ‰ (s.e.) (df= 11, p=0.9839). Concentrations of Mg, B, K and Ca were also less than half the value of the reference. In most other cases, nutrient concentrations in leaves showed values in the range of 'adequate nutrition'. Both *Triodia* species, particularly *T. basedowii*, accumulated extremely high levels of Mo ( $9.4 \text{ mg kg}^{-1}$ ) and Si ( $9.1 \text{ mg g}^{-1}$ ), being almost 95 and 18 times higher, respectively, than considered 'adequate' by Epstein and Bloom (2005).

## **Discussion**

### *Plant community characteristics on dunes and interdunes*

Similar representation of major family groups (e.g. Myrtaceae, Fabaceae, Proteaceae and Poaceae) on adjacent dunes and interdunes may be attributed to similarities in soil type for each landform element. However, the segregation of closely related and often congeneric species according to habitat is repeated many times and highlighted by the exclusive occurrence of *T. schinzii* on the dune and restriction of *T. basedowii* to the interdune (Table 3.1).

Total projected plant cover values were similar across the two habitats (42 - 49%). Such uniform cover is evidence to suggest that rainfall infiltrates locally and there is no run-off/run-on distribution occurring from the dunes to the interdunes. Cover values reported here are in the mid to upper range of values reported for spinifex communities elsewhere; 5% for young spinifex stands (Bell 1981), 40% for spinifex dominant stands (Winkworth 1967) and up to 77% for mature, mixed stands (Hesse and Simpson 2006). This is largely due to the absence of fire from the area for many years. Considerable amounts of dead leaf material within hummocks, especially in the centre of old, ring-form *T. basedowii* clumps is visual evidence of this explanation.

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Whilst *T. basedowii* is killed by fire and regenerates entirely from seed, the dune species *T. schinzii* is able to resprout and recover after fire (Rice and Westoby 1999). Vegetative reproduction is considered advantageous on sand dunes as establishment from seed is extremely difficult due to wind exposure causing detachment or burial (Danin 1996). With survival of below ground parts, it is not surprising the root system of *T. schinzii* is larger and capable of extending to twice the depth (~2 m) of its fire-killed relative, *T. basedowii*. This dramatic difference in rooting depth is likely to give *T. schinzii* greater access to water stored deeper in the soil and thus a better water status further into the dry season.

#### *Water relations of plants on dunes and interdunes*

Leaf conductance to water vapour ( $g_l$ ) and photosynthesis ( $A$ ) were greatest when water was most available during the wet season for both *Triodia* species (Figure 3.3). Being C<sub>4</sub> plants, the combination of high temperatures and plentiful rainfall during the summer season permitted very high rates of  $A$ . If expressed on an area basis, using projected area of the measured leaves, such rates of photosynthesis equate to around 39  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for *T. schinzii* and 26  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for *T. basedowii*. This conversion of gas exchange rates from a dry mass basis to an area basis is for comparison purposes only and is considered valid as there were no significant differences in SLA between species. Photosynthesis rates for other grass species from semi-arid regions are generally less than these values. Reported photosynthesis values for the C<sub>4</sub> grass *Paspalum plicatulum* Michx., are around 24  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (Gifford and Morison 1985) and for *Andropogon gerardii* Vitman., around 25  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (Knapp *et al.* 1993). Semi-arid zone C<sub>3</sub> grasses often display lower net photosynthesis values, typically between 12-15  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for species such as *Stipa tenacissima* L. from the dry Mediterranean (Pugnaire *et al.* 1996) and *Festuca idahoensis* Elmer, from the rangelands of North America (Doescher *et al.* 1997). Net photosynthesis rates greater than 40  $\mu\text{mol m}^{-2} \text{s}^{-1}$  are, however, common for crop species such as *Zea mays* L. (Crafts-Brandner and Salvucci 2002) and *Sorghum bicolor* (L.) Moench (Peng *et al.* 1991) under well watered conditions.

Very low photosynthetic rates were displayed by both spinifex species in the middle and late parts of the dry season, with  $A$  values almost 10% of those of the summer wet season maxima (Figure 3.3). Leaf conductance responded in a similar manner to photosynthesis throughout the seasons, and ranged from 1.2  $\text{mmol g}^{-1} \text{s}^{-1}$  (around 350  $\text{mmol m}^{-2} \text{s}^{-1}$ ) in the wet season to less than 0.1  $\text{mmol g}^{-1} \text{s}^{-1}$  (below 30  $\text{mmol m}^{-2} \text{s}^{-1}$ )

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during the middle of the dry season. Whilst there were no differences in  $g_l$  between *T. schinzii* and *T. basedowii* at any time of year, higher rates of photosynthesis in the wet season by *T. schinzii* indicated greater photosynthetic water-use efficiency. Significantly lower  $C_i/C_a$  values substantiated this assessment and were in line with significantly less negative foliar  $\delta^{13}C$  values in *T. schinzii* than *T. basedowii*. It can be concluded that following wet season rains, the dune species *T. schinzii* assimilates more carbon per unit water lost than its congeneric relative, *T. basedowii*, in the interdune.

With respect to leaf anatomy, the arrangement of sunken stomata only on the inner (adaxial) surface of *T. schinzii* leaves but on both sides of *T. basedowii* leaves seems counterintuitive considering the latter is distributed across the drier regions of the Australian continent. However, the tightly interlaced folds at the entrance of the abaxial, deeply sunken stomatal crypts of *T. basedowii* (Figure 3.2d) potentially offer better protection than the trichomes in the main groove. The lack of external stomata on leaves of the dune species, *T. schinzii*, may also confer an advantage to coping with higher wind speeds and sand-blasting typical on dune crests (Seely 1991; Bowers 1996; Fet *et al.* 1998).

Both *Triodia* species displayed a modified ‘Kranz’ anatomy where bundle-sheath cells extended beyond the vascular bundle and surrounded the mesophyll. Foliar  $\delta^{13}C$  values of around -14 ‰, confirm that these species employ the  $C_4$  photosynthetic pathway (Lambers *et al.* 1998). Iodine staining indicated starch accumulation, predominantly in the chloroplasts of the bundle sheath cells, and, somewhat surprisingly, in mesophyll and even parenchyma cells. Starch is typically found only in the bundle sheath cells of  $C_4$  species (Echeverria and Boyer 1986), so its presence in the mesophyll and parenchyma is atypical. However it has been noted previously that *Triodia* grasses are unusual and difficult to categorise into a particular  $C_4$  sub-group due to oddities of chloroplast position in the bundle sheath and their mesotome character (Hattersley and Watson 1976; Craig and Goodchild 1977; Hattersley and Browning 1981).

Improved water availability during the summer wet season resulted in the least negative predawn and midday leaf water potentials for both species (Figure 3.4). At this time and in the middle of the dry season, *T. schinzii* displayed significantly less negative  $\Psi$  values at predawn than *T. basedowii*. This finding indicates soil moisture reserves were diminished more quickly from the rhizosphere of the interdune species than *T. schinzii*

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from the dune. By the end of the dry season, however, both species attained the same predawn  $\Psi$  value of around -1.5 MPa. Little water is available in sandy soils below -1.5 MPa, a point at which moisture content is around 0.1% v/v (Noy-Meir 1973). Extremely low leaf conductance rates for both species late during the dry season support this assertion. Predawn  $\Psi$  values reported here are within a similar range to those of other xeric species growing in sandy, arid sites elsewhere (e.g., Pavlik 1980- *Swallenia alexandrae* (Poaceae); Monson and Smith 1982- *Baccharis sarothroides* (Asteraceae); Rosenthal *et al.* 2005- *Stipa hymenoides* (Poaceae)).

The rapid decline in midday  $\Psi$  from -1.5 MPa in the wet season to -3.0 MPa in the early part of the dry season for *T. basedowii* indicates that soil moisture reserves in the interdune were less than in the dunes. However, the slightly greater proportion of clay + silt in the interdune (5.5% compared with only 1% for the dune), may hold more water per unit volume of soil and yield moisture with more negative water potentials (Sperry and Hacke 2002). Considering leaf conductance rates were similar for both species in all seasons, despite more negative  $\Psi$  values exhibited by *T. basedowii*, there is some evidence that even this small fraction of fine soils is influencing leaf water potentials.

If such small textural differences are influencing water storage properties of these soils, then the 'inverse texture effect' is also likely to be affecting dune and interdune habitats differently. Considering this effect is most significant when rain falls in brief showers, followed by warm, dry, and windy conditions, small rain events may be lost more quickly to evaporation from the interdunes. The seasonal development of a cryptogamic crust, although patchy, could have some moderating effect by reducing water loss from the soil to the atmosphere (George *et al.* 2003; Austin *et al.* 2004). However, this resistance layer can also reduce infiltration rates and result in greater runoff on slopes (Yair 1990, Yair *et al.* 1997). Because of the well vegetated nature of the dune slopes and absence of any crust here, runoff did not occur and water soaked in locally.

Continuous rain from large cyclonic events will infiltrate deeply in both dunes and interdunes and therefore be largely unaffected by any inverse texture effect differences. Water that percolates beyond the rooting zone of the *Triodia* grasses is then utilised by shrubs and trees with extensive root systems, some of which can be over 8 m deep, as is the case for *Corymbia chippendalei* on the dune (see Grigg *et al.* 2008 - Chapter 2). It is proposed that both plant communities, with their functional diversity and stable plant

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cover, utilise most of the rainfall in average years, with little being lost to deep drainage. Other studies in semi-arid areas, including those conducted on sandy soils, have reported minimal deep drainage beneath mature, undisturbed native vegetation (Allison *et al.* 1994; Gee *et al.* 1994; Yair *et al.* 1997).

The results of this study complement the findings of Pavlik (1980-Eureka Dunes, California) and Rosenthal *et al.* (2005-Little Sahara Dunes, Utah). Taking into consideration the various climatic, physical and hydrological conditions presented by these and other studies on desert dune and interdune systems, I conclude that sand dunes offer more readily available water than interdunes and off-dune habitats when rainfall is 100-350 mm per annum. In the two studies conducted on locations where rainfall was less than 100 mm (Gries *et al.* 2003- Taklamakan Desert NW China; Niu *et al.* 2005 Hunshandak Sandland, Inner Mongolia), the presence of a water table became more influential on plant water status than soil water storage fluctuations.

#### *Nutrient relations of spinifex on dunes and interdunes*

Concentrations of most macro- and micro-nutrients in soil were significantly higher in the interdunes than the dunes (Grigg *et al.* 2008 - Chapter 2). However, there were few differences in foliar nutrient concentrations for *T. schinzii* and *T. basedowii* (Figure 3.5). Accretion mounds created by the long-term accumulation of organic matter and top-soil dust by *T. schinzii*, evidently offset the generally poorer soils in bare areas on the dunes. The resprouting strategy, long life-span, and deep roots of *T. schinzii* evidently provide additional advantages other than re-establishment after fire and anchoring in the loose soils. In the interdunes, *T. basedowii* is killed by fire so does not live long enough to form significant accretion mounds. Both spinifex species exhibited relatively low macronutrient concentrations, especially of P and N (Figure 3.5). Koerselman and Meuleman (1996) proposed that N:P ratios greater than 16:1 are indicative of P limitation and those less than 14:1 are indicative of N limitation for temperate herbaceous vegetation. However, tropical grasses are typically more N efficient than temperate ones, so N:P ratios as low as 12 can be considered indicative of P limitation (Lambers *et al.* 1998; Ludwig *et al.* 2001). In the current study, *T. schinzii* from the dune habitat displayed an N:P ratio of 16:1, whilst that of *T. basedowii* in the interdune was 30:1. This finding denotes that P, rather than N was the major limiting nutrient in both habitats for this part of the Great Sandy Desert, particularly in the interdunes. Termites and/or cryptogamic crust organisms may be contributing enough N to ensure

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this element is not a severely limiting factor in the Great Sandy Desert ecosystem. One study in another part of the Pilbara region, 400 km west of the current investigation, did not find termite activity or cryptogamic crust development (Bennett and Adams 2001). At this site, the C<sub>4</sub> grass *Themeda triandra* Forsskal, displayed an N:P ratio of 7:1. Fertiliser trials confirmed that N was indeed the major limiting nutrient in that study (Bennett and Adams 2001).

With respect to the other nutrients examined in the foliage of the two spinifex species, concentrations of K, Ca, Mg, B and to some extent Cu were all well below the values considered 'adequate' (Epstein and Bloom 2005). Concentrations of S and Zn were very close to the reference values, whilst those of Fe, Mn, Mo and Si were greater than those considered adequate by at least a factor of two. Si concentration for *T. basedowii* foliage was 9.1 mg g<sup>-1</sup>, and the element in greatest abundance followed by N (3.5 mg g<sup>-1</sup>) and K (3.4 mg g<sup>-1</sup>). At a concentration 19 times higher than that considered 'adequate', Si presumably enhances structural integrity and defence capabilities of the needle-like leaf blades (Epstein and Bloom 2005). *T. basedowii* also accumulated almost 100 times more Mo than considered 'adequate'. Such high levels of Mo far exceed the requirements for enzyme production, mainly associated with acquisition or utilisation of nitrogen, so the purpose and reason for this hyper-accumulation requires future research.

#### *Concluding remarks*

Differences in community composition, highlighted by the separation of spinifex species on dunes and interdunes, depend more on soil depth and associated water storage than soil texture and mineral nutrition. Significantly greater water status, coupled with higher rates of photosynthesis displayed by *T. schinzii* indicate that the dunes offer a more readily available store of water. The short roots exhibited by *T. basedowii* are likely to place this species at a competitive disadvantage in the dune habitat but ensure it is better adapted to the shallow, gravelly interdune soils. Bearing in mind that *T. schinzii* dominates the wetter (>350 mm annual rainfall) northern latitudes of spinifex distribution in Australia, and *T. basedowii* the drier (<300 mm) more southern interior, I suggest that the deep sandy dunes, with their ability to efficiently capture and hold moisture, permit the occurrence and passage of *T. schinzii* further south into the more arid interior.

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## Chapter 4

### Using ecophysiological parameters to diagnose problems associated with minesite rehabilitation: a case study on *Acacia* and *Triodia* species

#### Abstract

Successful rehabilitation and establishment of vegetation on mined land is essential to prevent contaminated soil and water dispersing into the surrounding landscape. It is vital, therefore, to monitor the progress of rehabilitation and to identify problems early-on so corrective measures can be taken, if necessary. The present study aimed to diagnose the reasons why plant health and vegetation cover were relatively poor on a mine-rehabilitation site compared with plants in natural vegetation. Plant water relations and mineral nutrition were assessed for three *Acacia* shrub species and two *Triodia* grass species. Soil physical, chemical and hydrological properties were also quantified. *Acacia* species at the rehabilitation site displayed signs of water stress including lower stomatal conductance and sap velocity during the dry season, and higher leaf  $\delta^{13}\text{C}$  values. Leaf water potentials at predawn were more negative at the rehabilitation site, although the finer-textured soils complicate interpretation for defining water stress to some extent. *Triodia* species also demonstrated more negative  $\Psi$  values, but no differences between sites for the other parameters. Concentrations of N, P and K in foliage were similar for most species in natural and rehabilitation sites. Foliar Cu, Fe, Zn, and particularly Al concentrations were significantly higher at the rehabilitated site. Heavier-textured waste-material likely caused mechanical difficulties for root penetration, and alkaline pH and high metal concentrations likely compounded this problem. Plants occurred only where sandy cover soils were >0.2 m due to the combined benefits of greater depth for root exploration and the 'capillary-break' effect reducing evaporative losses from the waste material. A 'store-and-release cover' with a range of greater soil depths (0.5 – 3 m) and reduced slope angles ( $\leq 14^\circ$ ) is recommended to improve water management, plant cover, biodiversity, and reduce erosion and water ingress to potentially acid-forming sulfidic material within the waste-rock dump

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## Introduction

Rehabilitation of degraded land resulting from mining is a requirement in many countries and must comply with environmental standards defined by legislation and government regulatory bodies. In general, rehabilitation projects are carried out to re-establish a natural or managed ecosystem that is safe, stable, non-polluting, resilient and self-sustaining (Aronson *et al.* 1993; Environmental Protection Agency 1995). However, reconstructed landforms and artificially established ecosystems often impose altered conditions for plant growth, with few original native species suited to the new habitat. To identify why certain plant species fail to establish and grow in these modified conditions requires an understanding of these species' ecophysiology in both natural and mine-affected sites (Schmidt *et al.* 1999).

Environmental parameters that influence the ecophysiology and health of plants on rehabilitation sites include: the chemical toxicity of mine residues (Bradshaw 1983; Baker and Proctor 1990; Cunningham *et al.* 1995; Tordoff *et al.* 2000; Archer and Caldwell 2004), soil physical properties (compaction, texture and erodability (Paniagua *et al.* 1999; Arunachalam *et al.* 2004; Li and Shao 2006; Szota *et al.* 2007)), soil nutrient status and organic-matter content (Wong 2003; Prober *et al.* 2005), and biological fertility, including the presence of micro-organisms (rhizobia, mycorrhizal fungi (Daft and Hacskeylo 1977; Jasper *et al.* 1989; Bentham *et al.* 1992; Rao and Tak 2002; Thrall *et al.* 2005)) and invertebrate fauna (Majer *et al.* 1984; Majer and Nichols 1998; Andersen *et al.* 2002). In addition to these, it is almost axiomatic that water availability is important on mine-rehabilitation sites, particularly in arid and semi-arid regions (Wong 2003).

To date, very little has been published on plant water status and water use on mine-rehabilitation sites. This is surprising considering the importance of water extraction from rehabilitation soil covers, especially where it is necessary to prevent the ingress of water into buried, hazardous mine residues. The few studies that have been conducted report that mature plants on mine-rehabilitation sites are often more water stressed than those in their natural habitat (Enright and Lamont 1992; Schmidt *et al.* 1999). Seedlings, however, may display higher water status on mine rehabilitation sites than natural sites until roots come into contact with adverse subsoils and competition for

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water increases (Bleby 2003). Plant water stress is likely due to poor infiltration and excessive runoff from slopes, and/or insufficient volume of hospitable soil for root establishment (Carroll *et al.* 2000; Szota *et al.* 2007). Soil water storage and availability for plants is most important in seasonally dry environments, particularly where rainfall volume and timing are unpredictable. These issues pose additional challenges for rehabilitation in semi-arid regions, where many mining activities occur (Lubke and Avis 1998; Tordoff *et al.* 2000; Rao and Tak 2002).

This study was conducted in a semi-arid part of the Great Sandy Desert in north-western Australia. The natural vegetation in this region is dominated by spinifex hummock grasses of the genus *Triodia*, and scattered woody shrubs and trees including different species of *Acacia*, *Grevillea*, *Corymbia* and *Eucalyptus*. Sand dunes and interdunes are stable, well vegetated (with 42% and 49% cover, respectively, and 165 species), and display distinct plant communities (Grigg *et al.* 2008a,b - chapters 2 and 3). This is in marked contrast to the rehabilitation site, which displays poor plant cover, evidence of mass-mortality among seedlings, and heavily eroded slopes. Anecdotal reports of seedling performance after the first twelve months of establishment indicated uniform seedling density and reasonable species richness ( $\geq 20$ ; pers. comm. Phil Davidson, Nifty Copper Operation Environmental Manager). However, this study was conducted seven years after establishment, by which time only five native species were found at the rehabilitation site; three *Acacia* shrubs and two *Triodia* grasses. In the natural desert ecosystem, these plants occur in a variety of habitats; in the interdunes, *A. ancistrocarpa* Maiden & Blakely exists where conglomerated gravels form a hardpan 2-2.5 m below the surface; *A. translucens* (Cunn. ex Hook) inhabits shallower soils where the gravel hardpan is typically 0.5-1 m below the surface; and *A. hilliana* (Maiden) exists in very shallow soils (~0.1 m) on shale rock outcrops. Co-existing with acacias in the interdunes is the grass species *T. basedowii* (E. Pritzel), whilst *T. schinzii* (Henrard-Lazarides) occurs only on the deep sandy dunes. Depth of native sandy soil at the rehabilitation site was approximately 0.2 m over mine-waste material. It was anticipated that the mine-waste material was physically and/or chemically hostile to root growth and that the limited cover soil layer was insufficient to support plant water requirements.

The aim of this investigation was to gain an understanding of the ecophysiological requirements of plants in natural vegetation and through comparison of plant

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functioning, apply this knowledge to diagnose the causes of poor plant cover and health on the mine-rehabilitation site. To assess the hospitability of soils, I determined their chemical characteristics, and physical and hydraulic properties. I examined seasonal plant water-use patterns (gas exchange, stem sap velocity), water status (leaf water potential), and an integrated measure of water use-efficiency ( $\delta^{13}\text{C}$  - Farquhar *et al.* 1989; Pate and Dawson 1999). The effects of soil texture on hydraulic properties and plant water potentials are considered (Sperry *et al.* 2002; Sperry and Hacke 2002; Hultine *et al.* 2005). Plant nutrition (foliar macro- and micro-nutrients and  $\delta^{15}\text{N}$ ) was studied to reveal nutrient deficiencies or toxicities, and the likely importance of  $\text{N}_2$ -fixation (by acacias). This suite of ecophysiological tools should complement other methods for assessing ecological integrity, such as Landscape Function Analysis (Tongway and Hindley 2000; Ludwig *et al.* 2004), and assist in the design and monitoring of future rehabilitation efforts.

## **Materials and Methods**

### *Study site location, soils and vegetation cover*

Fieldwork was conducted on a mine-rehabilitation site at Nifty Copper Operation (21°40'S 121°35'E) and in nearby (within 5 km) natural vegetation in the Great Sandy Desert of north-western Australia. The sites were 350 km inland of the west coast and the landscape is characterised by vegetated and stable red sand dunes of Quaternary origin (Bowler 1976; Nanson *et al.* 1992; Rhodes *et al.* 2004). As a whole, the landscape is remarkably flat; however, sand dunes averaging 12 m in height occur at varying distances apart; 50 m for braided dunes, and up to 1500 m for linear dunes (Beard 1969). Interdunes have sandy soils, with dense gravel layers starting typically within 0.5 m of the surface and grading to a hardpan by 2-3 m.

The mine-rehabilitation site was located on the sloping (~18°) sides of the waste-rock dump, which contained potentially acid-forming chalcopyrite rock encapsulated beneath relatively inert mine-waste materials. The outermost layer of mine-waste material was a white, mudstone shale (sedimentary) recovered from 10-30 m below the interdune surface. Upon exposure to water or physical disturbance this material readily delaminates and breaks into finer particles, forming a slaking silty loam. Heavy machinery was used to construct the waste-rock dump, spread a cover soil layer, and deep-rip along the contours to a depth of 0.5 m and at a spacing of 1 m. Between rip



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lines, compaction from heavy machinery movements was evident. The cover soil layer consisted of a mixture of dune and interdune soil to an average depth of 0.2 m (range 0.0-0.4 m), although there was considerable mixing with the silty mine-waste material in the rip lines. The physical and chemical characteristics of soils from the natural interdune site, cover soils and exposed waste material at the waste-rock dump rehabilitation site are summarised in Table 4.1, and more detailed descriptions and analysis methods are described in Grigg *et al.* (2008a) (Chapter 2). The rock fraction of the mine-waste material was removed by sieving (5 mm mesh size) and the soil fraction only was analysed.

The natural vegetation at this site has never been exposed to livestock grazing or any other non-indigenous land-use prior to the exploration and opening of the mine. The prevalence of *Triodia* grasses and associated woody taxa (predominantly Myrtaceae, Proteaceae and Fabaceae) in the Nifty Copper Mine area, is typical for the Great Sandy Desert and the broader region of northern and central Australia (Grigg *et al.* 2008a - Chapter 2). Plant species composition was recorded at both the natural and rehabilitation sites, whilst total projected plant cover (%) was determined using image analysis of digital photographs taken from a helium balloon-mounted camera at low altitudes (usually 10 to 100 m – see methods in Grigg *et al.* 2008b - Chapter 3). The three *Acacia* shrubs (*A. ancistrocarpa*, *A. translucens* and *A. hilliana*) and two *Triodia* grasses (*T. schinzii* and *T. basedowii*) that occur at the rehabilitation site are all found in natural vegetation within 3 km of the mine site. At the commencement of this study, all plants at the rehabilitation site were approximately seven years old. All of five species were selected for ecophysiological measurements at both natural and mine rehabilitation sites.

#### *Climate and seasons*

Most rain occurs during the summer (January to March) and is associated with tropical low-pressure systems and cyclones. The long-term average rainfall for the study area is around 330 mm, although this is extremely variable. In 2000, 849 mm of rain fell in the area, making it one of the wettest years on record. This study began in 2001, which was also a wetter than average year (523 mm), and continued until the end of 2002, which was slightly drier than average (274 mm) (Bureau of Meteorology 2008). Little to no rain may occur for several months at a time, especially between July and November. Total potential evaporation (Class A pan) far exceeds rainfall in every month; averaging

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over 4000 mm per year (Bureau of Meteorology 2008). Vapour pressure deficit (VPD) can be as high as 8 kPa between October and January, a time when daily maximum temperatures are often higher than 40°C (Grigg *et al.* 2008a - Chapter 2). During winter (June to August), temperatures typically range between 26°C in the day and 10°C at night.

For the purposes of this study, seasons were classified according to the time since summer rains. The ‘wet’ season included January, February and March. During the two years of this study, monsoonal precipitation was well above average and over 200 mm of rain fell in the month before these sampling times. April to June were considered the ‘early’ part of the dry season and a time when moisture availability was moderate, but in decline. July to September were termed the ‘middle’ of the dry season and sampling was carried out when there had been no rain for at least two months. October to December was termed the ‘late’ part of the dry season and displayed little rainfall. For detailed records of weather data, please refer to Grigg *et al.* (2008a) (Chapter 2).

#### *Leaf gas exchange*

Measurements of photosynthesis ( $A$ ) and stomatal conductance ( $g_s$ ) were made *in situ* on the youngest, fully matured, healthy leaves on the north (sun-exposed) side of each plant using a Li-Cor 6400 portable infra-red gas analyser (LI-COR Inc. Lincoln, NE, USA). At least three measurements were taken on each plant and between three and five individuals were assessed for each species at all sampling times. Sampling was between 10:00 and 14:00 hours Western Standard Time (WST). An artificial light source of red and blue LEDs was used to administer a light-saturating photosynthetic photon flux density of 1500  $\mu\text{mol m}^{-2} \text{s}^{-1}$  at all times. Vapour pressure and temperature in the chamber were maintained as close as possible to those of ambient air. Reference gas  $\text{CO}_2$  concentration was set at 380  $\mu\text{mol mol}^{-1}$  and flow rates regulated so leaf chamber  $\text{CO}_2$  concentration was between 360 and 375  $\mu\text{mol mol}^{-1}$ . Leaf temperatures were calculated using an energy balance equation (Li-Cor 6400 Manual 2000).

Measured leaf sections were sealed in zip-lock plastic bags, chilled and taken to the laboratory where their leaf areas were measured on a back-lit flatbed scanner at a scanning resolution of 0.2  $\mu\text{m}$  (WinRhizo V3.0.3 1995, Regent Instruments Quebec City, Canada). Leaves were then oven dried (70°C) for one week, and dry weights recorded. Due to changing degrees of leaf rolling between seasons for *Triodia* species, I

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expressed photosynthesis and leaf conductance ( $g_l$ , incorporating boundary layer effects) on a dry mass basis.

Eight sampling periods were conducted roughly three months apart, with each of the above-mentioned seasons (wet season, early dry, mid dry and late dry) captured twice.

#### *Leaf water potentials*

Leaf water potentials ( $\Psi$ ) were measured at predawn (03:00-05:00 h WST) and midday (12.00-14.00 h) using a Scholander-type pressure chamber (PMS Instruments, Corvallis, OR, USA). For each sample period, leaf water potentials were measured for three shoot sections from three to five randomly selected individuals. Shoot sections exhibited at least four leaves. Immediately after being excised shoot/leaf samples were sealed in zip-lock plastic bags with only the cut end protruding and placed inside the pressure bomb; all measurements were taken within one minute of cutting. These measurements were taken within one or two days of the gas exchange measurements during the eight fieldtrips mentioned above.

#### *Sap-velocity measurements*

The heat ratio method (Burgess *et al.* 2001a,b) was used to measure sap velocity in stems of four *A. ancistrocarpa* plants of similar size in natural and mine-rehabilitation sites. Probe construction followed design specifications set out in Burgess *et al.* (2001a), with two copper-constantan thermocouple junctions 5 mm and 15 mm back from the tip of each needle. One probe set was placed on north and south sides of each stem 0.3-0.4 m above the ground and attached via AM416 multiplexers to CR10X dataloggers (Campbell Scientific Inc. Logan, UT, USA). Measurements began in October 2001 and continued for nine months, after which stems were cut above and below the probes. Cut sections were wrapped in plastic to prevent drying from the exposed ends and the probes left running for two days. This created zero flow conditions, which were used to establish baseline values. In order to compare sites equally, sap velocity is expressed in relative terms. Sap velocity for each probe, at each half-hour sampling time, was averaged for each week and reported as a percentage of the maximum value displayed by that probe throughout the entire experimental period. The average of all four trees from each site is presented for three periods; first, when moisture availability was moderate due to a 23 mm rainfall event ten days earlier (weeks 1-5); second, during wet conditions following 256 mm of rain (weeks 14-18);

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and third, during the dry period when there had not been any rain for three months (weeks 27-31).

*Isotope composition: carbon and nitrogen*

Approximately 20 mature leaves, free from insect attack, were collected from the northern (sunny) side of four to six individuals of each species during the dry season (July) 2002. These were air-dried in the field, oven-dried at 70°C for one week, and ground using a ball mill.  $\delta^{13}\text{C}$  analysis was performed using continuous-flow mass spectrometry (Roboprep + Tracermass Ion Ratio Mass Spectrometer - Europa Scientific, Crewe, UK).  $^{13}\text{C}:^{12}\text{C}$  ratios of the  $\text{CO}_2$  produced by combustion at 1000°C in an oxygen atmosphere were compared with a cornflour standard (ANCA 53), calibrated in turn against the international standard NBS-22.  $^{15}\text{N}:^{14}\text{N}$  ratios were compared against a radish standard (ANCA 54) calibrated against international standards (IAEA-N1, IAEA-N2, IAEA-NO3). Analytical precision based on multiple replicate analyses for  $\delta^{13}\text{C}$  is  $\pm 0.2\text{‰}$  relative to the PeeDee Belemnite standard; for  $\delta^{15}\text{N}$  it is  $\pm 0.3\text{‰}$  relative to air. Analyses were performed at the Western Australian Biogeochemistry Centre (WABC).

*Nutrient composition of leaves*

The same leaf material collected for isotope analyses was sub-sampled for nutrient composition. Nitrogen concentration was determined colourimetrically (indophenol blue method) using an autoanalyser system after digestion with sulfuric acid and hydrogen peroxide (Yuen and Pollard, 1954). Another subsample of leaf material was digested with a mixture of nitric and perchloric acids (McQuaker *et al.* 1979), and then analysed by ICP-AES (Varian Vista axial spectrometer, Palo Alto, CA, USA) to determine concentrations of phosphorus, potassium, sodium, calcium, magnesium, sulfur, boron, copper, iron, manganese, molybdenum, zinc, aluminium and silicon. Analyses were performed at the Chemistry Centre (Western Australia).

*Soil hydraulic conductivity, runoff and erodability*

Saturated hydraulic conductivity ( $K_s$ ) was measured on soil cores using the constant-head method described by Reynolds (1993), adapted from that of Klute and Dirksen (1986). Intact cores, 50 mm long and 50 mm diameter, were collected from four sites; two natural sites (dune and interdune), and two rehabilitation sites – one site where cover soils were deep (~300 mm), and another site where waste material was exposed at the surface. At each location, 24 samples were taken: 12 at the soil surface, and 12 at

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200 mm depth. Any cores that were cracking or crumbling were rejected. In the laboratory, cores were gradually saturated from the bottom up. To ensure stable  $K_s$  measurements were attained, test duration for the mine-waste material was 6-8 hours, whilst for the sandy, natural soils, 1 hour was sufficient.

Runoff and soil erodability were measured for the mine-waste material. *Ex-situ* soil trays (750 x 750 x 200 mm) were filled to the top, angled at 10°, 15° or 20°, and exposed to a simulated rainfall intensity of 75 mm h<sup>-1</sup>. The rainfall simulator used is described in detail by Loch (2000a, 2001). ‘Rain’ was produced from flat fan Veejet 80-100 nozzles and swept back and forth across each plot. Droplet size, terminal velocities and kinetic energy at impact with the soil surface were representative of natural rain at the same intensity (~30 J m<sup>-2</sup> mm<sup>-1</sup>) (Rosewell 1986; Kinnell 1987). Runoff samples were collected in 1-L jars, and changeovers for new jars were timed. After a settling period of five days, bulk water was decanted and weighed; wet soil remaining in the contained was also weighed. These soils were oven dried at 70°C for one week then weighed. The mass of water lost from the soil during the drying process was added to the mass of water decanted so exact calculations of runoff could be made.

### *Statistics*

*Acacia* and *Triodia* species were examined separately. Completely randomised designs were used to assess relationships between ecophysiological parameters and dependent variables. For leaf water potential, photosynthesis, and stomatal conductance, three-way ANOVAs with the factors: site, season and species (either *Acacia* or *Triodia*) were performed. For mineral concentrations, isotope concentrations, and relative sap-velocity values, two-way ANOVAs with the factors site and species were performed. Factors were treated as fixed and interactions between factors were included in the model (first-order and second-order). Homogeneity of variances was assessed using Cochran’s test and data transformed ( $\log_{10}$ ) if group variances were heterogeneous. Pairwise comparisons were carried out using Tukey’s *post-hoc* test when ANOVAs indicated significant treatment (or interaction) effects (Quinn and Keough 2002). *F* values with their associated degrees of freedom (total and interaction if appropriate), are reported along with *P* values;  $\alpha= 0.05$ . Analyses were conducted using JMP V4 software (SAS Institute Inc., Cary, NC, USA).

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## Results

### *Vegetation cover and root morphology*

Projected plant cover on the mine-rehabilitation site was 12 %; about one quarter of that at the natural site (49% - Table 4.1, Figure 4.1a, b, c). The natural site displayed a moderately diverse flora, with 165 native species documented, whilst at the rehabilitation site only five native species were in reasonable abundance. Dead stems were numerous ( $>400 \text{ ha}^{-1}$ ) and many dislodged individuals were found in erosion gullies. With over 85% bare ground, unstable soils, and steep slopes ( $\sim 18^\circ$ ), severe rill and tunnel erosion was widespread at the rehabilitation site (Figure 4.1d). Excavations at the rehabilitation site revealed that all three *Acacia* species displayed dimorphic roots, with laterals restricted to the relatively sandy top 0.2 m of cover soil. Sinker roots did penetrate the mine-waste material but tapered sharply at the interface and were not found further than 0.3 m below this ( $\sim 0.5$  m below surface level). In its natural habitat, *A. ancistrocarpa* displayed a highly lateralised root system and a sinker root that descended at least 1.5-2 m into conglomerated gravels but was thought unlikely to penetrate far into the hardpan beyond this point. Similar root morphology was observed for *A. translucens*, although shallower gravel layers and hardpan (0.5 – 1 m) restricted its root depth further. *A. hilliana* on the shale rock outcrops displayed roots that headed along and into fissures in the rock and lateral roots that exploited the little soil available above this. In their natural habitat, roots of the *Triodia* grasses were fibrous but woody in appearance; *T. schinzii* in the dune habitat displayed roots down to 2 m, whilst *T. basedowii* in the interdune displayed roots down to 1 m or shallower (but at least 0.2 m) where gravels were heavily conglomerated. At the rehabilitation site, both *Triodia* grasses required cover soils at least 0.2 m deep and roots were not found further than 50 mm into the mine-waste material.

### *Landform topography and soil properties*

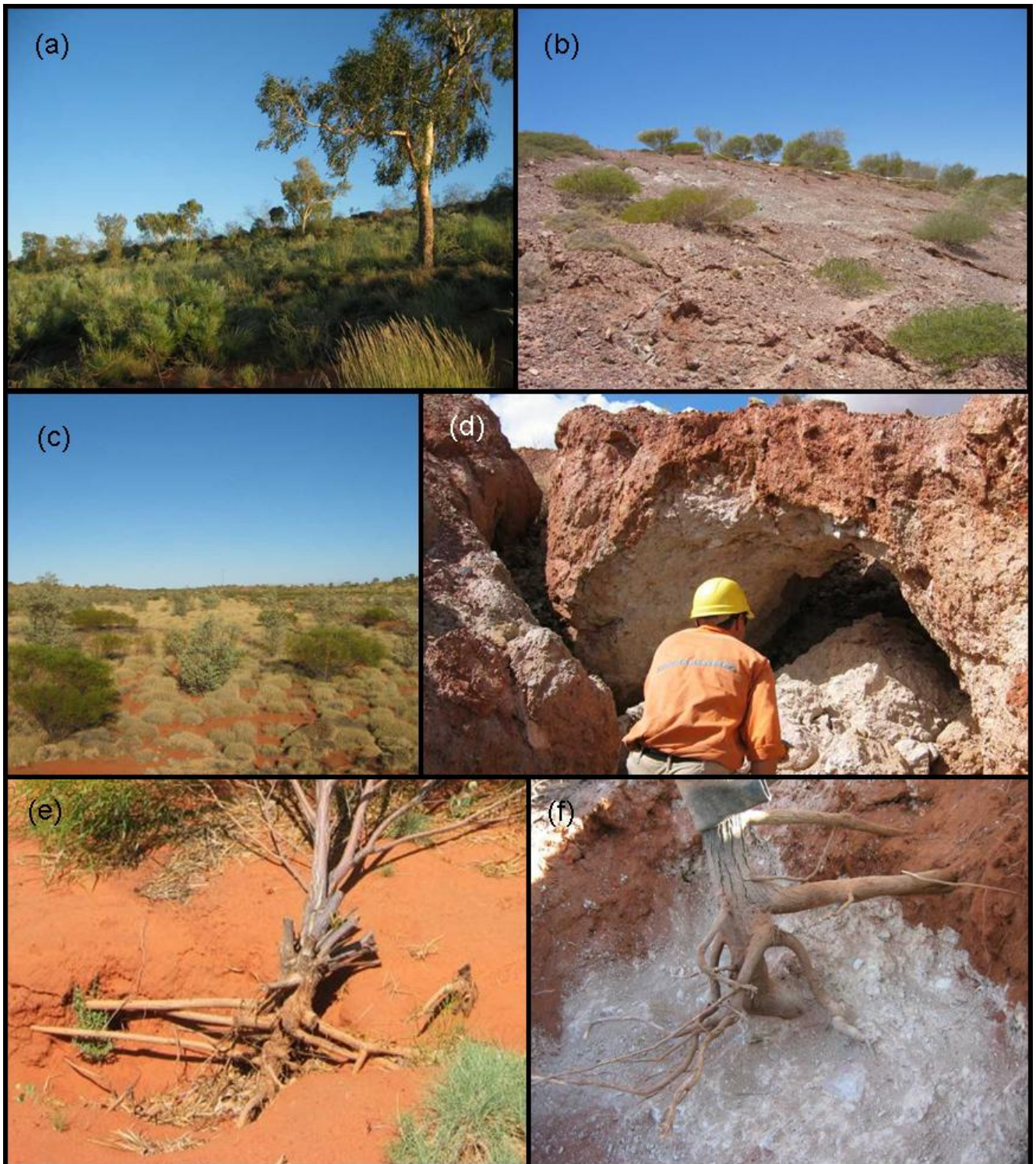
Slope angles of vegetated native dunes were generally similar ( $14^\circ$  to  $18^\circ$ ) to those of the rehabilitation site, but water erosion and runoff were never observed as the sandy soils absorbed all rainfall locally (see Figure 4.1a, b). Soil texture and structure was very different between sites. Native interdunes and particularly dunes were extremely sandy (Figure 4.1e), but the rehabilitation site was a combination of these sandy soils overlying mine-waste material at  $<0.2$  m depth (Figure 4.1f). The mine-waste material was a silty loam and quite compacted in between rip lines.

**Table 4.1** Total projected plant cover and soil physical and chemical properties for undisturbed natural and rehabilitation sites and for mine-waste material.

Attribute	Natural	Rehabilitation	Mine Waste
Total projected area vegetated (all plant matter)%	49 ± 2	12 ± 2	0 or Buried
Soil pH (0-0.1 m)	5.9 ± 0.07	7.3 ± 0.06	8.7 ± 0.1
Soil EC 1:5 w/v (0-0.1 m) mS/m	1 ± 0	21 ± 7	46 ± 16
Sand Content (0-0.1 m) %	94.5	88	35
Silt Content (0-0.1 m) %	0.5	7	45
Clay Content (0-0.1 m) %	5	5	20
Soil Texture Class	Sand	Loamy Sand	Silty Loam
Bulk Density (kg m <sup>-3</sup> )	1570 ± 12	1600 ± 16	1600 ± 22
Water Holding Content at Capacity (%)	11 ± 2	16 ± 3	25 ± 3
Cation Exchange Capacity (NH <sub>4</sub> Cl m.eq%)	1 ± 0	2 ± 0	5 ± 1
Organic Carbon (0-0.1 m) mg g <sup>-1</sup>	1.1 ± 0.06	1.1 ± 0.25	0.6 ± 0.02
Soil (0-10 cm) N - µg g <sup>-1</sup>	89 ± 5	193 ± 18	545 ± 145
Soil (0-10 cm) P - µg g <sup>-1</sup>	2 ± 0.1	2 ± 0.6	20 ± 6
Soil (0-10 cm) K - µg g <sup>-1</sup>	14 ± 0.6	65 ± 12	145 ± 35
Soil (0-10 cm) Ca - µg g <sup>-1</sup>	42 ± 7	280 ± 130	1850 ± 450
Soil (0-10 cm) Mn - µg g <sup>-1</sup>	40 ± 5	42 ± 13	198 ± 173
Soil (0-10 cm) Fe - µg g <sup>-1</sup>	18 ± 1	20 ± 1	43 ± 25
Soil (0-10 cm) Mg - µg g <sup>-1</sup>	12 ± 1	87 ± 17	755 ± 125
Soil (0-10 cm) Na - µg g <sup>-1</sup>	2.3 ± 0.9	44 ± 38	260 ± 60
Soil (0-10 cm) S - µg g <sup>-1</sup>	1.3 ± 0.3	90 ± 58	133 ± 57
Soil (0-10 cm) Cu - µg g <sup>-1</sup>	0.3 ± 0.07	28 ± 3	10 ± 7
Soil (0-10 cm) Co - µg g <sup>-1</sup>	0.31 ± 0.05	0.89 ± 0.19	1.65 ± 0.37
Soil (0-10 cm) Zn - µg g <sup>-1</sup>	0.1 ± 0	0.3 ± 0.03	1.05 ± 0.85
Soil (0-10 cm) B - µg g <sup>-1</sup>	0.13 ± 0.03	0.13 ± 0.03	0.5 ± 0
Soil (0-10 cm) Ni - µg g <sup>-1</sup>	<0.1 ± 0	0.17 ± 0.03	1 ± 0.7
Soil (0-10 cm) Mo - µg g <sup>-1</sup>	0.01 ± 0	0.01 ± 0	0.05 ± 0.03

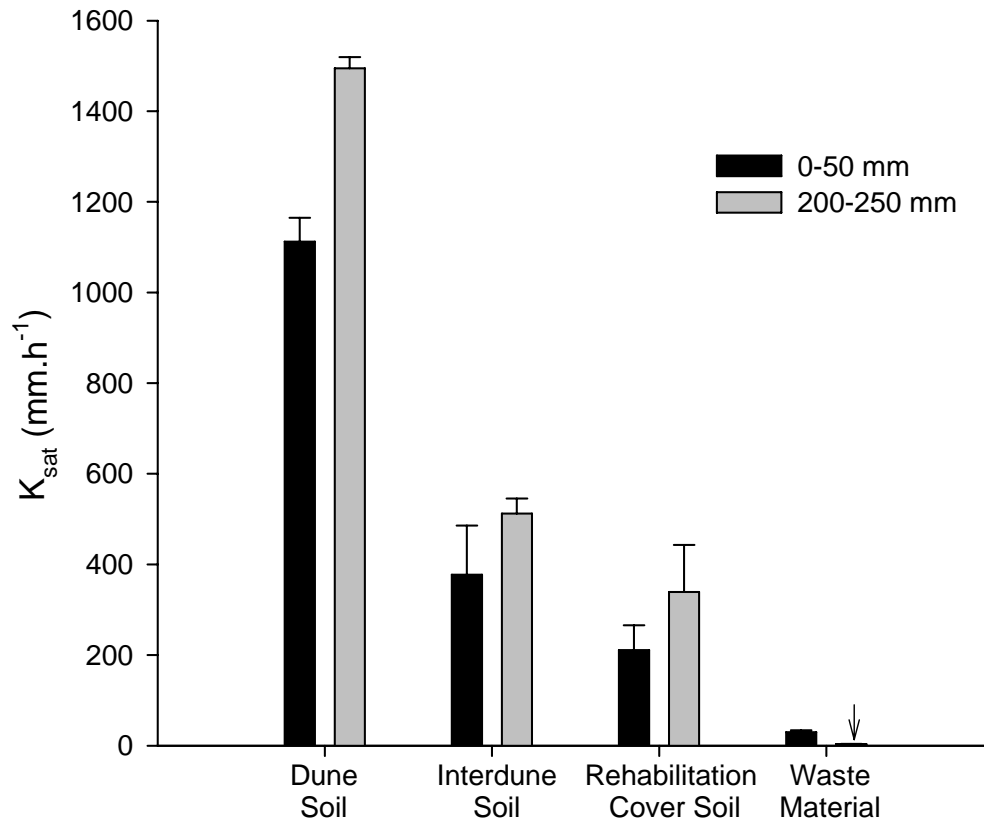
Hydraulic conductivity ( $K_{sat}$ ) of waste material was extremely low (<30 mm h<sup>-1</sup>) compared with all other soils, especially the sand from the dune, which had  $K_{sat}$  values over 50 times higher (Figure 4.2). Rainfall-simulator tests on *ex situ* re-packed soil trays of waste material demonstrated that over 70% of rainfall was lost to runoff when the slope angle was 10° (Figure 4.3a). Runoff increased to ~ 75% at 15°, and over 80% at 20° (Figure 4.3a). Initial runoff (first five minutes) was much faster for the 20° slope than the 10° slope, with 80% of flow running off compared to 25%. Maximum rates of sediment loss occurred within the first five minutes for the 20° slope, peaking at 4.2 kg m<sup>-2</sup> h<sup>-1</sup> (Figure 4.3b). Sediment loss was ~ 0.75 for the 10° slope, and 2 kg m<sup>-2</sup> h<sup>-1</sup> for the 15° slope (Figure 4.3b). After 15 minutes, runoff rates levelled off, and rates of sediment loss were around 1.1, 1.5 and 1.7 kg m<sup>-2</sup> h<sup>-1</sup> for the 10°, 15° and 20° slope

angles, respectively. Aggregate stability of the waste material was extremely poor, with complete slaking occurring within minutes but only minor particle dispersion.



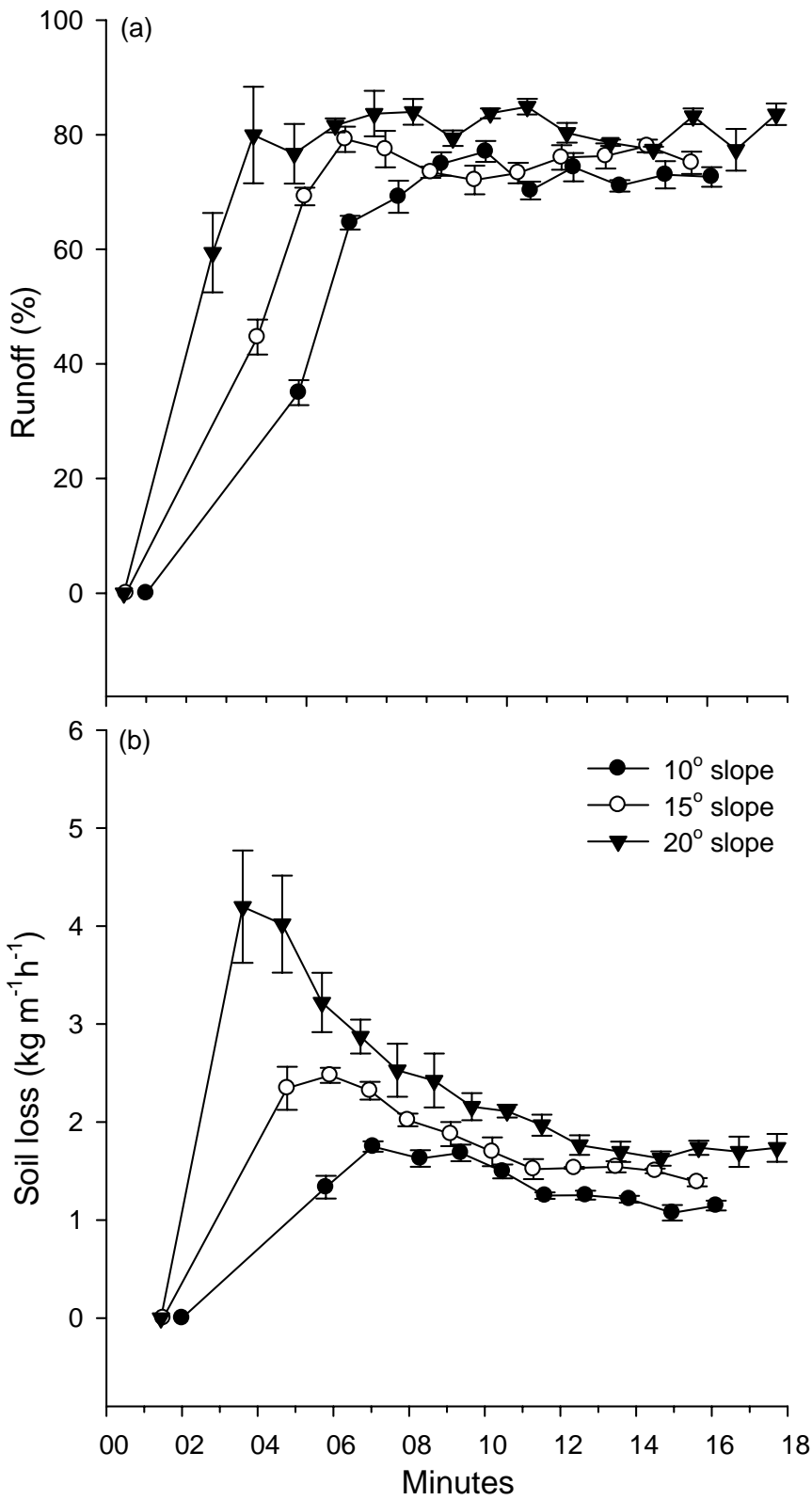
**Figure 4.1** Photographs of the study site illustrating (a) natural site with sand dunes covered by a diverse flora including species of *Acacia*, *Grevillea*, *Corymbia* and *Triodia*; (b) mine-rehabilitation site showing scattered *A. hilliana* in the foreground and *A. ancistrocarpa* with *A. translucens* in the background; (c) natural interdune vegetation dominated by *A. ancistrocarpa*, *G. wickhamii* and *T. basedowii*; (d) severe gully and tunnel erosion through minesite rehabilitation and white silty shale mine-waste material; (e) natural interdune *A. ancistrocarpa* with exposed root system; (f) *A. ancistrocarpa* root excavation to 30 cm depth into white shale waste material at the rehabilitation site; note the poor development of lateral roots into the waste material.





**Figure 4.2** Hydraulic conductivity for intact soil cores from two depths (0-50 mm and 200-250 mm). Samples collected from sand dunes and interdunes in the natural habitat, and from cover soils and exposed mine-waste material at the mine-rehabilitation site.

The pH of soils varied considerably between the natural and rehabilitation sites; native soils were mildly acidic (pH 5.9), cover soils at the rehabilitation site were close to neutral (pH 7.3), and the underlying waste material was alkaline (pH 8.7) (Table 4.1). Electrical conductivity (EC 1:5 w/v) was extremely low for native soils (<1 mS m<sup>-1</sup>), but relatively high for the waste material (46 mS m<sup>-1</sup>). If considered in terms a saturated soil paste extract (ECe) rather than a 1:5 w/v extract, the waste material equates to an ECe of ~ 460 mS m<sup>-1</sup>. Cover soils overlying the waste material displayed an EC approximately halfway between that of the native soils and the waste material (Table 4.1). Cation-exchange capacity of mine-waste material was five times that of native soils, and more than double that of cover soils. Concentrations of all elements tested were many times greater for the mine-waste material than for native soils, especially the macro-nutrients N, P and K. Sodium concentration was also very high in the mine-waste material, over 100 times that of soil from the natural site (Table 4.1).



**Figure 4.3** Runoff (a, % of rainfall) and sediment loss (b) from mine-waste material at slope angles of 10°, 15° and 20° during high-intensity rainfall ( $75 \text{ mm h}^{-1}$ ) from a rainfall simulator.

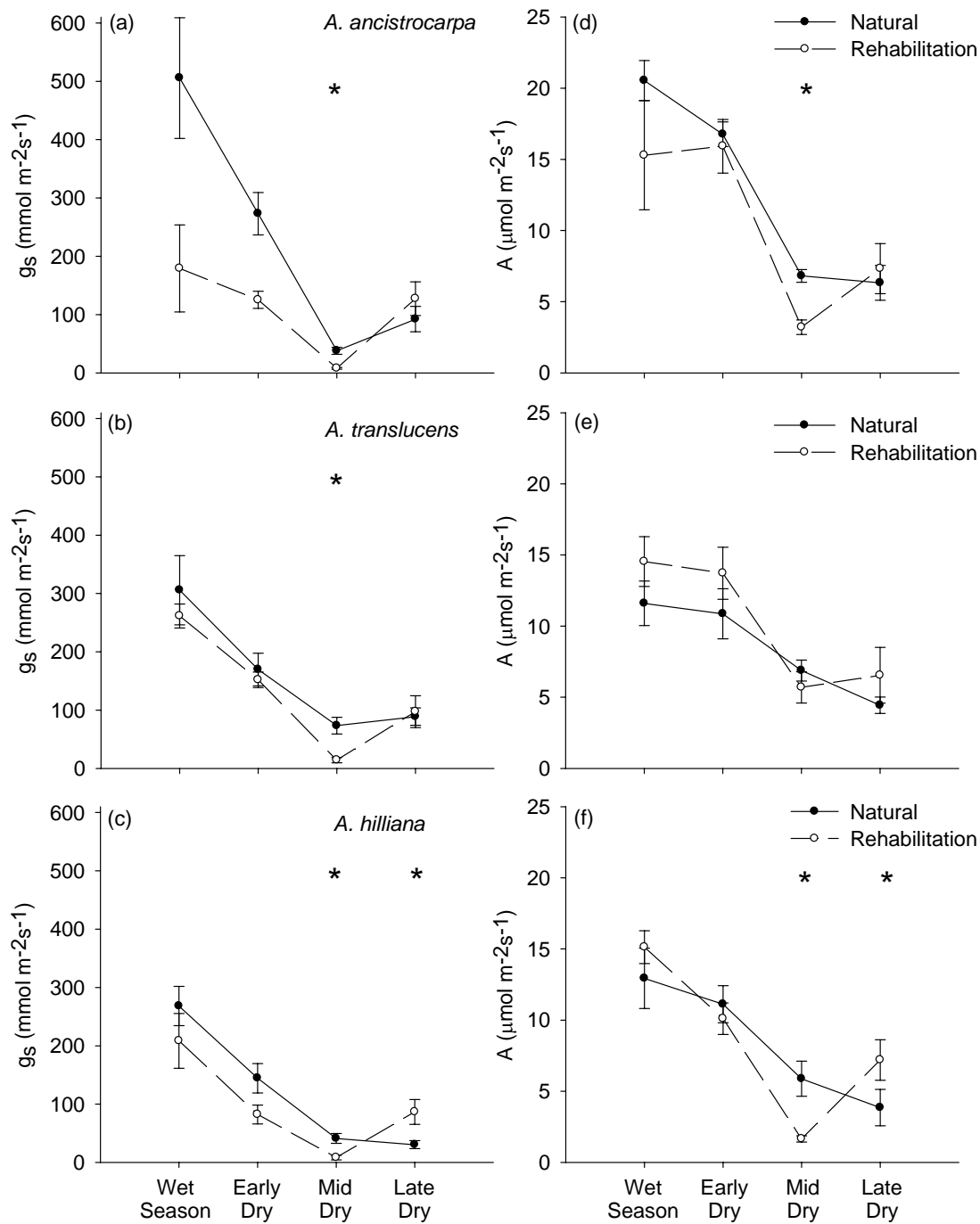
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### Leaf Gas Exchange

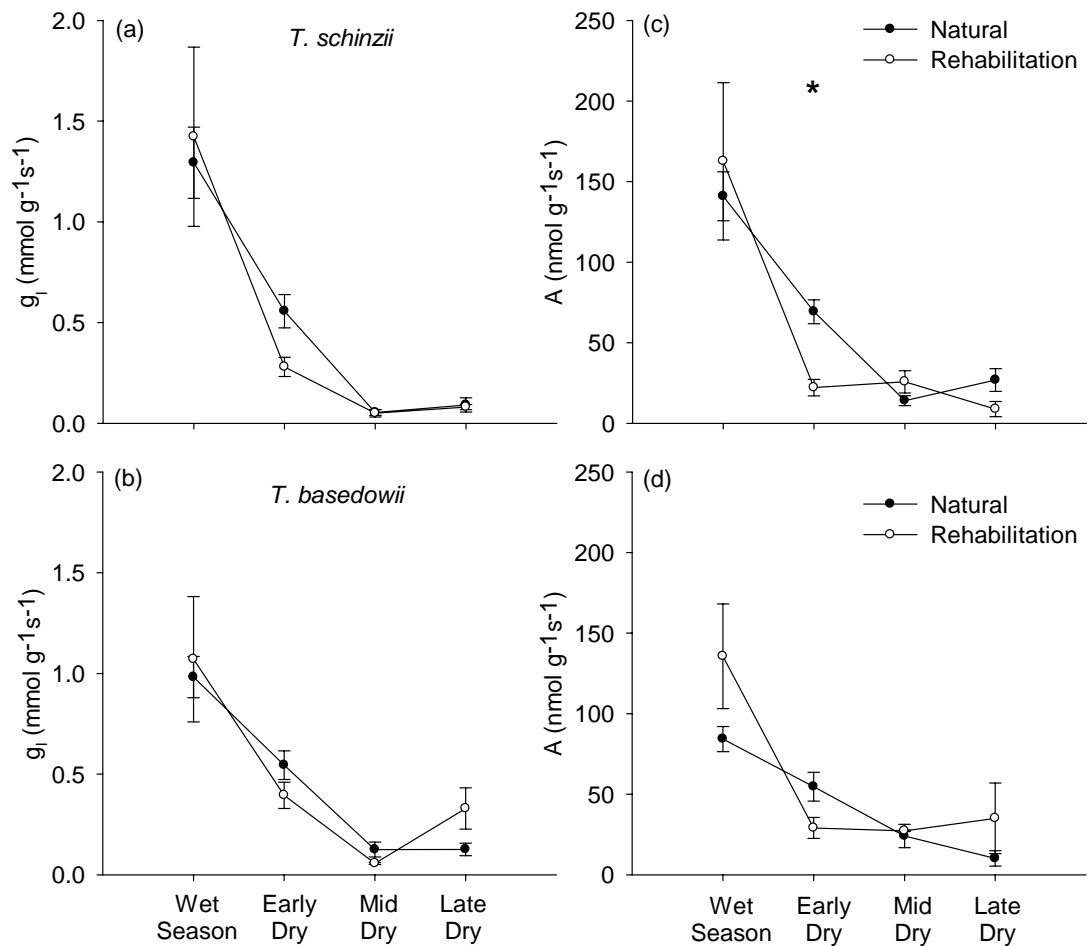
Site-related differences in leaf conductance ( $g_s$  or  $g_l$ ) and photosynthesis ( $A$ ) were complicated by interactions with season for both *Acacia* [for  $g_s$  ( $F_{(3,161)}=20.1$ ,  $P<0.001$ ) and for  $A$  ( $F_{(3,161)}=7.34$ ,  $P<0.001$ )] and *Triodia* species [for  $g_l$  ( $F_{(3,105)}=3.47$ ,  $P<0.05$ ) and for  $A$  ( $F_{(3,105)}=6.26$ ,  $P<0.001$ )]. *Post-hoc* tests on *Acacia*  $g_s$  data revealed that site-related differences occurred predominantly during the middle of the dry season, when conditions were extremely dry. At this time, all three species displayed lower stomatal conductance at the rehabilitation site (Figure 4.4a,b,c). Net photosynthesis was lower at the rehabilitation site during the mid-dry period for *A. ancistrocarpa* and *A. hilliana*, but not for *A. translucens* (Figure 4.4d,e,f). *Post-hoc* tests for *Triodia* species revealed no difference between sites for leaf conductance, and only one site difference for net photosynthesis; *T. schinzii* at the rehabilitation site had lower  $A$  during the early part of the dry season (Figure 4.5c).

### Leaf Water Potentials

Site-related differences in predawn or midday water potentials were complicated by soil textural differences. Finer-textured soils, such as those at the rehabilitation site, are inherently associated with more negative  $\Psi$  values for a given water content. Interactions among site, season, and species within each genus were significant (*Acacia*  $\Psi_{pd}$   $F_{(6,438)}=6.59$ ,  $P<0.001$ ; *Acacia*  $\Psi_{md}$   $F_{(6,432)}=4.76$   $P<0.001$ ; *Triodia*  $\Psi_{pd}$   $F_{(3,302)}=5.83$ ,  $P<0.001$ ; *Triodia*  $\Psi_{md}$   $F_{(3,302)}=5.83$ ,  $P<0.001$ ), and therefore main effects were discounted. *Post-hoc* tests of predawn  $\Psi$  values revealed that plants at the rehabilitation site had lower values than those at the natural site for four of the five species (two of the three *Acacias* and both *Triodia* species) during most seasons (Figure 4.6 a,b,d,e). Patterns in midday  $\Psi$  values were not as clear; site differences were less frequent (only occurring for one or two seasons) and the direction of the difference varied among species. At the rehabilitation site, lower  $\Psi_{md}$  values occurred for *A. translucens* and both *Triodia* species during some seasons; higher  $\Psi_{md}$  values were found for *A. hilliana* and *A. ancistrocarpa* during the early part of the dry season (Figure 4.6). All species showed seasonal fluctuations in midday leaf water potentials with the exception of *A. ancistrocarpa*, which consistently displayed values around -2 MPa throughout every season. Soil texture effects are elaborated upon in the discussion.



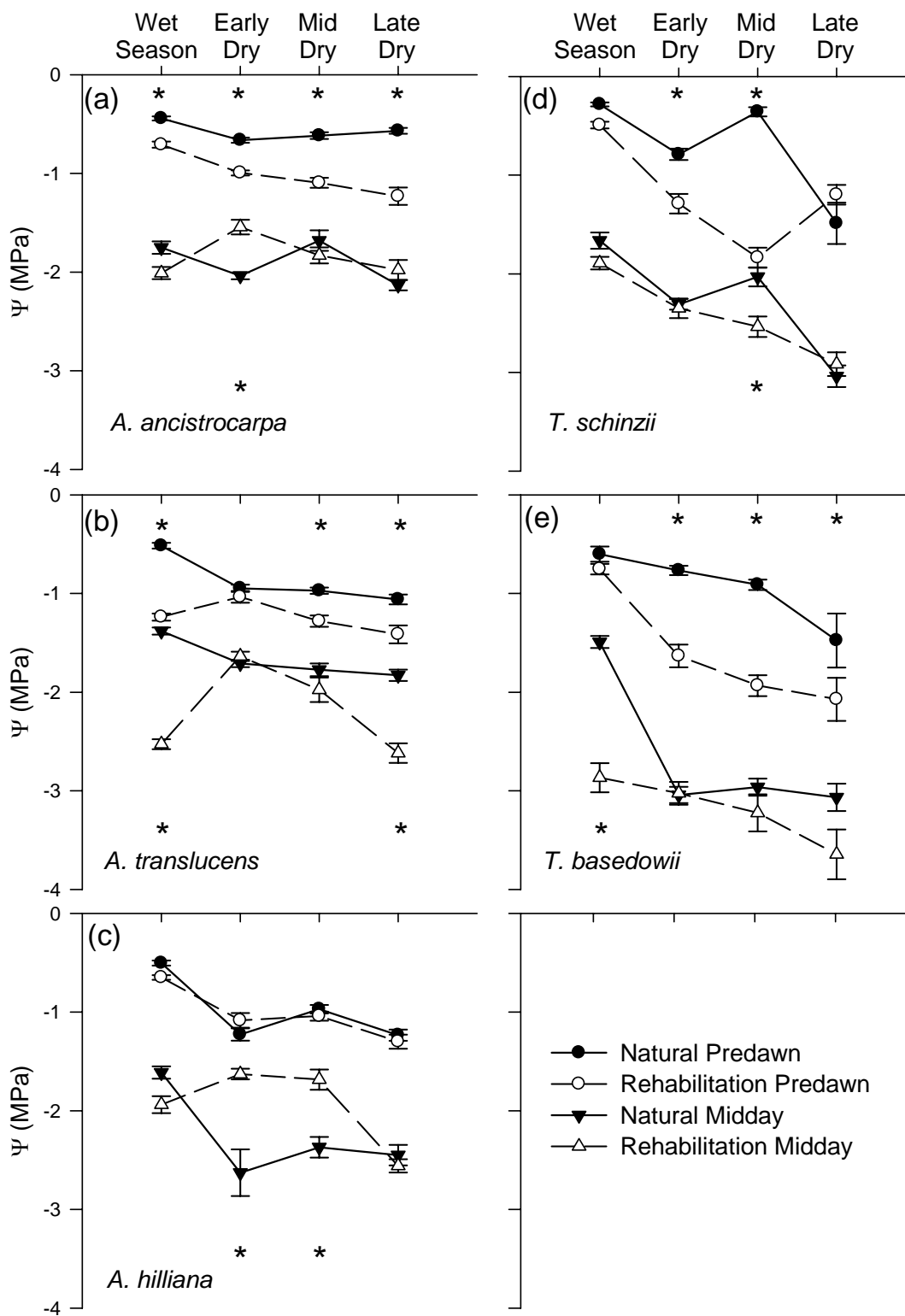
**Figure 4.4** (a-c) Mean stomatal conductance and (d-f) mean net photosynthetic rate for *Acacia ancistrocarpa*, *A. translucens* and *A. hilliana* from natural and rehabilitation sites throughout all four seasons. Error bars are standard errors of the mean. Symbols marked with an asterisk (\*) denote significant differences ( $P < 0.05$ ).



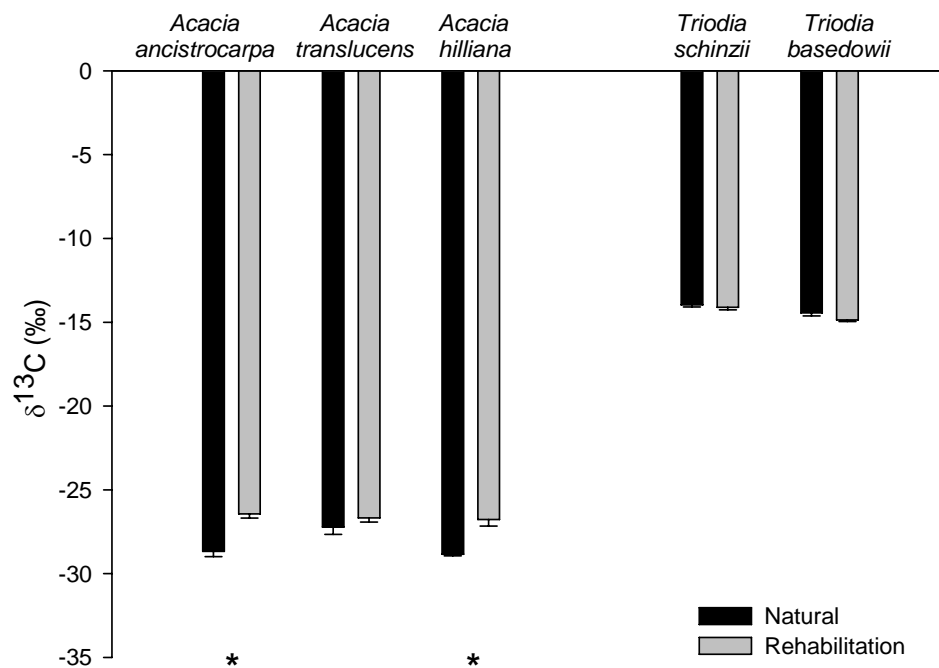
**Figure 4.5** (a-b) Mean leaf conductance and (c-d) mean net photosynthetic rate for *Triodia schinzii* and *T. basedowii* from natural and rehabilitation sites throughout all four seasons. Error bars are standard errors of the mean. Symbols marked with an asterisk (\*) denote significant differences ( $P < 0.05$ ).

#### Carbon-Isotope Composition

Plant  $\delta^{13}\text{C}$  values were significantly higher (less negative) at the rehabilitation site for *Acacia* species ( $F_{(1,24)}=31.8$ ,  $P < 0.001$ ) but not for *Triodia* species ( $F_{(1,21)}=3.22$ ,  $P > 0.05$ ). Interactions between site and species were not significant for both models ( $P > 0.05$ ). *Post-hoc* tests revealed that site differences occurred for *A. ancistrocarpa* and *A. hilliana* but not for *A. translucens* (Figure 4.7). All three *Acacia* species at the rehabilitation site displayed similar  $\delta^{13}\text{C}$  values around  $-26.5$  ‰; *A. ancistrocarpa* and *A. hilliana* at the natural site had  $\delta^{13}\text{C}$  values of around  $-28.8$  ‰. *Triodia* species at both sites displayed values around  $-14.2$  ‰.



**Figure 4.6** Leaf water potentials of (a) *Acacia ancistrocarpa*, (b) *A. translucens*, (c) *A. hilliana*, (d) *Triodia schinzii* and (e) *T. basedowii* at predawn and at midday for plants at the natural site and on rehabilitation sites throughout the wet season, early part of the dry season, the middle of the dry season, and late in the dry season. Error bars are standard errors of the mean. Asterisks (\*) denote significant differences ( $P < 0.05$ ).



**Figure 4.7** Foliar  $\delta^{13}\text{C}$  values for *A. ancistrocarpa*, *A. translucens*, *A. hilliana*, *T. schinzii* and *T. basedowii*. Error bars are standard errors of the mean. Symbols marked with an asterisk (\*) denote significant differences ( $P < 0.05$ ).

#### *Sap velocity*

Stem sap velocity differed between sites for *A. ancistrocarpa*, the one species for which this parameter was measured. Plants from the rehabilitation site had relatively lower sap velocities than plants from the natural site ( $F_{(1,23)} = 5.40$ ,  $P < 0.05$ ). Differences were most pronounced during the dry season (Figure 4.8). Sap velocity also differed seasonally (i.e. with soil moisture availability); greater relative rates occurred during moderate and wet periods compared with dry periods ( $F_{(2,23)} = 13.99$ ,  $P < 0.05$ ). There was no significant interaction between site and season ( $F_{(2,23)} = 1.56$ ,  $P > 0.05$ ). During the dry period average day-time sap velocity was  $4.7 \text{ cm h}^{-1}$  for plants at the natural site, and  $3.0 \text{ cm h}^{-1}$  at the rehabilitation site. Sap movement started 1-2 hours earlier at the natural site (around 05:30 WST), and remained higher for 2-3 hours longer at the end of each day (Figure 4.8).

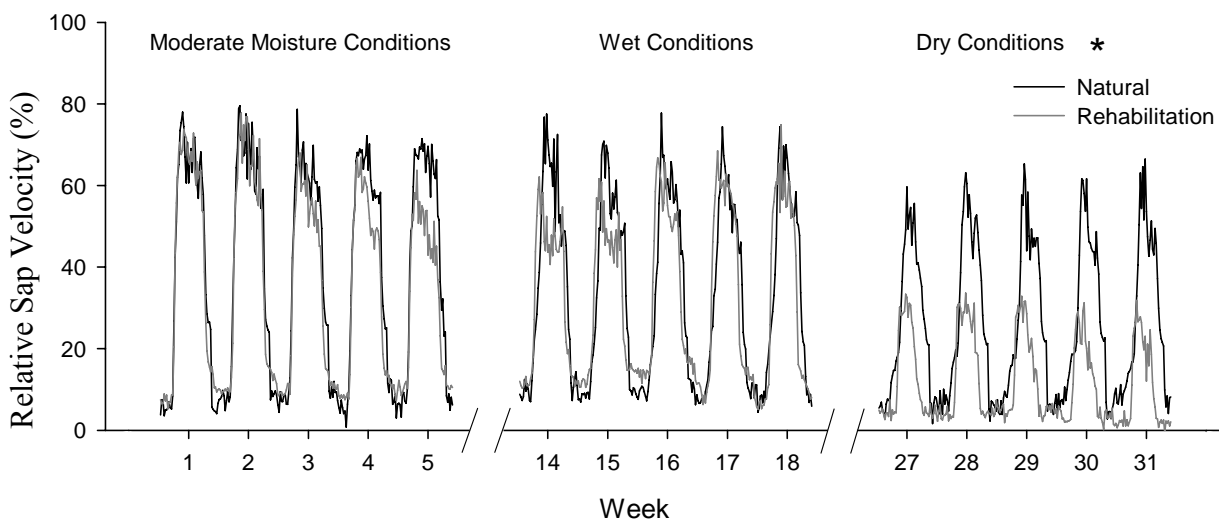
#### *Plant nutrition*

Foliar concentrations of most macro- and micro-nutrients (N, P, K, Ca, Mg, S and Mn) did not differ between sites for the five species studied (Table 4.2). However, concentrations of Cu, Fe, and Zn were significantly higher in the foliage of most species at the rehabilitation site, often being more than double the concentration at the natural site (Table 4.2). Aluminium (Al) displayed the most significant site differences, the

concentration being three to five times higher at the rehabilitation site than at the natural site for all species.

Compared with values in the literature considered adequate for plant nutrition (Epstein and Bloom 2005), *Acacia* species at both sites displayed similar concentrations of all macro- and micro-nutrients except P, which was only 14-32% of the above standard. *Triodia* species displayed lower nutrient concentrations than *Acacias* in almost all cases. For the *Triodia* species, the nutrient in lowest concentration relative to the Epstein and Bloom (2005) standard was P (5-17%), then N (23-38%), followed by B, Mg, Ca and K.

*A. ancistrocarpa* and *A. translucens* displayed  $\delta^{15}\text{N}$  values close to zero at the natural site, but significantly more positive values for plants at the rehabilitation site (Table 4.2). The rock outcrop species *A. hilliana* and both *Triodia* grasses displayed  $\delta^{15}\text{N}$  values around 1.3‰ at the natural site and similar or higher values at the rehabilitation site.



**Figure 4.8** Diurnal stem sap velocity averaged over each week and expressed in relative terms to maximum sap velocity including a period with moderate moisture conditions, a wet period after rain and a very dry period. Measurements taken for *A. ancistrocarpa* occurring at the natural site and at the rehabilitation site. An asterisk (\*) denotes significant differences between sites throughout that period ( $P < 0.05$ ).



**Table 4.2** Selected macro- and micronutrient concentrations and  $\delta^{15}\text{N}$  in foliage of *Acacia ancistrocarpa*, *A. hilliana*, *A. translucens*, *Triodia schinzii* and *T. basedowii* occurring at the undisturbed natural site and also at the mine-rehabilitation site. Asterisks (\*) denote significant differences ( $P < 0.05$ ), dashes (-) indicate no significant differences ( $P > 0.05$ ), and NA denotes data were not available. Values for 'adequate' nutrition are defined by Epstein and Bloom (2005).

Species Element	<i>A. ancistrocarpa</i>		<i>A. translucens</i>		<i>A. hilliana</i>		<i>T. schinzii</i>		<i>T. basedowii</i>		"Adequate" nutrition
	Natural	Rehab	Natural	Rehab	Natural	Rehab	Natural	Rehab	Natural	Rehab	
P (mg g <sup>-1</sup> )	0.39 (± 0.05)	0.45 (± 0.07)	0.58 (± 0.06)	0.65 (± 0.01)	0.28 (± 0.02)	* 0.60 (± 0.03)	0.26 (± 0.04)	- 0.28 (± 0.02)	0.11 (± 0.01)	* 0.35 (± 0)	2
N (mg g <sup>-1</sup> )	17.3 (± 0.52)	- 15.4 (± 2)	19.7 (± 0.87)	- 18.8 (± 0.76)	11.3 (± 0.41)	- 13.8 (± 0.2)	4.1 (± 0.41)	- 3.9 (± 0.08)	3.5 (± 0.16)	* 5.8 (± 0.12)	15
K (mg g <sup>-1</sup> )	8.8 (± 0.85)	- 4.9 (± 0.99)	8.0 (± 0.63)	- 6.1 (± 1.13)	8.3 (± 0.48)	- 9.3 (± 1.22)	5.7 (± 0.5)	- 4.4 (± 0.18)	3.4 (± 0.15)	- 4.0 (± 0.1)	10
Ca (mg g <sup>-1</sup> )	6.1 (± 0.6)	- 7.1 (± 0.68)	11.9 (± 1.04)	- 9.1 (± 0.29)	8.1 (± 0.65)	- 9.2 (± 1.22)	2.9 (± 0.29)	* 1.4 (± 0.18)	2.3 (± 0.3)	- 1.8 (± 0.12)	5
Mg (mg g <sup>-1</sup> )	2.09 (± 0.31)	- 2.73 (± 0.38)	2.98 (± 0.39)	- 2.73 (± 0.38)	1.70 (± 0.11)	- 3.33 (± 0.34)	0.70 (± 0.1)	- 0.83 (± 0.03)	0.48 (± 0.06)	- 0.75 (± 0.1)	2
S (mg g <sup>-1</sup> )	1.63 (± 0.11)	- 1.63 (± 0.22)	3.02 (± 0.21)	- 3.57 (± 0.28)	1.05 (± 0.06)	- 1.33 (± 0.19)	1.01 (± 0.11)	- 0.83 (± 0.03)	0.82 (± 0.04)	* 1.35 (± 0.05)	1
B (mg kg <sup>-1</sup> )	25 (± 4.3)	- 27 (± 1.5)	21 (± 3.6)	- 32 (± 7.0)	18 (± 1.5)	- 39 (± 6.6)	4 (± 1.4)	- 6 (± 0.5)	4 (± 0.9)	- 9 (± 0.5)	20
Mn (mg kg <sup>-1</sup> )	154 (± 14)	- 167 (± 9)	87 (± 10)	- 73 (± 18)	59 (± 7)	- 112 (± 8)	119 (± 16)	* 55 (± 3)	105 (± 22)	- 89 (± 2)	50
Fe (mg kg <sup>-1</sup> )	88 (± 6)	* 323 (± 34)	113 (± 16)	* 263 (± 26)	114 (± 7)	* 253 (± 17)	251 (± 84)	- 548 (± 80)	524 (± 110)	- 910 (± 133)	100
Cu (mg kg <sup>-1</sup> )	17 (± 2.4)	* 34 (± 1.7)	20 (± 2.3)	- 26 (± 2.3)	10 (± 0.4)	* 28 (± 3.5)	4 (± 0.4)	* 12 (± 1.1)	5 (± 0.8)	* 30 (± 3)	6
Zn (mg kg <sup>-1</sup> )	39 (± 5.0)	- 38 (± 4.1)	14 (± 5.0)	* 38 (± 3.1)	23 (± 2.5)	* 48 (± 3.1)	28 (± 14.1)	- 40 (± 4.2)	17 (± 5.4)	* 79 (± 1.9)	20
Mo (mg kg <sup>-1</sup> )	≤1 (± 0)	- ≤1 (± 0)	≤1 (± 0)	- 1.33 (± 0.33)	≤1 (± 0)	- ≤1 (± 0)	3.17 (± 0.87)	- 5.25 (± 0.85)	9.4 (± 1.86)	- 12.0 (± 2.04)	0.1
Si (mg kg <sup>-1</sup> )	270 (± 69)	- 203 (± 23)	188 (± 5)	- 183 (± 23)	130 (± 22)	- 177 (± 27)	3983 (± 538)	- 5175 (± 403)	9120 (± 1327)	- 6125 (± 269)	200
Al (mg kg <sup>-1</sup> )	97 (± 12)	* 627 (± 67)	95 (± 9)	* 467 (± 35)	123 (± 8)	* 413 (± 15)	99 (± 20)	* 530 (± 134)	179 (± 44)	* 843 (± 89)	NA
Na (mg g <sup>-1</sup> )	0.09 (± 0.004)	- 0.10 (± 0.001)	0.78 (± 0.063)	* 1.63 (± 0.176)	0.09 (± 0.006)	- 0.09 (± 0.007)	0.32 (± 0.087)	* 0.90 (± 0.041)	0.24 (± 0.06)	- 0.45 (± 0.029)	NA
$\delta^{15}\text{N}$ (‰)	-0.19 (± 0.12)	* 2.29 (± 0.13)	0.37 (± 0.13)	* 2.39 (± 0.95)	1.27 (± 0.34)	- 1.19 (± 0.65)	1.40 (± 0.35)	- NA (NA)	1.39 (± 0.59)	* 4.02 (± 0.49)	NA

## Discussion

This investigation examined a seven-year-old rehabilitation site that displayed poor plant cover, low species richness and severe erosion. The presence of many dead stems on the site indicated that mortality had been high. To diagnose potential stressors I compared ecophysiological parameters of plants at the mine-rehabilitation site with those at a natural site nearby. Findings are discussed in terms of landform topography; soil physical characteristics and erosion; plant water relations; soil chemistry and plant nutrition. Insights into the use of ecophysiological parameters as diagnostic tools, and their limitations are presented, followed by recommendations for the rehabilitation of this and other arid-zone mine sites displaying similar issues.

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### *Landform topography, soil physical characteristics and erosion*

Slope angles for the rehabilitation site and for natural sand dunes were similar at around 18°. However, erosion caused by rainfall impact and overland flow was a major problem on the rehabilitation site, yet was never observed on the native sand dunes. The stability of these dune slopes can be attributed to their greater vegetation cover (around 49%; see Table 4.1 and Grigg *et al.* 2008a - Chapter 2) and highly porous, deep sands. Rainfall, even from tropical cyclone events delivering up to 75 mm h<sup>-1</sup>, infiltrates rapidly, so runoff and rill erosion do not occur. This observation is in stark contrast to the low hydraulic conductivity (3-30 mm h<sup>-1</sup>; see Figure 4.2) and high runoff rates (70% to 80%; see Figure 4.3) displayed by the silty shale mine-waste material. These properties lead to poor retention of water on the rehabilitated slope and reduced water stores for vegetation.

Sediment loads associated with the runoff were also extremely high due to the unstable, slaking nature of this silty waste material. The importance of slope angle for erodability is highlighted by the fact that sediment loss during the first five minutes of rainfall was over two times and five times greater for the 15° and 20° slopes, respectively, than for the 10° slope. Once the soil surface was saturated after ten minutes of simulated rainfall, sediment loss slowed and stabilised to rates equivalent to 11, 15 and 17 t ha<sup>-1</sup> h<sup>-1</sup> for the 10°, 15° and 20° slopes, respectively. These results are within the range found by other studies on mine-waste materials employing various slope angles, and rainfall intensities (Lasanta *et al.* 2000; Loch 2000b; Johansen *et al.* 2001). They also support the conclusion that splash erosion is greatest during the first minutes of rainfall and the primary cause of particle detachment (Navas *et al.* 1990; Lasanta *et al.* 2000). Erosion rates from mine-waste facilities > 40 t ha<sup>-1</sup> year<sup>-1</sup> are considered unacceptable by mining-industry environmental regulators (Campbell 2004). Sediment loads from exposed mine-waste material on the 18° slope angles of the waste rock dump studied here are likely to exceed this limit after 3-4 hours of 75 mm h<sup>-1</sup> rainfall. Such high-intensity rainfall can occur at the study site, although usually for only short durations (<1 h), as a result of monsoonal cyclones. These findings highlight the effect of reducing slope angles on minimising erosion and runoff (Wilcox and Wood 1989; El-Swaify 1997; Carroll *et al.* 2000).

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### *Interactions between plant cover, erosion, microsites and root development*

Plant cover at the rehabilitation site was low (12%) and undoubtedly amplified erosion at the local scale, although a feedback between plant cover and erosion does exist. Without plant crowns (shrub and grass) protecting the soil surface from the erosive effects of rain droplet impact and soil particle detachment, higher allocation of rainfall to overland flow causes more sediment removal and rill erosion (Carroll *et al.* 2000; Wainwright *et al.* 2000; Greene and Hairsine 2004). In turn, this erosion exposes root systems, dislodging whole plants indiscriminate of species, and ultimately impacting upon plant cover. This escalation effect is thought to have been a significant issue shaping the vegetation patterns at the rehabilitation site. Superimposed on this biophysical interaction is the importance of slope design and engineering as certain parts of the landform will be more prone to erosion than others, e.g., where inwards-facing slopes conjoin to form a valley. The concentration of water runoff in these drainage lines ultimately form rills which cut away soil and dislodge whole plants, further reducing vegetation cover.

Plants at the rehabilitation site were found only in relatively favourable microsites that were sheltered from rill erosion, displayed at least 0.2 m of cover soil and localised run-on water harvesting. The finding that the only woody plants at the site were *Acacia* shrubs, adds to the evidence that this genus is particularly hardy and tolerant of disturbed conditions at mine-rehabilitation sites (Loch and Orange 1997; Grant and Loneragan 1999; Schmidt *et al.* 1999; Bell *et al.* 2003). Sinker roots of the three *Acacia* species were stunted and did not grow far into the waste material (~0.3 m), whilst lateral roots remained in the relatively sandy 0.2 m of cover soil. The fibrous root systems of the *Triodia* grasses were also largely confined to the cover layer with few roots extending beyond the interface with the mine-waste material. Major textural differences between the silty waste and the native desert sands likely caused mechanical difficulties for root penetration by the native plant species. Physically impeding substrates often limit root penetration on mine-rehabilitation sites (Enright and Lamont 1992; Tordoff *et al.* 2000; Szota 2007). The chemistry of the waste material was likely also a factor limiting root development and will be discussed in the section '*Soil chemistry and plant mineral nutrition*'.

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### *Plant water relations*

Ecophysiological measurement indicated that the three *Acacia* species at the rehabilitation site displayed more acute signs of water stress than the same species in their natural habitat at certain times of year, but not others. Evidence included: lower stomatal conductance during the middle of the dry season for all three species; lower rates of photosynthesis for two species (*A. ancistrocarpa* and *A. hilliana*) at this same time of year; higher foliar  $\delta^{13}\text{C}$  values (for the same two species), and reduced stem sap velocity during the dry period (for the one species examined, *A. ancistrocarpa*). Leaf water potentials at predawn were consistently more negative for plants at the rehabilitation site; however, the interaction with soil texture confounds interpretation of water stress and will be discussed in the following pages.

The above parameters indicate that *Acacia* species at the rehabilitation site had relatively less water available to them during the driest time of year, and so displayed more limited but efficient water use than plants in their natural habitat. These findings add support to the conclusions of others that have suggested water limitation is often experienced by native plants on mine-rehabilitation sites (Enright and Lamont 1992; Schmidt *et al.* 1999; Bleby 2003). For this study, limited water availability was probably caused by the combined effects of high runoff losses from the slope, limited water storage within the shallow cover soil layer (~0.2 m), and stunted root development into the silty waste material. Plants with shallow roots often display higher levels of drought stress and lower rates of gas exchange than plants with roots accessing more reliable moisture at depth (Flanagan *et al.* 1992; Donovan and Ehleringer 1994; Williams and Ehleringer 2000). That said, in order for these plants to have survived on the rehabilitation slope for seven years, I believe they must be obtaining water via lateral roots in the cover layer and from the waste material via the stunted sinker roots.

Fine-textured soils display greater water-holding capacity than sandy soils, so it is likely the silty waste material affords considerable moisture from the shallow depths where roots penetrate. Indeed, it is well established that plants occurring on finer-textured soils display shallower root systems than plants on coarser soils (Hacke *et al.* 2000; Jackson *et al.* 2000; Schwinning and Ehleringer 2001; Sperry and Hacke 2002). It may be argued that the waste material is not limiting root growth, but that roots penetrate only to this depth because that is as far as they need to go to obtain sufficient water.

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However, this is readily disproved by the facts that plants do not occur where cover soils are nonexistent (waste material at the surface) or extremely shallow (<0.2 m), and that plants are water stressed in the dry season, as explained above. The importance of cover soil depth cannot be overstated. Besides the direct implications for root development, the sandy cover layer acts as a capillary break limiting evaporative water losses from the soil surface (Stormont 1996; Fayer and Gee 2006; Yanful *et al.* 2006). The ‘dry mulching’ properties of coarse soils are central to the reason why sandy regions in arid environments exhibit more mesic vegetation with higher water status than those supporting plants in fine-textured soils; a concept known as the ‘inverse texture’ effect (Alizai and Hulbert 1970; Noy-Meir 1973; Sala *et al.* 1988; Sperry and Hacke 2002).

The effects of soil texture on leaf water potentials are well documented (Sperry *et al.* 1998; 2002; Hacke *et al.* 2000; Sperry and Hacke 2002; Hultine *et al.* 2005). Large pore spaces in sandy soils lead to a rapid decline in hydraulic conductivity, and soil water content with more negative soil water potentials. This decline is more gradual in clay and silt soils, and they hold more water than sands at a given soil water potential. Stronger matric forces require plants to display more negative water potentials where occurring on finer-textured soils than coarse soils (see references above). This explains why predawn leaf water potentials were more negative at the rehabilitation site for four of the five species; the exception was the rock-outcrop species *A. hilliana*. This species showed very similar  $\Psi_{pd}$  values in all seasons at both natural and rehabilitation sites. In its natural habitat roots were observed exploiting fissures in the shale rock which presumably contained sufficient, but sparingly available water to support transpiration demands. Other studies on shrubs and trees in shallow-soil habitats have also found evidence that plants obtain moisture from cracks and micropores in underlying rock (Zwieniecki and Newton 1995; Rose *et al.* 2003; Poot and Lambers 2008).

The species that showed the broadest range in stomatal conductance was *A. ancistrocarpa*; it displayed the highest  $g_s$  rates of any species when water was plentiful in the wet season, to amongst the lowest when it was scarce in the middle of the dry season. Considering this species often maintained the highest leaf water potentials, it appears to tightly regulate transpiration to maintain good hydraulic contact with the soil; a feature often displayed by plants on sands to limit xylem tensions and avoid cavitation (Sperry *et al.* 1998; Hacke *et al.* 2000; Jackson *et al.* 2000). Interestingly, midday leaf

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water potentials for *A. ancistrocarpa* were consistently around -2 MPa in all seasons at both natural and rehabilitation sites. Whilst such patterns can be indicative of plants approaching their hydraulic limit, another study on this species conducted during a drier year found even lower stomatal conductance rates ( $20 \text{ mmol m}^{-2} \text{ s}^{-1}$ ) and leaf water potentials ( $\Psi_{\text{md}}=-2.7 \text{ MPa}$ )(Chapter 5). These findings highlight the long-recognised view that yearly variability can be even more pronounced than seasonal variability in desert systems. Because of this, and complexities comparing water potentials between different soil types at natural and rehabilitation sites, determination of hydraulic limits for key species would be useful for future similar studies. This would involve determination of the proportion of embolised vessels, xylem vulnerability curves, xylem anatomy, as well as parameters outlined above (Tyree and Sperry 1988; Linton *et al.* 1998; Sperry *et al.* 1998). Taking into account that *A. ancistrocarpa* can display considerably more negative predawn and midday leaf water potentials (see Chapter 5), and that cavitation resistance of xylem tends to mirror the range in water potentials (Tyree and Ewers 1991; Sperry and Hacke 2002; Bhaskar and Ackerly 2006), I suspect this species was not significantly cavitated over the course of this two-year study.

The two *Triodia* species showed few site-related differences in water relations, particularly leaf gas exchange and foliar  $\delta^{13}\text{C}$  composition. These data indicate that plants at both natural and rehabilitation sites displayed similar levels of water access and confirm suggestions that significant differences in leaf water potential were due to the effects of soil texture. As was the case for the *Acacia* species, *Triodia* grasses also required favourable microsites with at least 0.2 m of cover soil, and showed very limited penetration of the mine-waste material. Whilst these soil depth conditions were similar from some interdune locations inhabited by *T. basedowii*, they were considerably different from the normally deep ( $\sim 2 \text{ m}$ ) rooting condition for *T. schinzii*. I suggest that the fibrous rooting strategy of these species facilitates a high degree of phenotypic plasticity to adjust to the shallow soils at the rehabilitation site. As a group, *Triodia* grasses occur across vast areas of arid and semi-arid Australia in a wide spectrum of habitats from rocky, shallow soils to deep sands (Lazarides 1997). They display a number of adaptations to strictly control water loss including tight rolling of leaf margins (forming cylindrical leaves with a sharp point), trichomes occluding the leaf groove, deeply-sunken stomata, resinous foliage and C4 photosynthesis (McWilliam and Mison 1974; Craig and Goodchild 1977; Jacobs 1984). All the above attributes undoubtedly help these grasses persist in the shallow soils at the rehabilitation site.

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### *Soil chemistry and plant mineral nutrition*

The sands at the natural site were slightly acidic (pH 6.7) whilst at the rehabilitation site, cover soils were slightly alkaline (pH 7.3) and the waste material was considerably alkaline (pH 8.7). The availability of most nutrients in soil is reduced by such alkaline pH (Binkley and Vitousek 1989; Lambers *et al.* 2008). Offsetting this issue to some extent is the fact that nutrients, including N, P and K, showed much higher concentrations in the waste material than in native soils (Table 4.1). Others have found similar results for mine-waste material (Schmidt *et al.* 1999); however, it is more common to find lower concentrations of essential nutrients (Tordoff *et al.* 2000; Wong 2003; Freitas *et al.* 2004). Most macro- and micro-nutrients (N, P, K, Ca, Mg, S and Mn) concentrations in foliage displayed little difference within species for plants on natural and rehabilitation sites (Table 4.2). Where differences did occur, concentrations were higher in plants at the rehabilitation site and more in line with concentrations defined as adequate by Epstein and Bloom (2005). For all species examined at both sites, the nutrient in lowest concentration relative to that considered adequate was P. For the *Triodia* grasses, the nutrient next most likely limiting growth was N.

Foliar  $\delta^{15}\text{N}$  values indicated  $\text{N}_2$  fixation by *A. ancistrocarpa* and *A. translucens* from the natural site, but not for the rock-outcrop species *A. hilliana* (Table 4.2). Significantly more positive  $\delta^{15}\text{N}$  values in foliage of plants at the rehabilitation site suggest relatively less  $\text{N}_2$  fixation and that the soil N source was different, possibly as a result of stronger N-cycling and  $^{15}\text{N}$  enrichment of the remaining soil N fraction (Nadelhoffer and Fry 1994; Schmidt *et al.* 1999).

Foliar concentrations of Cu, Fe, and Zn were significantly higher for plants at the rehabilitation site, although not to the extent that these were considered toxic (Sposito 1985; Alloway 1995; Orcutt and Nilsen 2000). Concentrations of the potentially toxic non-nutrient Al ranged between 400 and 900  $\text{mg kg}^{-1}$  at the rehabilitation site; three to five times higher than those for plants at the natural site. Such levels are comparable with Al concentrations for hyper-accumulating species and may have been toxic if plants were sensitive to high levels. However, there were no signs of leaf chlorosis or abnormal leaf morphology indicating this and associated conditions (P and Ca deficiencies); although Al toxicity also retards development of root meristems and reduces root growth (Rengel 1992; Delhaize and Ryan 1995). Evidence for this latter effect may have been obscured by root stunting caused by adverse textural properties of

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the waste material. Because of the alkaline nature (pH 8.7) of the waste material, these elements should not be available for plant uptake; Al for example, is not likely to be a problem unless soil pH  $\leq 4.5$  (Epstein and Bloom 2005). It is suggested that lateral roots in the more neutral cover soil are more likely responsible for absorbing these elements. This may have been facilitated by acidification of the rhizosphere (Lambers *et al.* 2008; Jones *et al.* 2003), a process associated with N<sub>2</sub> fixation in *Acacia* species (Little *et al.* 2005; Marcet *et al.* 2006; Marchante *et al.* 2008). Considering *Acacias* are known to be tolerant of metalliferous mining soils (Barnet *et al.* 1985; Lesueur *et al.* 1993; Musil 1993), Al toxicity may not be a problem for these species at the rehabilitation site. However, more sensitive local species may be affected and this could be a contributing factor as to why they do not occur at the rehabilitation site. Further research is needed to ascertain this, particularly in terms of soil-plant rhizosphere interactions, e.g., exudation of organic acids (Schöttelndreier *et al.* 2001).

The electrical conductivity of the waste material (EC<sub>1:5</sub> = 46 mS m<sup>-1</sup>), was below the level generally accepted to adversely affect glycophytes (~60 mS m<sup>-1</sup>) (Greenway and Munns 1980; Munns and Tester 2008). Considering soils at the natural site contained negligible amounts of Na (2.3 µg g<sup>-1</sup>) and very low EC (1 mS m<sup>-1</sup>), the finding that foliar Na concentrations were similar at both sites for most species indicates salt stress was not occurring at the rehabilitation site.

#### *Ecophysiological parameters as diagnostic tools: advice for the mining industry*

Where the goal of rehabilitation is to return the original native plant species, it is important to gain an understanding of their ecophysiological requirements *before* rehabilitation sites are designed and constructed. Primary consideration should be assessments of plant root morphologies and the physical and chemical properties of natural soils and mine-waste materials. Hospitability to root growth, hydraulic properties and erodability should dictate the depth of soil required for the establishment of target species. As highlighted by severe erosion problems at this study site, water management is paramount and failings in engineering design (e.g., excessive slope angles and uncontrolled escape of water from the flat upper sections) will undermine even the most concerted efforts to establish a vegetated cover. Landform-evolution modelling should be incorporated to inform management of the likely water shedding and erosion patterns of each design of a waste-rock dump. If these measures are not



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taken from the outset, the likelihood of problems and associated costs will be much greater in the long run.

For existing sites already showing problems, the above measures should be combined with ecosystem and an analysis of landscape function (Tongway and Hindley 2000; Ludwig *et al.* 2004) to characterise the plant cover and physical processes causing erosion. Ecophysiological parameters including plant nutrition, water relations and phenotypic attributes (morphology, hydraulic architecture and anatomy) offer the highest level of detail and opportunity to diagnose why problems are occurring. All of these components are required to gain the best-possible understanding of systems and processes in both natural and rehabilitation settings, ultimately improving the chances for successful rehabilitation and environmental approval of mine closure.

#### *Improving Plant Survivorship at the rehabilitation site*

Reducing slope angles from 18° to less than 14° will greatly reduce the severity of erosion. This can be achieved either by expanding the footprint of the waste rock dump if material is moved down slope, or keeping the same footprint and setting the top of the slope further back. The second approach would clearly increase the height of the landform, reduce the flat-top area and associated problems with pooling. Uncontrolled shedding of water from the flat top of the waste-rock dump is the cause of the largest and most catastrophic erosion gullies, so utmost attention must be given to water management here. Without suitable materials to construct rock-lined drains and controlled shedding of water, the only option for the flat top is a deep store-release cover. Considering the water-holding capacity of the sands are ~10%, a depth of 3 m of native soils would absorb the average annual rainfall and prevent deep drainage if plants similar to the natural habitat were established. However, the costs involved with establishing this over the entire waste-rock dump would be prohibitive, so it could be employed only where deep drainage is of greatest concern above encapsulated pyrite bodies. For the remainder of the waste-rock dump, including other parts of the flat top and the sloping sides, a cover of at least 0.5 m would be needed to support the minimum amount of vegetation. Species selection for these areas should concentrate on those that have already proved their ability to survive such conditions, and others in the area known to inhabit shallow, gravelly or heavier soils (e.g., *Eucalyptus victrix*, *Jacksonia aculeata* and *Melaleuca lasiandra*; Grigg *et al.* 2008a,b – chapters 2 and 3). Particular attention should be given to establishing a dense cover of *Triodia* grasses due to their

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low ground-covering nature protecting the soil surface from the impact of rain-droplet erosion. Their dense fibrous root systems also bind the sandy soils and prevent wind erosion, a particular issue on such an elevated landform. In and around the 3 m deep 'islands' on top of the waste-rock dump, a broad selection of dune and interdune species could create a similar cover and leaf area index to the native vegetation. Climate change in this part of Australia is projected to increase the amount of rainfall (Bureau of Meteorology 2009), so a diverse flora will be needed to allow continued plant cover to stabilise the rehabilitation site for the long term.

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## Chapter 5

### Changes in water relations for *Acacia ancistrocarpa* on natural and mine-rehabilitation sites in response to an experimental wetting pulse

#### Abstract

Vegetation plays an essential role in mine-site rehabilitation as it serves to reduce erosion and extract moisture from the soil cover, thus minimising deep drainage to potentially hazardous materials below. Plant water-use patterns and root development are likely to be impacted where subsoils are physically and/or chemically inhospitable and close to the surface, particularly in arid and semi-arid environments where pulses of rainfall are infrequent and interspersed with long dry periods. The aim of this investigation was to determine how plant water relations of the woody shrub species *Acacia ancistrocarpa* (Maiden and Blakely) were affected by a summer wetting pulse on a degraded mine-rehabilitation site and a pristine natural site in the Great Sandy Desert of north-western Australia. At both the natural and rehabilitation sites, 20 m<sup>3</sup> of water was applied to emulate an 80-mm rainfall event comparable with cyclones that occur during the summer wet season. I found that plants responded with significant increases in stomatal conductance, leaf water potential and sap velocity in lateral roots within three days of irrigation at the natural site and two days at the rehabilitation site. At the rehabilitation site this response occurred despite the fact that sinker roots were stunted by impeding physical properties of the mine-waste material. Sap velocity, measured using the heat ratio method, in lateral and primary sinker roots was close to zero at night and positive during the day for trees at both sites during the dry period before the irrigation. These data indicate hydraulic redistribution was not occurring between the primary sinker and lateral roots at night, and water was transported along the laterals towards the crown, despite the fact they were in dry soil. Excavations revealed that lateral roots extended up to 6 m and displayed secondary sinker roots accessing water from deeper soil layers, even from mine-waste material. These morphological traits likely improved the water relations and survival of *A. ancistrocarpa* at the rehabilitation site. Considering these traits and the rapid pulse responsiveness of this species, I recommend *A. ancistrocarpa* for future rehabilitation projects at this and other mine-sites in the region.

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## Introduction

Water management on mine waste-rock dumps is of crucial importance to maintaining landform stability and preventing uncontrolled runoff and erosion. This is particularly important when potentially hazardous waste-rock materials are stored such as acid-generating pyrites, arseno-pyrites and heavy-metal containing ores. Acid mine drainage is a serious environmental problem and has caused substantial contamination to groundwater and river systems in many places throughout the world (Australia: Lottermoser 1999; Asia: Williams *et al.* 1996; Africa: Naicker *et al.* 2003; Europe: Johnson 1986; Achterberg *et al.* 2003; Gatzweiler *et al.* 2001; North America: Evangelou and Zhang 1995; Mays and Edwards 2001; Johnson and Hallberg 2005). In seasonally dry environments, one strategy to mitigate or prevent infiltration of water into waste material is to construct a suitably engineered and substantial layer of soil over the mine waste to act as buffer volume, known as a store-release cover or evapotranspiration cover (Caldwell and Reith 1993; O’Kane 2003; Campbell 2004). If sufficient soil and regolith depth is provided, rainfall can then be absorbed and retained within the cover layer for release by plant and soil evapotranspiration during subsequent dry periods.

Natural vegetation in seasonally dry environments is likely to use all available rain-derived soil moisture and prevent deep drainage in all but the wettest years if the soil is of sufficient depth and favourable texture to allow unhindered development of plant roots (Phillips 1994; Smettem 1998; Van de Water *et al.* 2002; Seyfried *et al.* 2005; Mitchell *et al.* 2009). For a similar degree of extraction to occur on a store-release cover, suitable soil depth and texture must be accompanied with hospitable soil chemistry, water retention and landform topography (Gee *et al.* 1994; Campbell 2004). Furthermore, species used for revegetation must be able to tolerate the prevailing conditions, which are different from the conditions in their natural habitat, and also exhibit suitable root morphology and water-use patterns. Plant species that can persist throughout long dry periods and respond quickly and effectively to rain events are considered important to minimise deep drainage through the store-release cover.

### *Factors affecting pulse responsiveness*

The timing and magnitude of plant physiological responses to wetting pulses in seasonally dry environments depends on a number of environmental factors including rainfall amount and seasonality, soil texture, depth, slope angle and antecedent soil

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moisture and plant ecophysiological factors such as root morphology and plant size (Flanagan *et al.* 1992; Sperry and Hacke 2002; Fravolini *et al.* 2005; Zeppel *et al.* 2008). Rainfall seasonality and the evaporative conditions following a rain event interact strongly with soil type and slope angle (runoff) to influence the proportion of water that soaks in to the profile. Summer rainfall is typically followed by hot, dry conditions and relatively high losses to the atmosphere and as a result, a smaller proportion of rainfall enters the soil and penetrates to a shallower depth compared with winter rainfall (Williams and Ehleringer 1996, 2000; Golluscio *et al.* 1998; Loik *et al.* 2004). Short pulses of summer rainfall can be used only by plant species that maintain active shallow root systems (Ehleringer *et al.* 1991, Lin *et al.* 1996, Schwinning *et al.* 2003). This is particularly important for fine-textured soils as water is retained in shallow soil layers, and due to strong capillary forces, is readily evaporated from the surface (Seely and Louw 1980; Orshan 1986; Brown and Archer 1990). By contrast, sandy soils permit rapid infiltration of water to deeper soil layers and relatively weak capillary forces limit evaporative extraction from the soil surface, so a greater proportion of rainfall penetrates to depth; a process termed the ‘inverse texture effect’ (Noy-Meir 1973; Sala *et al.* 1988; Sperry and Hacke 2002). In concert with these factors, plant water status and the severity of stress caused by reduced antecedent soil moisture during interpulse periods further influences the recovery of transpiration and photosynthesis (Yan *et al.* 2000; Schwinning *et al.* 2002).

Root system functional type is the primary morphological attribute that determines pulse response capability (Noy-Meir 1973; BassiriRad *et al.* 1999; Ogle and Reynolds 2004; Huxman *et al.* 2004a). Many shrub species in seasonally dry environments display lateral roots to access nutrients and pulses of water in shallow soil layers, and sinker roots to access more reliable, deeply stored moisture (Caldwell and Richards 1986; Ehleringer and Dawson 1992; Jackson *et al.* 1996; Schenk and Jackson 2002). This combination permits hydraulic redistribution of water from deeper reserves to near-surface lateral roots in many species and allows them to maintain lateral root functioning during dry periods (Richards and Caldwell 1987; Caldwell *et al.* 1998; Hultine *et al.* 2003a; Burgess and Bleby 2006). Despite potential losses to the surrounding dry surface soil, hydraulic redistribution facilitates the rapid development of fine roots and utilisation of rainfall events (Dawson and Pate 1996; Ryel *et al.* 2004; Seyfried *et al.* 2005). Furthermore, it improves water availability for shallow-rooted understory species and for soil micro-organisms during interpulse periods (Caldwell

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and Richards 1989; Dawson 1993; Huxman *et al.* 2004a). Plant size is also important as small individuals, even juveniles of species that normally do exhibit hydraulic redistribution at maturity, may not have developed adequate root systems to facilitate transfer of water between different soil layers (Dawson 1996). Root morphology and root system size ultimately affect the pulse utilisation ability and the soil moisture thresholds at which plants alternate between deep and shallow water sources (Ehleringer and Dawson 1992; Lin *et al.* 1996; Gebauer and Ehleringer 2000; Gebauer *et al.* 2002).

Plant ecophysiological factors that are conducive to maximising the use of rain pulses depend on characteristics that promote rapid water use including high stomatal sensitivity to plant water status, high leaf conductance, large leaf area and high shoot:root ratio (Schwinning and Ehleringer 2001; Xu and Li 2006). However, these characteristics must be combined with the ability to respond in an equal but opposite direction for all such physiological and morphological adaptations in order to curtail water loss and to survive prolonged periods without rain (Noy-Meir 1973; Nobel and Sanderson 1984; Nobel 1988; Xu *et al.* 2007).

In semi-arid, and particularly in arid regions, dry periods often persist for several months at a time. Whilst plants have adapted to endure these stressful periods in their natural environment, the altered conditions on mine-rehabilitation sites potentially create additional stresses that affect the way plants deal with both pulse and inter-pulse phases. As far as I am aware, nothing has yet been published specifically on the effects of mine rehabilitation conditions on plant pulse responsiveness. However, a small body of literature exists on the ways in which modified soils on mined lands impact upon root morphology and plant water status. In general, plants are more water stressed on rehabilitation sites than in natural habitats, because of physically and/or chemically hostile subsoils, excessive runoff, poor water infiltration and insufficient depth for root establishment (Enright and Lamont 1992; Schmidt *et al.* 1999; Szota *et al.* 2007).

#### *Potential scenarios for pulse response at the mine-rehabilitation site*

The speed at which plants respond to wetting pulses at mine-rehabilitation sites compared with natural sites in water-limited environments may follow scenarios on either side of a spectrum. For example, a faster response may be observed if lateral roots are restricted to very shallow layers and maintained so they are able to enhance their water uptake after rain without requiring the formation of new roots (Cui and Calwell

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1997; Ong *et al.* 1999). This ‘use it rapidly, or lose it’ strategy (BassiriRad *et al.* 1999) may be feasible in at least two ways; first, if water is supplied to shallow roots, e.g. via hydraulic lift from the sinker root (Richards and Caldwell 1987; Sperry and Hacke 2002; Hultine *et al.* 2003a,b; Huxman *et al.* 2004b); or second and less likely, water is not supplied so shallow roots are isolated in dry soil and survive without losing water as per the ‘rectifier-like’ effect described for succulents (Nobel and Sanderson 1984). A slower response time to the pulse may be observed on a rehabilitation site if any of at least four possibilities occur including (1) the existing lateral roots are excessively cavitated and have lost hydraulic conductivity (Sperry *et al.* 1998); (2) if hydraulic lift is important in the species but not possible because of insufficient access to water by the sinker (Caldwell *et al.* 1998); (3) if new roots are required before uptake begins (Cui and Caldwell 1997; North and Nobel 1998) or (4) if existing lateral roots are preferentially placed at greater depth in response to more favourable moisture availability over the dry season; however, this will likely be at the expense of reduced ability to extract moisture from near the surface. Alternatively, plants on the rehabilitation site may respond at a similar rate to those at the natural site, either because they remain unaffected by the conditions, or because the responses to the various changes offset one another.

#### *Background and aims of the study*

The mine-rehabilitation site studied for this investigation displayed a number of symptoms indicating that the mine-waste material was inhospitable to plant root development, and it was suspected that the depth of native soil overlying the waste material was not sufficient to serve as a store-release cover. At the rehabilitation site plant cover was extremely poor compared with the natural site which was characterised by almost 50% projected cover (Grigg *et al.* 2008a,b – chapters 2 and 3). Large areas devoid of vegetation displayed exposed mine-waste material at the surface and severe rill erosion down the sloping sides. Biodiversity was also relatively poor as only five native plant species (three *Acacia* shrubs and two *Triodia* grasses) were typically found at the rehabilitation site compared with 165 species at the natural site. The presence of numerous dead stems indicated that initial establishment from the topsoil seed bank had been widespread, but high mortality rates had occurred in subsequent years. Preliminary observations found that (1) plants were surviving in areas where cover soils were at least 0.2 m deep over a white silty shale waste material, (2) lateral roots were restricted to the cover layer and (3) sinker roots displayed marked reductions in diameter at the

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interface with the underlying waste material. This white shale waste was used by the mining operation as an ‘inert’ waste layer at least 3 m deep to form a barrier over the top of more reactive, sulfide containing waste beneath. Differences in the physical properties (e.g. soil texture and bulk density) of the silty shale and the native sands were suspected to be the main reasons limiting root development into the waste material. Furthermore, different textural properties between sites will also have significant ramifications affecting the availability of water during dry periods, the movement of water after pulse events and the resulting water relations of plants.

The notion that pulse-responsive plant species are important on mine rehabilitation for the mitigation of deep drainage was an underlying rationale at the inception of this study. Here, I investigate the pulse responsiveness of one shrub species, *Acacia ancistrocarpa*, that occurs on the on the mine-rehabilitation site and in nearby natural vegetation in the Great Sandy Desert of north-western Australia. In its natural interdune habitat *A. ancistrocarpa* displays a dimorphic root system and occurs where ~ 2 m deep sandy soils overly a gravel hardpan layer (Grigg *et al.* 2008a – Chapter 2). Summer rainfall accounts for the majority of the annual precipitation at the site, so it is expected that *A. ancistrocarpa* is adapted to quickly utilise this source of water. One factor thought to be important for rapid pulse responsiveness was hydraulic redistribution from the sinker to sustain hydration and function of lateral roots. Numerous other species with dimorphic roots in water-limited environments display hydraulic lift to maintain shallow root activity, especially where summer rainfall is sufficiently reliable (Ehleringer and Dawson 1992; Burgess *et al.* 1998, 2000a; Hultine *et al.* 2003a, 2004). It was predicted that upward hydraulic redistribution (hydraulic lift) from the sinker to lateral roots would be diminished in plants at the rehabilitation site because of stunted sinker root development in mine-waste material. Specific goals of the study were to (1) define how quickly and to what extent the water relations of *A. ancistrocarpa* respond to a large wetting pulse at the rehabilitation and natural sites and (2) determine lateral root and primary sinker root activity throughout the dry-to-wet transition period in order to establish if hydraulic redistribution was occurring. For all parameters investigated, emphasis is placed on relative differences through time within site in recognition of the effects soil texture has on plant water relations (Hacke *et al.* 2000; Sperry and Hacke 2002). The wetting pulse, equivalent to an 80 mm rainfall event, was chosen because such events are common for tropical cyclones that occur during summer and because



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such large events are most likely to penetrate through the cover soils at the rehabilitation and potentially lead to acid mine drainage.

## Materials and Methods

### *Location, climate and physical characteristics of the study site*

This experiment was conducted in the Great Sandy Desert of north-western Australia on the Nifty Copper Operation mining lease (21°40'S 121° 35'E). Situated approximately 350 km from the coast, the area is classified as semi-arid and has an average annual rainfall of around 330 mm, although this is highly variable (Bureau of Meteorology 2008). Most rainfall occurs during the summer (December to February ~ 54%) and autumn (March to May ~ 32%) as a result of tropical thunderstorms that occur between one and four times per year bringing 40 mm to sometimes over 120 mm of rain. Outside this summer wet season, rain is often minimal for several months at a time, with winter (June to August) rainfall accounting for around 9% of the long-term average, and spring (September to November) only 5%. Potential evaporation (Class A pan) exceeds rainfall in every month by several-fold and totals approximately 4000 mm per year (Bureau of Meteorology 2008). At the very end of the dry season, just before the break of the wet season, it is extremely hot (>40°C) and vapour pressure deficit can be as high as 8.5 kPa. It was during such a time that the present study was conducted.

Two experimental sites were established, one in pristine natural vegetation, and the other on a rehabilitated slope of the Nifty Copper mine waste-rock dump; the sites were about 3 km apart. The natural site was a flat interdune area; soils were predominantly red sands with 5% clay, 0.5% silt and a lateritic gravel fraction that increased with depth until forming a cemented hardpan 2-3 m below the surface (Grigg *et al.* 2008a – Chapter 2). This soil displayed a field-capacity water content of 0.12 m<sup>3</sup> m<sup>-3</sup>. At the rehabilitation site, the cover layer was typically less than 0.3 m of mostly native sandy soil over a white, silty shale waste material; the resulting profile structure was reminiscent of a texture-contrast duplex soil. There were large areas where cover soils were non-existent and waste-rock material was exposed as a result of poor initial application of soil and/or erosion by wind and water. At the interface between cover soils and the waste material, there was often a mixing zone caused by deep ripping to a depth of 0.5 m. In general, the top 0.1 m of cover soil displayed typically 88% sand, 5% clay and 7% silt with a field capacity of 0.25 m<sup>3</sup> m<sup>-3</sup>. The white shale waste material



**Figure 5.1** (a) *Acacia ancistrocarpa* in natural vegetation; (b) scattered acacias on the mine-rehabilitation site; (c) irrigation drip-line and tank setup at the natural site; (d) excavated root system of *A. ancistrocarpa* on the mine-rehabilitation site displaying stunted lateral root growth into the silty mine waste shale material; (e) sap-velocity probes for the heat ratio method in the stem of *A. ancistrocarpa* at the natural site.

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was composed of 35% sand, 20% clay and 45% silt. This material readily delaminated, was easily eroded when exposed to rainfall and had a high slaking ability. Soil chemistry also differed among sites as pH and EC (1:5 w/v extract) were lower in native soils ( $5.9 \pm 0.07$ ;  $1 \pm 0 \text{ mS m}^{-1}$ ), than cover soils ( $7.3 \pm 0.06$ ;  $21 \pm 7 \text{ mS m}^{-1}$ ) and waste material ( $8.7 \pm 0.1$ ;  $46 \pm 16 \text{ mS m}^{-1}$ ). Macro- and micronutrient concentrations were extremely low for native soils and often several fold lower than for waste material (e.g. phosphorus and nitrogen,  $2 \mu\text{g g}^{-1}$  and  $89 \mu\text{g g}^{-1}$  in native soils compared with  $20 \mu\text{g g}^{-1}$  and  $545 \mu\text{g g}^{-1}$  in mine-waste material) (Chapter 4). For more detailed information and methods, see Grigg *et al.* 2008a – Chapter 2).

#### *Vegetation and study species*

The natural vegetation is predominantly composed of spinifex (*Triodia*) grasses and a diversity of woody shrubs (e.g. numerous *Acacia*, *Grevillea*, and *Hakea* species); total projected plant cover averages 49% in the interdunes (Figure 5.1a; Grigg *et al.* 2008a – Chapter 2). *A. ancistrocarpa* (Maiden and Blakely) is a common shrub in sandy interdunes (Figure 5.1b). It displays a dimorphic root system with numerous lateral roots (5-12) in the top 0.4 m below the surface and one primary sinker root extending ~2 m into conglomerated gravels. Above ground, it has a multi-stemmed habit and isobilateral phyllodes (75 mm x 8 mm). Plants of this species are killed by fire and reproduction is entirely dependent on seed production; flowering typically occurs in May and seeds are dropped in October.

At the rehabilitation site, total projected cover is 12% with scattered pockets of *Acacia* sp. and *Triodia* sp. occurring in the least unfavourable microsites (Figure 5.1c). Surviving plants occur only where soil depth is greater than 0.2 m, rip-line furrows retain water and erosion rills are absent. Numerous dead stems of varying sizes for these and other woody species indicated that mortality had been a major issue, particularly in the early years after establishment of the rehabilitation site. Preliminary studies on partially excavated root systems revealed that lateral roots were confined to the shallow cover soils <0.2 m below the surface at the rehabilitation site. Primary sinker roots tapered abruptly upon coming into contact with the waste shale material, being reduced to a diameter of less than 5 mm, 0.25 m into waste material (Figure 5.1d). In their natural habitat, *A. ancistrocarpa* roots of this diameter were observed 1.5 m below the surface in heavily conglomerated gravel.

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### *Irrigation*

At both the natural and rehabilitation sites, three *A. ancistrocarpa* trees of similar size were employed for the irrigation experiment, and another three trees of similar size were identified well away (~50 m) from the edge of the irrigation zone to serve as controls. The irrigation involved the application of 20 m<sup>3</sup> of fresh water over a 250 m<sup>2</sup> area to replicate soil moisture conditions similar to those created by an 80-mm rainfall event (Figure 5.1e). The three experimental trees were situated at least 6 m from the edge of the irrigation zone in order to cover the lateral root area. Water was applied throughout this area using drip-line and sprinklers over a 24 hour period starting at 7 pm. The morning after the irrigation started, by which time roughly half the water had been administered, was called the beginning of day 1. A fire hose was also used to apply water to the shrub crown as stem-flow was considered important for *A. ancistrocarpa*. Due to logistical considerations with respect to site and equipment access, the irrigation was conducted on the 11<sup>th</sup>-12<sup>th</sup> November 2003 for the rehabilitation site, and the 5<sup>th</sup>-6<sup>th</sup> December 2003 for the natural site. Dry conditions had persisted at the site for over six months prior to the experiment. In the 200 days leading up to this study, the only rainfall recorded was a 6-mm event 92 days earlier (12/08/03), and a 4-mm event 135 days earlier (30/06/03). The effects of these events would have long since dissipated, so plants were likely relying upon sparingly available but steady reserves of moisture. Combined with the fact that weather conditions were similar throughout this time, the 24-day gap between irrigations would not have biased the results.

### *Soil Moisture Content*

Capacitance-type ECHO probes (trade name ECH2O, EC-20, Decagon Devices Inc., Pullman, WA, USA) were used to record volumetric soil moisture content every 30 minutes using a CR10x datalogger (Campbell Scientific Inc. Logan, Utah, USA). Probes were inserted into undisturbed soil at 0.1 m, 0.2 m and 0.4 m depth at both sites. In the natural bushland site, an additional probe was installed at 0.8 m depth. This was not possible at the rehabilitation site as large boulders and hard compacted shale layers were present below 0.5 m. For this reason, ECHO probes were placed in a ripped zone where native soils and silty waste material was well mixed and access to a depth of 0.4 m was not a problem. Calibrations for soil type and temperature were conducted under laboratory conditions.

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### *Leaf water potentials*

Leaf water potentials ( $\Psi$ ) were measured at predawn (03.00-05.00 hours Western Standard Time) and midday (12.00-14.00 hours) using a Scholander-type pressure chamber (PMS Instruments, Corvallis, OR, USA).  $\Psi$  measurements were taken for three shoot sections exhibiting three to five leaves from each of the irrigated and control trees at each site. Immediately after being excised from the parent plant, shoot/leaf samples were sealed in zip-lock plastic bags with only the cut end protruding and placed inside the pressure bomb to begin measurements within one minute of cutting. Measurements are presented for the dry period before the irrigation, on day 1 (when the 24-h irrigation was still occurring), day 2, day 3 and day 4 and day 14. For the rehabilitation site, measurements were taken on day 7 and day 21 and the midway point between them used for day 14 because site access was not possible. The difference between these points was small relative to the increase since the irrigation and similar enough for linear determination of the mid-point at day 14.

### *Stomatal Conductance*

A Li-Cor 6400 portable infra-red gas analyser (LI-COR Inc. Lincoln, NE, USA) was used to measure stomatal conductance ( $g_s$ ) *in situ* on the youngest, fully matured, healthy leaves on the north (sun-exposed) side of each plant. Measurements were conducted during the dry period before the irrigation started, as well as on days 1, 2 and 3 after it started. Sampling was carried out between 10.00 and 14.00 hours Western Standard Time and overlapped with midday leaf water potential measurements. At least three measurements were taken on each plant at all sampling times. An artificial light source of red and blue LEDs was used to administer a light-saturating photosynthetic photon flux density of  $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$  at all times. Vapour pressure and temperature in the chamber were maintained as close as possible to those of ambient air. The reference gas  $\text{CO}_2$  concentration was maintained at  $380 \mu\text{mol mol}^{-1}$  and flow rates adjusted to ensure leaf chamber  $\text{CO}_2$  concentrations were kept between 360 and  $375 \mu\text{mol mol}^{-1}$ . Leaf temperatures were calculated using an energy balance equation (Li-Cor 6400 Manual 2000) and were very high given the hot ( $>40^\circ\text{C}$ ) ambient conditions. Measured leaf sections were sealed in zip-lock plastic bags, cooled and taken to the laboratory where their leaf areas were measured on a back-lit flatbed scanner at a scanning resolution of  $0.2 \mu\text{m}$  (WinRhizo V3.0.3 1995, Regent Instruments Quebec City, Canada). Once areas were determined, leaves were oven-dried at  $70^\circ\text{C}$  for one week, and dry weights recorded. Transpiration ( $E$ ) was used for calculation of leaf-area

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based whole plant hydraulic conductance ( $K_{\text{plant}}=E/\Delta\Psi$ ) according to the evaporative flux method (Sperry *et al.* 1998; Tsuda and Tyree 2000). For the determination of  $\Delta\Psi$ , the whole-plant water potential gradient, predawn leaf water potential was used as an estimate of  $\Psi_{\text{soil}}$ , and midday leaf water potential for  $\Psi_{\text{leaf}}$  (Eamus *et al.* 2006).

### *Sap-velocity measurements*

The heat ratio method (Burgess *et al.* 2000b, 2001a) was used to measure sap velocity ( $V_h$ ) in stems, lateral and sinker roots of all three irrigated *A. ancistrocarpa* plants in natural and mine-rehabilitation sites (Figure 5.1f). Probe construction followed design specifications set out in Burgess *et al.* 2001a, with two copper-constantan thermocouple junctions 5 mm and 15 mm back from the tip of a 35 mm needle. Five probe sets were used in each tree: two in stems at opposite sides, one in each of two lateral roots and one in the primary sinker root. Probe sets were placed in stems within 0.5 m of ground level where stem diameters were 30-60 mm, and in roots, within 0.4 m of the root-stem junction and at least 15 mm in diameter. However, only the largest shrubs at the rehabilitation site fulfilled this requirement. To keep plant sizes similar across sites, they were compared with individuals at the natural site that were merely average size for that habitat.

Different probe depths were trialled during the dry period before the experiment started so thermocouple junctions could be located either side of the maximum flow point; the outermost (15 mm) thermocouple was generally placed within 5-10 mm of the cambium. Probes were wired to CR10X data-loggers via AM416 multiplexers (Campbell Scientific Inc. Logan, UT, USA). Measurements began several weeks before the irrigation event and continued for three months. At the end of the experiment, stems were cut above and below the probes and the cut sections were wrapped in plastic to prevent drying from the exposed ends. Probes and equipment were left running in the shade for three days in order to obtain zero flow conditions for baseline calibration. Once all equipment had been uninstalled, lateral roots were excavated up to 3 to 6 m from the base of the stem using digging tools and a high-pressure air-spade (Series 2000, Concept Engineering Group Inc, Verona, PA, USA).

Conductive sap wood area was determined for stems and roots at the end of the experiment by cutting sections and placing them in a solution of 0.1% basic fuchsin for up to 24 hours or until all dye had been absorbed. For stem sections, this was done on

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whole branches with leaves still attached, and the cut end submerged at least 50 mm into the dye solution. For roots, excised sections 100 mm in length were cut and distal ends placed in 40 mm of basic fuchsin. In the laboratory, serial sections were then cut from dyed surfaces backwards in 10 mm increments for stems and 5 mm increments for roots. Changes in the proportion of embolised and filled vessels between the dry period before and the wet period after the irrigation were considered a potential problem for determination of net sap flux, so  $V_h$  data were analysed in relative terms for each individual probe. This was done by representing values as a proportion of the maximum velocity recorded for that particular probe throughout the entire experimental period. These upward limit values (maximum of 1) were generally identified in the week following the irrigation. In order to compare between days, an average value was taken for each 24 hour period; these average values rarely exceeded 0.5 because day- and night-time values were included. Statistical analyses were performed on these proportionally transformed data for the three replicate trees at each site.

#### *Statistical analysis*

Repeated measures ANOVA was conducted for all comparisons involving plant water relations using Statistica V7.1 (Statsoft Inc, Tulsa, OK USA). Individual trees were within group subjects and there were three trees per treatment group ( $n=3$ ). For leaf water potential data, between group factors were Habitat (Natural site and Rehabilitation Site) and Wetting (Irrigated and Control); the within group factor was Time (dry conditions pre-irrigation and days after wetting d1, d2, d3, d4, d14). Prior to analysis, data were  $\text{Log}_{10}$  transformed to meet the assumptions of the parametric model. Homogeneity of variances was checked and confirmed using Levene's test. Normality was viewed using p-p plots. *Post-hoc* multiple unplanned comparisons were conducted using Tukey's HSD tests.

For stomatal conductance measurements, preliminary analysis of data revealed that variance differed between habitats. Transformations did not homogenise variance, so statistical comparisons were conducted separately for each habitat. The repeated measures ANOVA used Wetting (Irrigated and Control) as the between-group factor and Time as the within-group factor (dry conditions pre-irrigation and days after wetting d1, d2, d3). Assumptions of the model and *post-hoc* tests were performed as per leaf water potential. For sap-velocity measurements, the repeated measures ANOVA was conducted on the proportionally transformed data described above. The between-group

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factor was Habitat (Natural site and Rehabilitation Site) and the within-group factor was Time (dry conditions pre-irrigation and days after wetting d1, d2, d3, d4, d7, d14, d21 and d28). Assumptions of the model and *post-hoc* tests were performed as above. Statistical significance of all tests were set at  $p < 0.05$ .

## Results

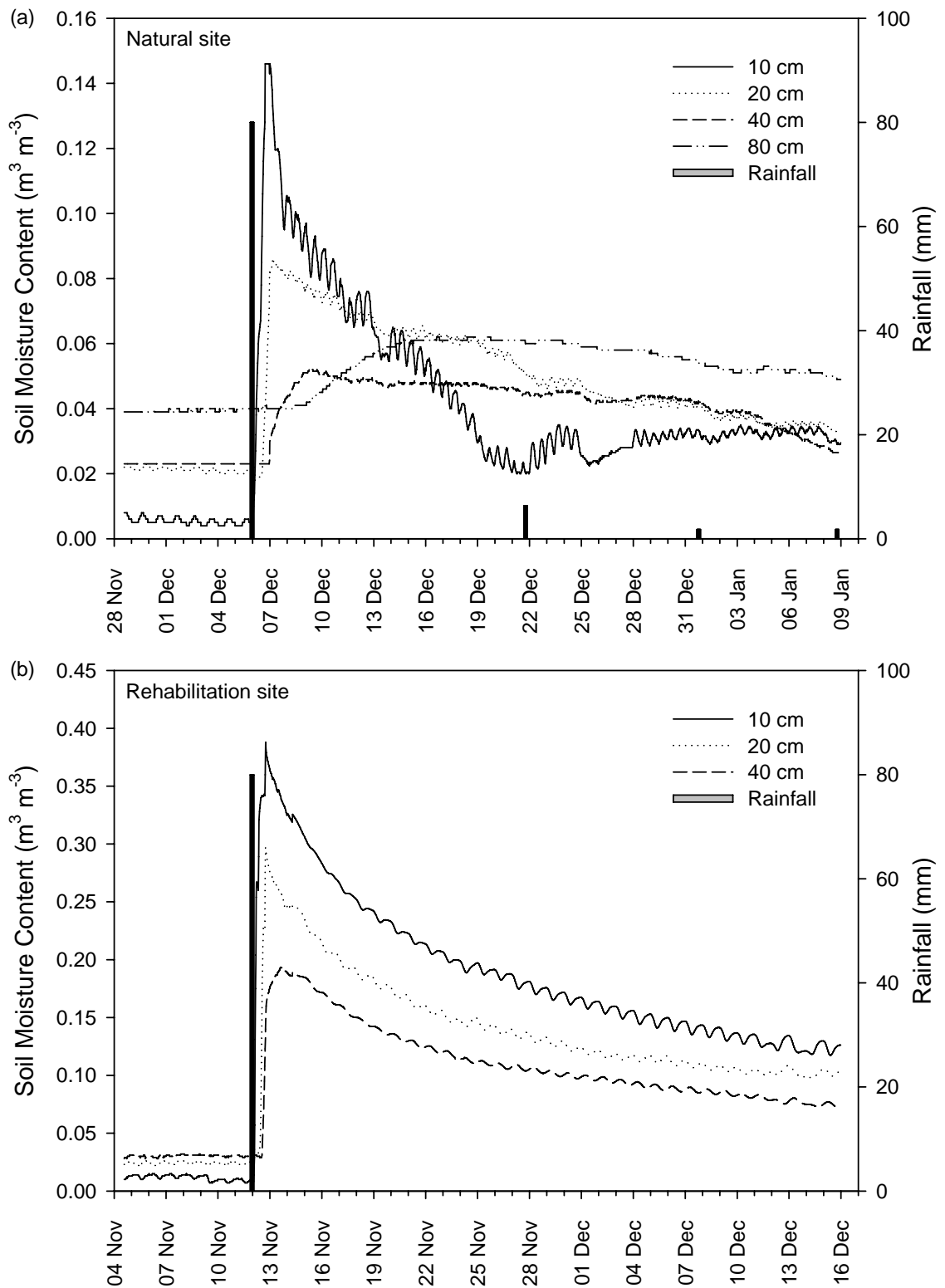
### *Soil Moisture Content*

Prior to the irrigation event, surface soils were very dry ( $< 0.01 \text{ m}^3 \text{ m}^{-3}$ ) for both the natural and rehabilitation sites (Figure 5.2) due to the absence of rainfall in the previous three months, and only 10 mm in the three months prior to that. Soil at a depth of 80 cm at the natural site displayed a volumetric water content of  $0.04 \text{ m}^3 \text{ m}^{-3}$ , almost double that of the value at 20 cm and 40 cm depth. Irrigation water infiltrated quickly at both sites, increasing soil moisture content at 10 cm depth within two hours of starting, by which time the equivalent of 7 mm of rain had been applied (Figure 5.2a, b). At the natural site, water content at the 10 cm depth declined sharply, whilst at the rehabilitation site, the decline was much more gradual due to the presence of finer materials mixed in with cover sands when the deep ripping occurred. The wetting front of the irrigation took three days to descend 80 cm at the natural site. Maximum values at 20 cm depth were around  $0.08 \text{ m}^3 \text{ m}^{-3}$  in the sandy soils at the natural site and around  $0.3 \text{ m}^3 \text{ m}^{-3}$  for the rehabilitation site, reflecting the higher water-holding capacity of the mixed silty waste material and sand. Volumetric moisture content at the rehabilitation site was slightly higher than field capacity during the irrigation event possibly due to super-saturation and pooling of water at the surface.

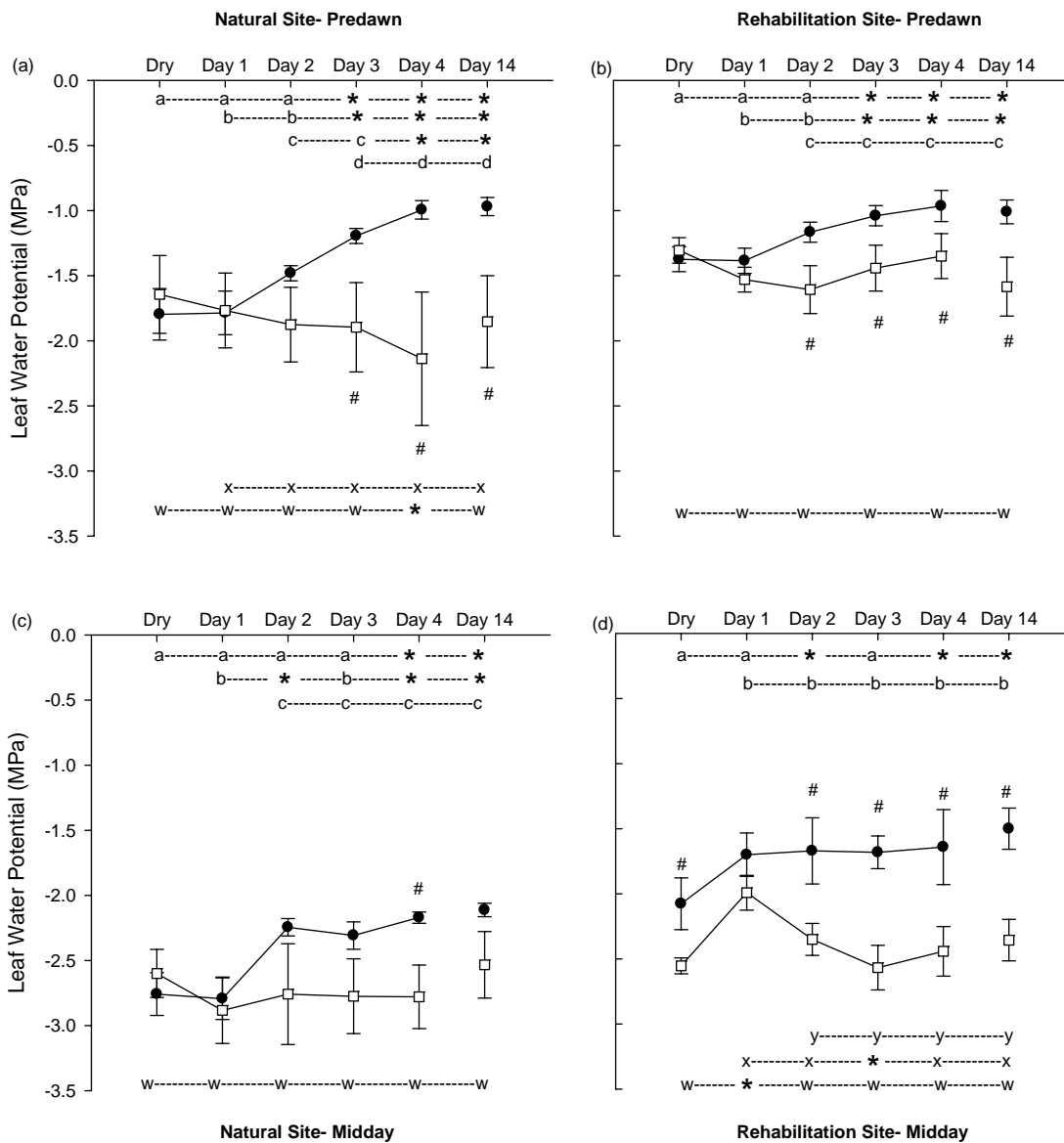
### *Plant Water Relations*

Leaf water potentials ( $\Psi_1$ ) of control plants were stable or declined slightly throughout the experimental period for both the natural and rehabilitation sites (Figures 5.3). For predawn  $\Psi_1$  values, there was a significant three-way interaction between time, habitat and irrigation ( $F_{5,40}=5.398$ ,  $p < 0.001$ ). *Post-hoc* tests comparing predawn  $\Psi_1$  values through time (within groups) revealed that irrigated plants in both natural and rehabilitation sites showed significant increases on day three (Figures 3a,b). Bearing in mind that the irrigation ran for 24 hours, predawn measurements on day three were taken approximately 57 hours since the watering started and 33 hours since it ended.





**Figure 5.2** Soil moisture content at varying depths at the natural site (a) and the mine-rehabilitation site (b) before, during and for one month after the irrigation event.



**Figure 5.3** Leaf water potentials for irrigated plants (black filled circles) and non-irrigated control plants (open squares) at predawn (top figures; a and b) and at midday (bottom figures; c and d) plants at the natural site (left figures; a and c) and rehabilitation site (right figures; b and d) during the dry period before the irrigation and for two weeks after the irrigation. Error bars are standard errors of the mean;  $n = 3$ . Statistically significant differences ( $p < 0.05$ ) between irrigated and control plants are denoted by the hash symbol (#). For differences within treatment over time, common letters across days denote similarity, whilst asterisks (\*) within a line of letters denotes statistical difference to the day at which the first letter appeared. In each panel, letters at the top refer to  $\Psi$  differences through time for irrigated plants; whilst those at the bottom refer to control plants.

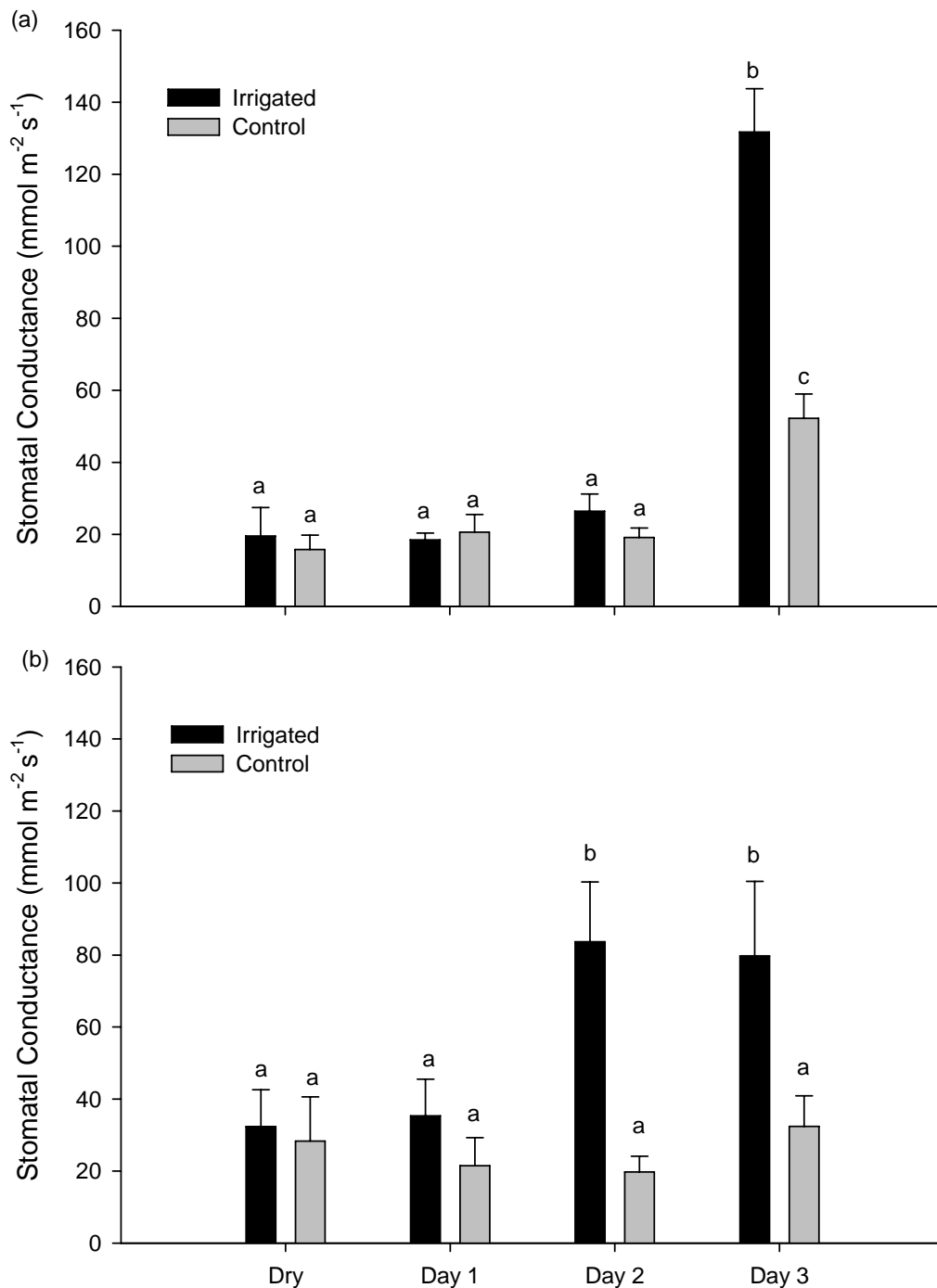
Values peaked on day four and remained significantly higher than those recorded pre-irrigation for at least ten more days at each site. Comparisons of predawn  $\Psi_1$  values between groups identified for irrigated plants were significantly less negative than for control plants from day 2 onwards at the rehabilitation site and from day 3 onwards at the natural site (Figure 5.3 a,b).

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For midday water potentials there were significant two-way interactions between time\*habitat ( $F_{5,40}=6.477$ ,  $p<0.001$ ) and time\*wetting ( $F_{5,40}=9.321$ ,  $p<0.001$ ). *Post-hoc* tests comparing midday  $\Psi_1$  through time revealed that values were statistically the same for day 1 and dry season measurements at both the natural and rehabilitation sites. Values for day 2 were significantly different from day 1 for the natural site and for the dry period for the rehabilitation site (Figures 5.3c, d). Differences between control and irrigated plants were identified by *post-hoc* tests on day 4 only at the natural site, but for all days except day 1 at the rehabilitation site. There were no significant differences between  $\Psi_1$  values of plants at the natural and rehabilitation sites at predawn or midday when the experiment began. Irrigated plants displayed significantly less negative midday  $\Psi_1$  values than at the start of the experiment for at least 14 days after the wetting event. Non-irrigated control plants displayed  $\Psi_1$  values typically between -2.5 MPa and -3.0 MPa throughout the measurement period. The difference between predawn and midday water potential ( $\Delta\Psi=\Psi_{pd} - \Psi_{md}$ ) was relatively constant for irrigated plants at both sites, remaining around 1.0 MPa for the natural site and 0.7 MPa for the rehabilitation site.

Stomatal conductance ( $g_s$ ) at the natural site displayed a significant interaction between time and wetting ( $F_{3,12}=23.067$ ,  $p<0.001$ ). *Post-hoc*-tests revealed a significant increase in  $g_s$  for irrigated plants on day three, with values approximately six-fold greater ( $132 \text{ mmol m}^{-2} \text{ s}^{-1}$ ) than those during the dry period prior to the irrigation and on days 1 and 2 (Figure 5.4a). Control plants at the natural site displayed stable values until day 3 when there was an unexpected increase, but values for the irrigated plants were still over 2.5 times greater and significantly different. For the rehabilitation site, a significant interaction between time and wetting also occurred ( $F_{3,12}=9.536$ ,  $p<0.05$ ). *Post-hoc* tests revealed there were no significant differences between control plants throughout the experiment. Stomatal conductance doubled on day 2 for irrigated plants at the rehabilitation site, a significant increase occurring one day earlier than for plants in the natural site (Figure 5.4b). There were no significant differences in  $g_s$  between sites for control plants, or for treatment plants during the dry period before the irrigation.

Increases in stomatal conductance occurred in the absence of changes in  $\Delta\Psi$  values over the course of the dry to wet transition period and were reflected in concomitant increases in whole plant hydraulic conductance ( $K_{\text{plant}}$ ) for irrigated plants. At the natural site,  $K_{\text{plant}}$  for irrigated plants increased from  $0.96 (\pm 0.23) \text{ kg m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$  in



**Figure 5.4** Stomatal conductance for irrigated and control *A. ancistrocarpa* plants at the natural site (a) and the mine-rehabilitation site (b) for the dry period before the irrigation and days one, two and three immediately following the irrigation event. Error bars are standard errors of the mean; n = 3. Statistically significant differences (p < 0.05) are denoted by different letters.

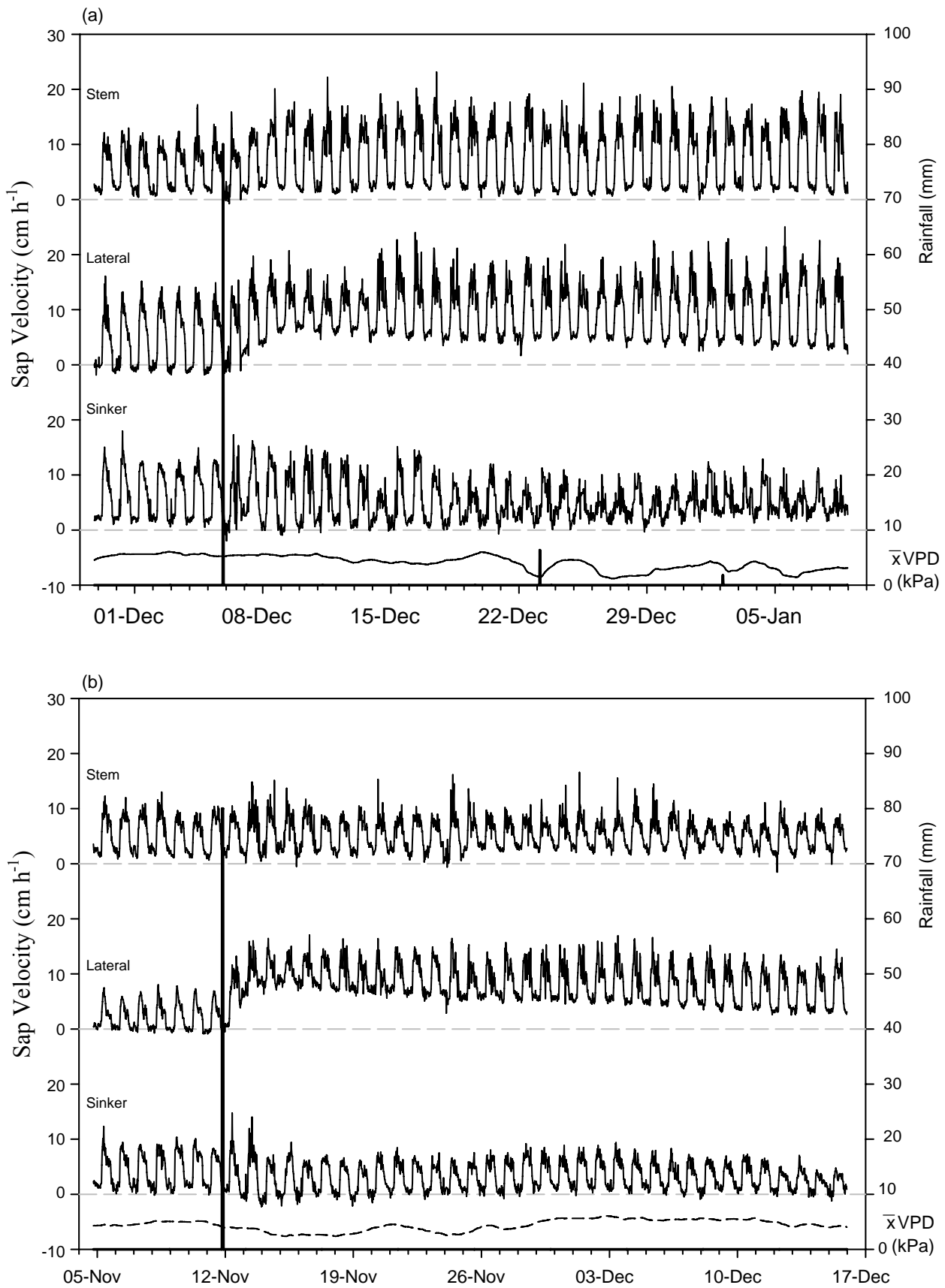
the dry period to a maximum of 6.22 ( $\pm 0.43$ ) kg m<sup>-2</sup> s<sup>-1</sup> MPa<sup>-1</sup> on day 3. For irrigated plants at the rehabilitation site, maximum  $K_{\text{plant}}$  values of 5.44 ( $\pm 0.83$ ) kg m<sup>-2</sup> s<sup>-1</sup> MPa<sup>-1</sup> occurred on day 2, an increase from 2.02 ( $\pm 0.40$ ) kg m<sup>-2</sup> s<sup>-1</sup> MPa<sup>-1</sup> at the sampling time before the irrigation. Control plants displayed  $K_{\text{plant}}$  values generally close to 1 kg m<sup>-2</sup> s<sup>-1</sup> MPa<sup>-1</sup>.

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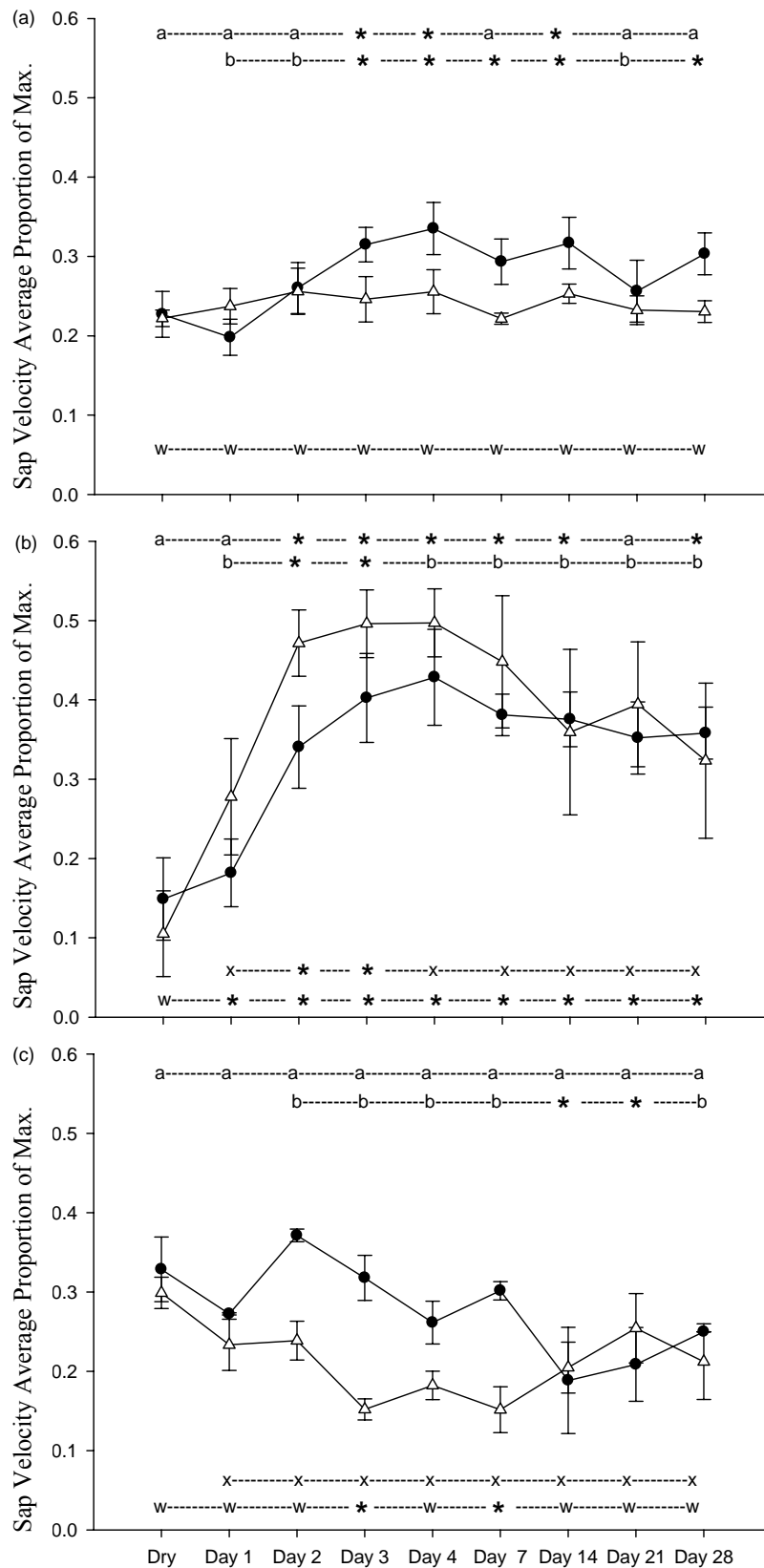
### *Sap velocity in stems and in lateral and sinker roots*

Sap velocities ( $V_h$ ) in stems during the dry period before irrigation were similar at the natural and rehabilitation sites, with daily maximum values around  $10 \text{ cm h}^{-1}$  (Figure 5.5a, b). The repeated measures ANOVA for relative sap velocity in stems revealed a significant interaction between time and site ( $F_{8,32}=3.44$ ,  $p<0.05$ ), as velocities did not change significantly for rehabilitation plants, but they did for plants in the natural site (Figure 5.6a). *Post-hoc* tests revealed a significant increase from pre-irrigation dry values on the third day after the irrigation for stems in the natural site (Figure 5.6a). Furthermore, stem  $V_h$  values in plants from the natural site remained significantly higher than pre-irrigation dry or day 1 values for day 7, 14 and 28 after the irrigation (Figure 5.6a). Basic fuchsin dye staining indicated that sap wood area extended to the centre of even the largest stems measured (50 mm).

Lateral roots of plants from the natural site during the dry period before the irrigation displayed average daytime  $V_h$  values of  $9.4 \text{ cm h}^{-1}$ , whilst those for plants in the rehabilitation site were only  $4.2 \text{ cm h}^{-1}$ . Night-time sap velocities pre-irrigation were close to zero for trees from both sites, although occasionally slightly negative ( $-1$  to  $-2 \text{ cm h}^{-1}$ ), indicating a minor degree of reverse flow for plants from the natural site (Figure 5.5a, b). For relative sap velocities there was a significant change through time ( $F_{8,32}=15.56$ ,  $p<0.001$ ) and there was no interaction with site. *Post-hoc* tests revealed a significant increase on day 3 for the natural site and on day 2 for the rehabilitation site (Figure 5.6b). These significantly higher values persisted for the following 28 days. For both sites, relative sap velocities on days 3 and 4 were also significantly higher than values displayed on day 1. After the wetting event, night time sap flow in lateral roots became positive indicating water uptake and movement towards the stem/root junction for plants at both sites. Excavations of lateral roots revealed that some roots extended further than 6 m at the natural site and up to 5 m for the rehabilitation site. Small secondary sinker roots emerged intermittently along their length at both sites. At the natural site, these roots displayed starting diameters between 5-12 mm and extended beyond 1 m depth where digging stopped. At the rehabilitation site, lateral roots were found only in the native soil cover layer, but small (3-8 mm), multi-branched secondary sinker roots did penetrate 0.2 m into the white shale waste material. The entire cross-sectional area of all lateral roots stained with basic fuchsin so no heartwood was found for plants at either site.



**Figure 5.5** Average sap velocities in stems, lateral roots, and sinker roots of irrigated *A. ancistrocarpa* plants occurring at a natural site (a) and the rehabilitation site (b) during the dry period before the irrigation and for one month after the irrigation;  $n = 3$ . Columns represent the irrigation and rainfall events (mm) and the smoothed line in the bottom section of each plot is mean VPD (kPa) averaged over a 24 hour period.



**Figure 5.6** Proportionally transformed sap velocities in stems (a), lateral roots (b), and a sinker root (c) of irrigated *A. ancistrocarpa* plants occurring at the natural site (solid circles) and the mine-rehabilitation site (open triangles) during the dry period before the irrigation and for selected days in the month following the irrigation event. Error bars are standard errors of the mean;  $n = 3$ . Common letters through time denote similarity within site through time, whilst asterisks (\*) within a line of letters denotes statistical difference ( $p < 0.05$ ) to the day at which the first letter appeared. In each graph, letters at the top refer to differences through time for the natural site; those at the bottom refer to the rehabilitation site.

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In sinker roots of plants from the natural site, sap velocities at night during the dry period were positive (3-4 cm h<sup>-1</sup>), but for plants at the rehabilitation site they were close to zero (Figure 5.5a, b). However, after the irrigation, night-time sap velocity for the natural site decreased to zero, whilst for those at the rehabilitation site it became slightly negative (around -2 cm h<sup>-1</sup>) for the following four nights. Statistical analysis of relative velocities for sinker roots identified a significant interaction effect between time and site ( $F_{8,24}=4.13$ ,  $p<0.005$ ) as values for the rehabilitation site declined more rapidly at first than for values in the natural site. There was a downward trend in relative sap velocities for both sites, but *post-hoc* tests revealed the only significant differences for the natural site were between day 2 and day 14 and 21 (Figure 5.6c). For the rehabilitation site, significant differences were between the pre-irrigation dry values, and day 3 and 7 (Figure 5.6c). Basic fuchsin dye staining indicated the entire cross-sectional area of the sinker roots was conducting at both sites and that average diameter 0.2 m below ground level was 36.2 mm at the natural site and 25.8 mm at the rehabilitation site. Given the absolute sap velocities presented in Figure 5.5 and assuming there were no differences in the proportion of conducting vessels for plants at both sites, total daily water movement via primary sinker roots was likely 2.5 to 3 times greater for plants from the natural site than the rehabilitation site during the dry period prior to the irrigation.

## Discussion

The water relations of *A. ancistrocarpa* on natural and rehabilitation sites were investigated at the end of the dry season and during the days and weeks following an irrigation with fresh water to simulate an 80-mm rainfall event - a pulse size typical of cyclones that occur during the summer wet season. With the overall objective to quantify how *A. ancistrocarpa* responds to such a pulse at the rehabilitation and natural sites, two specific aims were identified; first, to define the speed and extent of changes in plant water status and water-use patterns; and second, to ascertain if hydraulic redistribution was occurring between the primary sinker root and the lateral roots. It was anticipated that differences in the response by plants on the two sites would give some indication as to why high mortality rates had led to poor plant cover on the mine-rehabilitation site.

### *Pulse response*

Plants at the natural site displayed significant changes in water relations within three days of irrigation, whilst changes occurred generally one day earlier for plants at the



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rehabilitation site. Other studies have identified plants in water-limited environments that respond with significant changes in plant water relations within three days of a wetting event (BassiriRad *et al.* 1999; Huxman *et al.* 2004b; Burgess 2006) whilst others have found much longer response times or even none at all (Ehleringer *et al.* 1991; Phillips and Ehleringer 1995; Williams and Ehleringer 2000; Schwinning *et al.* 2003; Xu and Li 2006). This response time is likely due primarily to the enhancement of water uptake by existing roots near the surface (Cui and Calwell 1997; Ong *et al.* 1999) and, to a smaller extent the initiation of new roots (Dawson and Pate 1996; Ryel *et al.* 2004; Seyfried *et al.* 2005). Considering the six months prior to this experiment were all-but devoid of rainfall, this speed of uptake is noteworthy. The lack of water availability is highlighted by the fact predawn water potentials and stomatal conductance values at the natural site were much lower than those reported by an earlier, two-year study when rainfall had been greater (Grigg *et al.* 2008a, Chapter 2). With respect to the scenarios proposed earlier for pulse responsiveness of trees at the rehabilitation site, the suggestion most likely explaining the faster response is that lateral roots were restricted to shallower layers and their hydraulic function was maintained with a water supply. However, the mechanism by which this occurred was evidently not associated with hydraulic lift from the primary sinker root as anticipated, but from water supplied to the lateral roots by secondary sinker roots.

After the irrigation, stem sap velocity and stomatal conductance increased for plants at the natural site; however, the relative change in each was very different. Stem sap velocity was 20% higher on day 3 than it was during the dry period prior to irrigation, but stomatal conductance was 600% higher and almost three-fold higher than for unirrigated control plants for that day. This inconsistency was even more pronounced for irrigated trees at the rehabilitation site as there was no change in stem sap velocity, despite the fact that  $g_s$  tripled. Based on the reasonable assumptions there were no changes in leaf area and the relationship between transpiration and stomatal conductance was reasonably consistent over this short period of time, these data indicate that stem sap velocity is not proportional to transpiration for *A. ancistrocarpa*.

One possible explanation for this result relates to changes in the radial gradient of sap flux density (Salleo and Lo Gullo 1989; Salleo *et al.* 2000). Trials to determine velocity profiles using sap-flow probes were carried out weeks before the experiment, but were not possible once it had begun because of the necessity to avoid disturbance to probe

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position. The region of maximum flow, generally within 10 mm of the cambium, was most appropriate for probe placement so this was consistently used for all trees. Other studies have documented seasonal and diurnal changes in radial and circumferential sap flow using multiple-sensor probes that position thermocouples at varying depths throughout the conductive sap wood (Nadezhdina *et al.* 2002; Ford *et al.* 2004; Cohen *et al.* 2008). Multiple-sensor probes for the heat ratio method used here were not commercially available at the time of sampling. However, the ability of the heat ratio method to determine low velocities and reverse flows, its low power consumption and lack of perturbation by extremes in ambient temperature meant it was preferred over other methods for this particular study (Shackel *et al.* 1992; Becker 1998; Grime and Sinclair 1999; Burgess *et al.* 2001a,b; Green *et al.* 2003; Burgess and Bleby 2006). Considering the narrow diameter (30-60 mm) of stems and the fact that thermocouples in each sap-flow probe/needle were 10 mm apart, I am confident that probe placement accounted for between one third and two thirds of the conducting wood radius and in the region where sap velocity was greatest.

A second explanation to account for the discrepancy in stem sap velocity and stomatal conductance is that xylem cavitation was substantial during the dry period and that after the wetting pulse there was an increase in the proportion of conducting and non-conducting vessels. Water-stress-induced xylem cavitation caused by extremes in atmospheric demand coupled with insufficient moisture at the root-soil interface result in significant reductions in water loss (Tyree and Sperry 1989; Hacke *et al.* 2000; Davis *et al.* 2002). Re-watering of plants that remain hydraulically competent after a dry period can repair embolisms and ultimately regain lost conductivity (Salleo and Lo Gullo 1989; Meinzer *et al.* 2001). I suspect that during the dry period, plants at both sites displayed a substantial proportion of non-conducting vessels, but those that were still conducting displayed a peak daytime velocity of, for example 10 cm h<sup>-1</sup> in the case of the rehabilitation site. After the wetting pulse, cavitated vessels refilled and started conducting once again also with peak velocities around 10 cm h<sup>-1</sup>. Large increases in whole plant hydraulic conductance after the wetting event strengthens this explanation for irrigated plants at both sites. However, it can not be substantiated without determination of vessel percent embolism, or thresholds for cavitation ( $\Psi_{cav}$ ) and xylem vulnerability curves. Further research into the relationships among all the above parameters is needed. Considering sandy soils have a more abrupt decline in saturated hydraulic conductivity with downward changes in soil water potential (Hacke *et al.*

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2000; Sperry *et al.* 2002), and plants on sandy soils are more prone to xylem cavitation (Jackson *et al.* 2000; Sperry and Hacke 2002, Hultine *et al.* 2005), I suspect that plants at the natural site were more embolised than those at the rehabilitation site.

*Patterns in water uptake and hydraulic redistribution by roots*

During the dry period before the irrigation I expected that lateral roots would display little or no water uptake during the day and reverse flows at night supplied by hydraulically lifted water from the sinker root. Contrary to these expectations day time sap velocity in lateral roots was positive with rates similar to those of sinker roots whilst night time sap velocity was close to zero at both natural and rehabilitation sites. These findings indicate that water was being supplied to the lateral roots from deeper, wetter soil layers accessed by secondary sinker roots from distal portions and that hydraulic lift from the primary sinker was not occurring during the dry season. Secondary sinker roots have been identified for a number of species in water-limited environments (Jeschke and Pate 1995; Dawson and Pate 1996; Burgess *et al.* 2000a; Hultine *et al.* 2003a, b). Considering sap-velocity sensors were positioned close to the stem/root junction, I can state only that hydraulic redistribution from the *primary* sinker to the laterals was not a significant process; hydraulic lift of water from *secondary* sinkers to distal regions of the lateral root still remains a possibility. The absence of net water exchange between the primary sinker and lateral roots at night suggests there was no gradient in soil water potentials of the rhizosphere for active roots of both types prior to the irrigation. Future investigations are needed with sap-velocity sensors in secondary sinker roots and in lateral roots on either side of the junction (proximal and distal to the stem) to ascertain the possibility and extent of this phenomenon. These findings also highlight the need to fully excavate root systems (Pate *et al.* 1995; Dawson and Pate 1996; Jackson *et al.* 1996; Xu and Li 2006); had this not been done, positive sap flow in laterals during the day may have been ascribed to direct uptake without the contribution of secondary sinkers.

Positive sap flow in the primary sinker root during the days prior to the irrigation was not expected for plants at the rehabilitation site as I assumed that the sub-soil conditions of the mine-waste material would inhibit water uptake. However, positive flows during the day, and even at night during this time suggest water was being accessed. Excavations of root systems at the rehabilitation site revealed that lateral roots extended widely and were restricted typically to the native soil mixed surface layer. The primary

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sinker root and secondary sinkers originating from the laterals did enter the shale waste material, but were stunted in terms of their length and diameter compared with those of trees from the natural site. Taking into consideration the observed sap velocities, sinker roots for plants from the rehabilitation site displayed a water flux around one third that of sinker roots in the natural site. Given that plants were similar sizes, this finding indicates less water is accessed by primary sinker roots and that a greater proportion of uptake is sourced from the wide-spreading lateral root and secondary sinker root network at the rehabilitation site than at the natural site. The greater reliance on this wide-spreading network to obtain sufficient water means that each plant requires a greater 'footprint' area and partly explains the lower density of plants supported on the rehabilitation site.

After the wetting event, surface soils became saturated and there was evidence of a small amount of hydraulic redistribution down the primary sinker root from the laterals for at least three nights following the irrigation at the rehabilitation site, although not at the natural site. Transfer of water from wet surface layers to drier soil at depth via the root system has been observed in a number of studies on shrub and tree species in water limited environments (Burgess *et al.* 1998, 2001b; Schulze *et al.* 1998; Smith *et al.* 1999; Ryel *et al.* 2002, 2003). Night time water uptake by lateral roots at both sites was most likely used for refilling embolised vessels and for night time transpiration; positive sap flow in stems occurred most nights throughout this period.

#### *Root development and access to water*

The relationship between constraints in root development and pulse responsiveness is a more general issue indirectly examined here. The findings indicate that the stunted, relatively shallow roots displayed by trees at the rehabilitation site did not reduce the pulse responsiveness of *A. ancistrocarpa* so it is likely that the selection pressure for survival occurs during the interpulse (dry) period. It may be argued that shallow root depth into the silty waste material was not due to mechanical difficulties of penetration, but rather that plants were accessing sufficient moisture in the ~0.3 m below the interface with the cover soils. Other studies have found that in fine-textured soils, plants of a given crown size and leaf area need smaller root systems because such soils have higher water-holding capacities and shallower infiltration depths (Sperry *et al.* 1998; Jackson *et al.* 2000; Schenk and Jackson 2002; Seyfried *et al.* 2005). Whilst this effect is bound to be influencing rooting depth to some extent, if it was the dominant factor I

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would expect plant density and species richness to be much greater and not restricted to areas where cover soils were  $\geq 0.2$  m deep. A strong interaction with the depth of cover soils occurs not only because they are a more favourable growth medium for plant roots, but also because the high sand fraction acts as a ‘capillary break’ or dry mulch layer between the fine waste material and the atmosphere. In this way soil surface evaporation is reduced by cover soils and more water infiltrates the layers of fine material below the interface (Stormont 1996; Fayer and Gee 2006; Yanful *et al.* 2006).

With respect to species richness, I reiterate the point that the only woody species surviving at the rehabilitation site were Acacias. The presence of wide-spreading laterals with secondary sinker roots and primary sinker roots able to penetrate some depth into the waste material undoubtedly provides advantages over other species without these characteristics. I suspect that other woody species from the area, including Grevilleas, Hakeas and Eucalypts do not have these properties or the phenotypic plasticity required to survive in the shallow, modified soils at the rehabilitation site. Recent work on a number of *Hakea* species in south-western Australia found lower survivorship for deep-soil adapted species compared with shallow-soil endemics from ironstone outcrops when grown in reciprocal habitat conditions (Poot and Lambers 2008).

#### *Management implications*

On the mine-rehabilitation site, *A. ancistrocarpa* was one of the few species to survive where native soils were as shallow as 0.2 m over waste material. Therefore, if future rehabilitation efforts provide the same conditions, similar and unacceptably low plant densities (~12%) and poor species richness will result. I propose a range of soil depths for future rehabilitation efforts at this site with a minimum cover soil depth of 0.3 m in some areas, a depth at which Acacias will grow, to in excess of 2 m in other areas, in order to provide for other woody species adapted to natural dunes and interdunes. Greater depth of the store-and-release cover soil profile will provide a more reliable buffer volume for soil moisture, and support a greater leaf area and plant density, thus reducing the erosive potential of rain impact. The range of soil depths will also allow edaphic heterogeneity to support a broad range of plant functional types, greater root density and efficient extraction of moisture to prevent deep drainage and a more species-rich plant community. It is widely accepted that a high degree of biodiversity is required to ensure the long-term success of self-sustaining and functional ecosystems,

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especially in the face of climate change (Chapin III *et al.* 2000; Sala *et al.* 2000; Loreau *et al.* 2001; Midgley *et al.* 2002). All these parameters must be considered of utmost importance by government regulatory bodies before approving environmental closure to mining operations at the end of their economically viable life.

### *Concluding remarks*

This investigation has demonstrated that *A. ancistrocarpa* can survive prolonged dry periods and respond quickly to pulses of rain. Plants from the natural site displayed significant improvements in water relations within three days of the irrigation event whilst those at the rehabilitation site showed many of these changes one day earlier, despite stunted development of primary sinker roots. Hydraulic redistribution between the primary sinker and lateral roots was not found for plants at either site, and therefore not responsible for maintaining the hydraulic functioning of shallow roots in dry soil. Secondary sinker roots originating from laterals at various points along their length accessed deeper soil layers and presumably supplied water to fulfil this role and contribute significantly to the transpiration stream. I suggest that secondary sinker roots maintain the activity of lateral roots in dry soil and, in turn, facilitate rapid water uptake by these shallow roots following summer wetting events. Taking into account rapid pulse responsiveness, the ability to persist in dry periods and tolerance of shallow soils over mine-waste material, I concluded that *A. ancistrocarpa* is an ideal species for use in future rehabilitation efforts at this and other mine sites in the region.

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## Chapter 6

### General Discussion

The aims of this research were two-fold; first, to gain an understanding of the ecophysiology of plants and soil conditions in a natural habitat in the Great Sandy Desert in Western Australia; and second, to determine how the few native species occurring at a nearby mine-rehabilitation site were affected by the associated altered growing conditions. In this way, knowledge of abiotic conditions and plant functioning in the natural ecosystem were used as a reference to compare plant performance and diagnose problems causing poor plant cover at the rehabilitation site. A broad range of parameters were examined including ecological attributes (e.g., species composition and plant cover in each habitat); soil physical characteristics (e.g., texture, depth, hydraulic properties, erodability); soil chemical properties (e.g., pH, EC); soil and plant mineral nutrition (e.g., macro- and micro-nutrients); plant phenotypic traits (e.g., rooting patterns); and emphasis was placed on plant water relations (e.g., leaf gas exchange, leaf water potentials,  $\delta^{13}\text{C}$ , sap velocity in stems and roots). These findings are discussed in relation to habitat characteristics in the natural ecosystem, interactions between water availability and plant responses, and the likely impacts of climate change in this area. The causes of poor plant cover at the rehabilitation site are then discussed, followed by recommendations for improving rehabilitation practices, and broader implications for the mining industry.

#### *Factors affecting vegetation patterns and ecophysiology in the natural ecosystem*

The study sites in the natural habitat displayed two plant communities, discretely separated according to the two desert landscape elements: dunes and interdunes. Closely related and often congeneric species occurred in each habitat, but individual species were rarely found in both. These differences were highlighted by the distribution pattern of the dominant grass species; *Triodia schinzii* occurred only on dune ridges, whilst *T. basedowii* was restricted entirely to the interdunes (Chapters 2, 3). In addition, the largest tree species in the landscape, *Corymbia chippendalei*, occurred only on the upper slopes of the dunes. Relatively small and scattered *Acacia* and *Grevillea* shrubs dominated the woody component of most interdunes, but in lower-lying areas with shallow gravelly soils small-statured *Eucalyptus victrix* trees occurred (Chapter 2).

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Plant cover on dunes and interdunes were similar (42% and 49%, respectively; Chapter 3) and in the upper end of the spectrum for desert ecosystems (Winkworth 1967; Aguiar and Sala 1999; Hesse and Simpson 2006). Such high plant cover values are due to a combination of relatively high annual rainfall (~330 mm) and coarse-textured soils. Rapid infiltration of water into sandy soils and limited capillary rise results in relatively low soil surface evaporation compared with fine-textured soils (Alizai and Hulbert 1970; Noy-Meir 1973). This ‘inverse texture’ effect is central to the reason why sandy soils in arid environments support greater vegetation cover than fine-textured soils (Noy-Meir 1973; Sala *et al.* 1988; Sperry and Hacke 2002).

Dunes and interdunes displayed similar and extremely sandy surface soils (99% and 95% sand, respectively). However, the depth of these soils differed greatly at contrasting sites; the dunes were on average 12 m high and composed of homogeneous sands, whilst most interdunes displayed sands over increasingly dense gravel layers that generally formed a hardpan ~ 2 m below the surface. It was hypothesised that the greater depth of sands would provide a larger store of water and facilitate higher water use further into the dry season for plants in the dune habitat than closely related species in the interdunes. Nutrient availability was also considered a possible factor influencing plant habitat preferences. Considering that the interdunes displayed much greater termite activity, cryptogamic crust patches, and the tendency for organic matter accumulation because of the lower landscape position, it was hypothesised that plants on interdunes would display higher nutrient concentrations. This study found that nutrient concentrations were higher in interdune soils, but there were few differences in foliar nutrient concentrations between habitats, and no consistent patterns for any nutrient among all eight woody and non-woody species examined (Chapters 2, 3). In both habitats, phosphorus was the nutrient evidently most limiting growth, followed by nitrogen. I concluded that the availability of nutrients was not a direct factor shaping the different vegetation patterns in this ecosystem. However, water relations parameters indicated that plants in the dune habitat displayed greater access to soil moisture than plants in the interdunes, particularly during the dry season (Chapters 2, 3). This was facilitated by uninhibited root growth through the homogeneous deep sands in the dunes. I conclude that soil depth and associated moisture storage are the primary factors determining the plant-habitat associations in the natural desert environment.



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Root morphologies were generally similar for closely related species on both habitats, although some rooting patterns for dune species were not replicated in the interdunes. Roots of the *Triodia* grasses were fibrous at both sites, but those for *T. schinzii* penetrated 2 m into the dune soils, whilst *T. basedowii* roots were 1 m deep or less if they encountered gravels closer to the surface (Chapter 3). Dimorphic roots were common for woody shrubs throughout the dune and interdune habitats (Chapter 2). Ehleringer and Dawson (1992) proposed that dimorphic roots confer an advantage where summer rainfall is sufficiently reliable, as near-surface lateral roots allow uptake of summer precipitation events and tap roots access to deep stores of moisture. Considering the vast majority of rainfall at the study site occurs during the summer monsoon, Ehleringer and Dawson's (1992) proposal explains why the dimorphic rooting strategy is the optimal phenotype for most shrub species in the Great Sandy Desert. The tree species, *C. chippendalei* displayed a unique root morphology, which was not emulated by any species in the interdune. Near-surface lateral roots were absent, and the root crown was often 1-2 m below the surface. Dozens of substantially-sized diagonal roots originated from the root crown and were often greater than 10 mm diameter after 8 m (Chapter 2). Clonal species devoted to vegetative means of dispersal with shoot-bearing rhizomes were common in the dune habitat (e.g. *Acacia jensenii*) but not in the interdunes. The diversity of root morphologies found at this site highlights the variety of trade-offs between pulse water use and access to deep moisture stores (Schwinning and Ehleringer 2001). This diversity facilitates spatial and temporal separation of niches for water uptake, and promotes species co-existence (Walter 1971; Caldwell and Richards 1986; Neilson 1995; Weltzin and McPherson 1997). Furthermore, it allows maximum utilisation of resources and leads to greater ability of the vegetation to respond to inter-annual variations in rainfall and climate change (Schlesinger *et al.* 1990; Casper and Jackson 1997; Williams and Ehleringer 2000; Lavorel and Garnier 2002).

A clonal habit and the ability resprout after fire were common for species occurring on the dunes (e.g., *C. chippendalei* and *T. schinzii*); whilst in the interdunes, species tended to be killed by fire and regenerate from seed (e.g., *A. ancistrocarpa*, *T. basedowii*) (Chapter 2, 3). Establishment from seed is very difficult on sand dunes after disturbance (e.g., fire or clearing) because of wind exposure causing sand-blasting, seedling burial or detachment; and because water is only available in surface layers for short periods after rain (Danin 1996). Resprouting species display longer life-spans and larger

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root:shoot ratios than seeder species (Pate *et al.* 1990; Bell *et al.* 1996; Verdu 2000). These traits facilitated the long-term accumulation of nutrient-rich fine particles (organic matter and topsoil dust) and greater exploration for deep water sources. *T. schinzii* hummocks were particularly effective at accumulating particles, often forming accretion mounds up to 0.5 m high on the dune crests (Chapter 3). The greater ability for resprouter plants in the dune habitat to create ‘islands of fertility’ (Schlesinger *et al.* 1996) likely offsets the higher concentrations of nutrients in the interdunes. This helps to explain the similarities in foliar nutrient concentrations for closely related species on dunes and interdunes (Chapter 2, 3).

Soil moisture availability varies spatially (vertically and horizontally) and temporally in desert environments and shapes ecosystem processes and vegetation dynamics (Walter 1971; Noy-Meir 1973; Reynolds *et al.* 2004; Schwinning and Sala 2004). Based on well-founded hypotheses for soil and plant interactions, Schwinning and Sala (2004) proposed, the ‘hierarchy of pulse responses’, which considers the size and duration of water pulses in terms of soil moisture availability. This model recognises that large rainfall events, clustered storms and very wet seasons allow water to infiltrate to great depths, but these events occur infrequently (yearly or decadal time scales) for most desert systems. These ‘high-order’ events result in long, steady pulses that may carry over from one year to the next (Schwinning and Sala 2004). In the years leading up to and during this study in the Great Sandy Desert, ‘high-order’ events dominated the rainfall. During this time, half the rainfall was in the form of tightly clustered events (the sum of rain over 4 days) greater than 60 mm, and over 90% of these events occurred during the summer half of the year (Appendix I, Figure I.3, Bureau of Meteorology 2006). Extreme rainfall clusters (cyclones >150 mm) contributed over 15% of the rainfall during this time. The monsoon before this study started was one of the wettest in record (849 mm in 2000) and resulted in the flooding of some low-lying interdunes. The effects of this deep soaking clearly persisted throughout the two-year seasonal study (2001-2002) on water relations, as indicated by much higher than expected leaf water potentials and gas exchange rates for plants on both dunes and interdunes (Chapters 2, 3). Had this study been conducted following average rainfall conditions, relatively lower water availability in the interdunes than the dunes might have been more accentuated than presented here. Evidence for this is found in the comparison of that for *A. ancistrocarpa* between the two-year seasonal study (Chapter 2) and the pulse response study which occurred at the end of the 2003 dry season

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following two years of average rainfall (~330 mm) (Chapter 5). In the early study, predawn leaf water potentials ( $\Psi_{pd}$ ) never dropped below -0.5 MPa, whilst stomatal conductance ( $g_s$ ) values were 50 mmol m<sup>-2</sup> s<sup>-1</sup> during the driest times of year (Chapter 2). For the later study values were markedly lower:  $\Psi_{pd}$  values were -1.7 MPa and  $g_s$  values were 20 mmol m<sup>-2</sup> s<sup>-1</sup> (end of 2003; Chapter 5). These findings highlight that inter-annual variability can be more significant than intra-annual (seasonal) variability, and that long-term studies of arid and semi-arid environments are needed to understand the dynamics of water availability in these ecosystems (Zeppel *et al.* 2006).

The effects of ‘high-order’ events will be longer-lasting in the dunes than the interdunes because the much deeper sands provide a larger buffering capacity. Plants with deep roots are reliant on ‘high-order’ events to recharge deep soil layers (Schwinning and Sala 2004). Shallow-rooted species are more dependent on the frequency of rain pulses rather than their size (Dougherty 1996; Knapp *et al.* 2002; Schwinning *et al.* 2003; Reynolds *et al.* 2004). Both extremes in water source dependence were demonstrated by species examined in this study. The tree species *C. chippendalei* in the dune habitat displayed predominantly deep roots and moderate stomatal conductance, with little variation between wet and dry seasons; a pattern reflecting a “long pulse duration” as described by Schwinning and Sala (2004). All other species displayed greater fluctuations in water use over the seasons, particularly the *Triodia* grasses and woody species in the interdunes. In the interdunes, the relatively shallow soils result in greater depletion of soil moisture reserves within years, creating a greater necessity for tolerance of broad fluctuations in water availability.

Trends in rainfall over the past few decades have shown that most of Australia has been getting drier; however, north-western Australia is one of the few regions getting wetter (Appendix I, Figure I.4, Bureau of Meteorology 2009a). When this project began the long-term average rainfall for the area was 332 mm (Telfer measurements since 1974). Due to a series of very wet years over the past decade, the long-term average is now close to 365 mm. This has been the result of increasingly severe tropical cyclones with higher rainfall intensities (Bureau of Meteorology 2009b). If this kind of rainfall continues, changes in community structure and species composition are likely. Greater penetration of moisture to depth tends to favour woody species with deep roots more than species with shallow roots such as grasses (Walter 1971; Schwinning and Sala 2004; Fensham *et al.* 2005). This process is accentuated on deep, sandy soils due to

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rapid infiltration rates through the profile (Knoop and Walker 1985; Fravolini *et al.* 2005; Potts *et al.* 2006a). I predict that the density of woody plants will increase throughout the Great Sandy Desert, particularly on the flat crests of dunes which are currently only sparsely vegetated (21%; Chapter 3). Such ‘woody thickening’ has been observed in other areas where increases in rainfall have occurred over preceding decades (Brown *et al.* 1997).

Climate change and associated alterations in rainfall patterns are well recognised as factors influencing shifts in the distribution of many plant species (Midgley *et al.* 2002; Parmesan and Yohen 2003; Root *et al.* 2003; Hulme 2005). In the Great Sandy Desert, increased rainfall will likely cause shifts in species distributions at both local and regional scales. Locally, species adapted to the more-mesic dunes may encroach onto the interdunes if they display sufficient plasticity in root morphology to establish on the shallower soils. One species that has the potential to be an indicator of this shift is *Grevillea stenobotrya*, and evidence for this encroachment may already be available. This tree-shrub ( $\leq 3$  m tall) normally inhabits sand dunes throughout the broader region; however, small individuals ( $\leq 1.3$  m tall and  $< 10$ -years old) were observed throughout interdunes with *G. wickhamii* and *A. ancistrocarpa* (Chapters 2, 3). Another potentially good indicator species is *T. schinzii* as it predominantly occurs in higher-rainfall sub-tropical areas further north. I propose that greater water availability in the dunes allows this species to occur at the study site; an area more arid than expected for ‘soft’ spinifex species (Chapter 3). Whilst this species normally occurs on the dunes, it can acclimate to shallower soils, as evidenced by its tolerance of conditions at the mine-rehabilitation site. These properties should allow *T. schinzii* to compete with its more arid-adapted relative *T. basedowii* in the interdunes. Greater penetration of cyclones into the southern interior should also facilitate the latitudinal spread of *T. schinzii*, and other species of sub-tropical origin, into the dune-fields of the Gibson and Great Victoria Deserts. Monitoring the distribution patterns and densities of these and other species will undoubtedly prove useful for gauging the effects of climate change in this region.

#### *Diagnosing the causes of poor plant cover at the rehabilitation site*

At the rehabilitation site, plant cover was less than a quarter of that at the natural site, and it was a key objective of this study to determine the reasons why. In terms of their distribution, plants were found only in patches away from erosion rills and where cover soils were at least 0.2 m deep. The only species in reasonable abundance included three

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*Acacia* shrubs and two *Triodia* grasses. A marked decline in plant density and species richness had apparently occurred during the seven years prior to the start of this investigation; anecdotal reports indicated uniform seedling cover and reasonable biodiversity ( $\geq 20$  species) after the first twelve months of establishment (pers. comm. Phil Davidson, Nifty Copper Operation Environmental Manager). The presence of numerous dead individuals, both standing and dislodged in erosion gullies, provided supporting evidence for this. High mortality in areas where cover soils were shallow or non-existent indicates that plants were adversely affected by the underlying mine-waste material. Indeed, root development was severely impeded, with roots penetrating no more than 0.3 m below the interface between the cover soils and waste material (Chapter 4). This was in marked contrast to roots of plants in their natural habitat, particularly *A. ancistrocarpa* (2-2.5 m) and *T. schinzii* (2 m). To determine why plants were adversely affected by the waste material, soil chemical and physical properties were investigated, in conjunction with the associated effects on plant nutrition, root development and water relations.

Soil chemistry of the waste material was different from that of the native soils (Chapter 4). It displayed mild salinity levels ( $EC_{1:5} = 46 \text{ mS m}^{-1}$ ), and although higher than the natural soils ( $EC_{1:5} = 1 \text{ mS m}^{-1}$ ), the salinity level was below that generally accepted to adversely affect all but the most sensitive glycophytes ( $\sim 60 \text{ mS m}^{-1}$ ) (Greenway and Munns 1980; Munns and Tester 2008).  $\text{Na}^+$  concentrations in foliage were not significantly different for most species at natural and rehabilitation site indicating no salt stress. Soil pH of the desert sands was 6.7 whilst the pH of the waste material was 8.7; high enough to significantly reduce the availability of many mineral elements (Lambers *et al.* 2008). However, higher concentrations of macro- and micro-nutrient in the waste material likely offset this to some extent, because concentrations in foliage at both sites were similar. Notable exceptions included concentrations of Cu, Fe and Zn, and particularly that of the potentially toxic non-nutrient Al; these were significantly higher in foliage of plants at the rehabilitation site. Foliar Al concentrations were similar to those of hyper-accumulating species and may have been toxic if these plants were sensitive to such levels (Rengel 1992; Delhaize and Ryan 1995; Lambers *et al.* 2008). However, there were no signs of leaf chlorosis or abnormal leaf morphology for any of the five species currently occurring at the rehabilitation site. Some *Acacia* species are tolerant of metalliferous mine soils (Barnet *et al.* 1985; Lesueur *et al.* 1993; Musil 1993; Bell *et al.* 2003), so it is possible that other species in the local area (e.g., *Grevillea*,

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*Hakea* and *Eucalyptus*) are more sensitive and unable to tolerate the mine-waste material. Further research is needed into the role of Al affecting plant development at this site.

Soil physical properties were extremely different at the natural and mine-rehabilitation sites (Chapter 4). The sandy and gravelly native soils were texturally dissimilar from the fine, compacted silty, shale waste material. Such physically impeding characteristics likely caused mechanical difficulties for root penetration and were considered the primary cause of stunted root growth. Soils from the natural site displayed high hydraulic conductivities, whilst these were very low for waste material. Because the natural site displayed highly transmissive soils and considerable vegetation cover, runoff and erosion were never observed, not even on the slopes of the dunes during the most intense cyclonic rain events. By contrast, slow infiltration rates, low plant cover and the unstable, slaking nature of the waste material led to high runoff and erosion at the rehabilitation site. A rainfall-simulation experiment on the mine-waste material revealed that for slope angles similar to those at the rehabilitation site, 70 to 80% of water would be lost to runoff with a rainfall intensity similar to that associated with tropical cyclones ( $75 \text{ mm h}^{-1}$ ). The experiment also revealed that compared with a slope angle of  $10^\circ$ , erosion rates were two-fold and five-fold greater for  $15^\circ$  and  $20^\circ$  slopes during the first five minutes of rainfall. Once the soil surface was saturated after ten minutes, erosion stabilised to 11, 15 and  $17 \text{ t ha}^{-1} \text{ h}^{-1}$  for the  $10^\circ$ ,  $15^\circ$  and  $20^\circ$  slopes, respectively (Chapter 4). These rates are consistent with findings of others in similar experiments on unstable mine-waste materials (Lasanta *et al.* 2000; Johansen *et al.* 2001; Loch 2000), and are unacceptably high by mining-industry standards (Campbell 2004).

High runoff losses at the rehabilitation site, in combination with limited cover soil depth to retain moisture were anticipated to reduce water availability for plants. Ecophysiological measurements indicated that conditions at the rehabilitation site adversely affected the water relations for woody plants but not for grasses. *Acacia* species at the rehabilitation site generally displayed poorer water relations (lower  $g_s$ , lower stem sap velocity, higher  $\delta^{13}\text{C}$  values, more negative leaf water potentials) than plants at the natural site during the middle of the dry season (Chapter 4). It is proposed that this was caused by limited root penetration and reduced access to deep stores of moisture. However, this was partly offset by the fine texture and associated higher

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water-holding capacity of the waste material. Even with relatively shallow root systems, plants were accessing limited water from the waste material during the dry season, as indicated by positive (upwards) sap flow in the sinker roots of *A. ancistrocarpa* (Chapter 5). In addition, sap flow in lateral roots during the day was facilitated by uptake via secondary sinker roots descending from distal regions into the waste material. *Triodia* species showed virtually no differences between sites at any time of year (Chapter 4). The fibrous rooting strategy of these species and their ability to tolerate shallower soils at the rehabilitation site suggests a high degree of phenotypic plasticity. *Triodia* species are adapted to relying on moisture in shallow soil depths, whilst *Acacia* species have greater dependence on deeper sources and are thus more affected by limited root penetration at the rehabilitation site.

Reduced access to deep moisture because of physically hostile sub-soils at the rehabilitation site leads to a selective advantage for species that are shallow rooted, able to tolerate extended dry periods, and respond quickly to wetting pulses. Desert grasses are well known to display these qualities (Sala and Lauenroth 1982; Pugnaire *et al.* 1996; Schwinning *et al.* 2002; Potts *et al.* 2006b); and were demonstrated here by the success of the two *Triodia* species. Woody plants with near-surface and deep roots can potentially respond quickly to rainfall events, but the seasonality of the rainfall greatly influences the timing and extent of uptake (Lin *et al.* 1996; Williams and Ehleringer 2000; Fravolini *et al.* 2005). In response to an 80-mm experimental wetting event *A. ancistrocarpa* displayed significant increases in stomatal conductance, leaf water potential, and sap velocity in lateral roots after two days for plants at the rehabilitation site and after three days at the natural site (Chapter 5). The faster response at the rehabilitation site was attributed to the confinement of lateral roots closer to the surface compared with plants at the natural site. These response times were similar to those of other woody species with near-surface roots in water-limited environments (BassiriRad *et al.* 1999; Huxman *et al.* 2004; Burgess 2006). The initial phase of this response is attributed to enhanced water uptake by existing roots more so than newly-grown roots (Cui and Caldwell 1997; Ong *et al.* 1999). Secondary sinker roots descending from distal sections of lateral roots were evidently responsible for supplying water to the crown and maintaining hydraulic function of lateral roots in dry soil. I suggest, therefore, that they are important for enabling rapid pulse responsiveness in *A. ancistrocarpa*. The presence of secondary sinker root also explains the absence of hydraulic redistribution between the primary sinker root and the lateral roots as both

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types of sinker roots are likely experiencing the same soil water potentials. The importance of secondary sinker roots and the role they play in water sourcing and hydraulic redistribution has received very little attention in the literature, and is suggested as an important topic for future research.

Trends for increasing annual rainfall in the region might lead to the expectation that plant cover should improve at the rehabilitation site (Appendix I, Figure I.4). However, climate models indicate summer cyclones will be more severe, and there will be less winter rainfall (Bureau of Meteorology 2009b). The greater severity of cyclones is forecast to increase peak rainfall intensities by 20-30%, and will heighten problems with erosion and plant dislodgment. For plants that do remain on the rehabilitation slopes, wetter summers, and drier winters mean greater fluctuations in moisture availability. Although winter rainfall is a relatively small component (10-15%) of annual inputs, its importance is amplified because a high proportion of it penetrates to deeper layers during the cool months (Williams and Ehleringer 1996, 2000; Golluscio *et al.* 1998; Schwinning and Sala 2004). Hotter temperatures in the future will increase soil surface evaporation offsetting higher summer rainfall to some extent, and exacerbate demands for moisture during the winter dry season.

The dominance of 'high-order' rain events (Schwinning and Sala 2004) resulting from summer thunderstorms and cyclones in the Great Sandy Desert demands that deep cover soils are needed at the rehabilitation site. Ideally, the soil layer should retain all rainfall and allow plants to extract this moisture over the dry months. An effective 'store-release' cover should prevent deep drainage into the underlying mine-waste materials (Campbell 2004). Determination of cover soil depth should be dictated by the volume, timing and intensity of rainfall, evaporation (soil/litter surface and canopy interception), the water-holding capacity of the soil profile occupied by plant roots and the extraction rate. Taking into account most rainfall occurs between January and March, and the prospect of increasingly large cyclones in the future, at least 350 mm of rainfall should be budgeted for. Evaporation losses following rain will reduce this amount by 10 and 20% (Daamen *et al.* 1995; Carlyle-Moses 2004; Wildy 2004). Plant extraction of water in the immediate term following short periods of high intensity rainfall will be negligible so should not affect the calculation of required soil depth. Taking into account losses of about 50 mm from the initial 350 mm of rain amount, and water-holding capacity of the native sands is 10% (Chapter 3), then approximately 3 m of cover soil is needed to



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avoid deep drainage. Plant roots should not be relied upon to extract moisture from the waste material, although this will likely be necessary if deep drainage is to be prevented following very wet years. A cover soil depth of 3 m would support similar vegetation cover to the natural habitat and allow the establishment of a broad number of species. The practical aspects of implementing a 3 m cover soil depth are discussed in the management implications section below.

*Issues for consideration in future mine-rehabilitation studies*

Similar investigations as this should ideally begin with assessments of vegetation characteristics and plant requirements before mining operations disturb an area so plans can be developed early for the rehabilitation strategy. Where operations are already running, assessments of rehabilitation progress should start at the very beginning or within the first twelve months of establishment. Important information such as seedling densities and species richness early on would have provided useful benchmarks for comparison, but unfortunately are lacking here. Ecophysiological measurements should start within two years as by this time, signs of adverse affects should be apparent, particularly problems directly associated with soil physical or chemical properties. Seedlings are likely to be more susceptible to water shortages, salt stress, temperature extremes as well as problems common to post-mining soils such as acidic or alkaline pH, and toxic concentrations of heavy metals (Enright and Lamont 1992; Grant *et al.* 1996; Bell 2001). Earlier commencement of this study may have provided additional insights into the ecophysiological problems experienced by native species once present at the rehabilitation site. For example, species that no longer occur at the rehabilitation site may have been sensitive to metal toxicities (e.g., Al). With respect to problems relating to water availability, the full extent of these may not be realised until plants have exhausted initial moisture reserves, need to utilise deeper stores of water, if available. Indeed Bleby (2003) found that leaf water potentials for small saplings were higher at a mine rehabilitation site than an adjacent forest site, but large saplings did not show this difference. Where a single site can not be followed through time, chronosequence studies of different aged plots side-by-side can be a useful alternative. I suggest that monitoring of ecophysiological parameters should be done at least yearly, and should concentrate on the first five years of establishment or until it is evident that the re-vegetation community has reached an equilibrium. By this time, all problems should be evident and properly substantiated advice can be given on ways to improve ensuing rehabilitation efforts.

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With respect to methodological recommendations for future similar studies, a larger suite of parameters for defining water stress should be considered to overcome inherent complexities comparing between soil types at natural and rehabilitation sites. Pressure volume curves, xylem vulnerability curves and quantification of the proportion of embolised vessels would greatly complement methods used in this study (Tyree and Sperry 1988; Sperry *et al.* 1998; Linton *et al.* 1998). They would also help to explain discrepancies between sap velocity and stomatal conductance identified here for *A. ancistrocarpa* (Chapter 5). Continuous monitoring (data logging) of other parameters such as stem water potentials (with stem hygrometers – e.g., Naor and Cohen 2003), and fluctuations in stem diameter (with fine-scale, band dendrometers – e.g., Mäkinen *et al.* 2003; Graham and Nobel 2005), would also be helpful and provide additional information on diurnal and seasonal responses to water availability.

It is important to recognise that ecophysiological parameters must always be considered in concert with broader ecological issues such as erosion and plant cover when determining problems at mine-rehabilitation sites. As evidenced by the present research, ecophysiological measurements offer a great deal of insight into the functioning of plants in natural and rehabilitation sites alike, and should be included as one of the many tools used for diagnosing problems affecting plant growth. Coupled with ecologically based assessment procedures such as Landscape Function Analysis (Tongway and Hindley 2000; Ludwig *et al.* 2004) they can assist in diagnosing problems and monitoring the success of rehabilitation by industry and government regulatory bodies.

#### *Management implications and recommendations for rehabilitation at this site*

Directly or indirectly, the two fundamental issues at the centre of all problems at the rehabilitation site are: 1) cover soil depth, and 2) slope angle. Problems associated with the hostile mine-waste material (e.g., poor plant root penetration and plant mortality), runoff and erosion can be mitigated if sufficient cover soil depth is provided and slope angles are reduced. Wherever potentially hazardous mine wastes are buried within constructed landforms, it is of utmost importance to prevent the ingress of water and mobilisation of toxic substances. For many deep mines (open pit or underground), including Nifty Copper Operation, sulfide-containing rocks (e.g., pyrites and chalcopyrites) are unearthed and stockpiled on waste-rock dumps. If buried without

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adequate coverings of inert mine-waste material and hospitable soil for plant growth, deep percolation of water can lead to acid-mine drainage and leaching of heavy metals into the environment. Fundamentally, this is a water-management issue and options exist along a continuum from complete water shedding off the landform, to water retention on the landform.

At Nifty Copper Operation, the first of these options will not be feasible because no inert, stable (non-eroding) rocks were present for the creation of rock-lined drains and rock-armoured slopes. The only feasible alternative is a store-release cover that controls water locally so that shedding is minimised to prevent erosion. Based on calculations described earlier, approximately 3 m of dune sand is required to hold the rainfall from one average wet season. Assuming plants exhaust the previous years' rainfall completely, drainage beyond the cover layer should be prevented. In very wet years, even this soil depth will not prevent percolation beyond the cover layer, but the roots of *Acacia* species that penetrate as far as 0.3 m into the waste material may extract some of this water. Whilst it is beyond the scope of this thesis to carry out the cost-benefit analysis of implementing a 3 m cover depth, it is appreciated that the cost of construction would be prohibitive. From the perspective of the mining company, they demand a compromise that is financially realistic, practical for operational reasons and minimises environmental impacts enough to obtain approval for mine closure from government regulators. For this reason, a minimum soil depth of 0.5 m is advised in order to establish a sufficient density of only waste-tolerant species to reduce, but not wholly prevent impacts of erosion and deep drainage. Over the top of hazardous encapsulated pyrite bodies, at least 2 m of cover soil is still advised because of the threat of acid-mine drainage. A range of soil depths will also create habitat heterogeneity throughout the rehabilitation site and lead to the improvement of plant biodiversity.

The practical requirement for extracting water from the cover layer and reducing the likelihood of deep drainage should be complimentary to establishing a species rich plant community. A range species should be selected with a variety of root morphologies in order to optimise water extraction (Pate and Bell 1999; Schwinning and Ehleringer 2001; Schenk and Jackson 2002). Based on findings from this research, interdune plants should be targeted because they are better adapted to the proposed soil depths ( $\geq 0.5$  m), are more tolerant of fluctuations in water availability and display greater pulse responsiveness. Species with a dimorphic rooting strategy include *Grevillea wickhamii*,

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*Hakea lorea*, *Jacksonia aculeata*, *Melaleuca lasiandra* and the three *Acacia* species (*A. ancistrocarpa*, *A. translucens* and *A. hilliana*) are recommended for areas  $\geq 0.5$  m deep areas. The tree species *Eucalyptus victrix*, may be particularly successful because of its tolerance of dense gravelly soils spreading nature (Chapter 2). Small woody and herbaceous species with roots that penetrate dense gravelly or rocky soils should also be included; e.g., *Goodenia scaevolina*, *Scaevola parvifolia* and *Ptilotus calostachys*. Particular attention should also be paid to the grasses *T. basedowii*, *T. schinzii* and others such as *Eriachne aristidae* because their low crowns offer excellent protection of the soil surface from the erosive effects of rain droplet impact and their fibrous roots are effective at binding surface soils limiting inter-rill and even rill erosion. On the 2-3 m deep sections, dimorphic-rooted dune species including *G. stenobotrya*, *Crotalaria cunninghamii* and transplanted root stock of the clonal species, *A. jensenii*, could offer long term stability in the event of fires. Whilst I believe every effort should be made to return edaphic conditions to that inhabitable by species local to the area, I also believe that other species better adapted to shallow, heavy soils from the broader region (<400 km) should be considered for use in the revegetation strategy. This, however, requires a shift in accepted practice by government regulatory bodies that demand the use of provenance seed collected from the local area (<20 km). Taking into account climate change and associated shifts in species distribution ranges, inclusion of plants from the broader region may simply pre-empt their natural encroachment into the area and be advantageous in the long-term.

Appropriate design and construction are primary to the long-term stability of the waste-rock dump, and if not done correctly can undermine even the most conscientious rehabilitation efforts. Failures in these areas are apparent at the landform studied here, as evidenced by the massive erosion gullies several metres deep. As described earlier, this has been caused by the uncontrolled escape of water from the flat top section of the waste dump. Whilst a 3 m cover soil on this flat area would prevent this, it is unlikely that a depth of 0.5 m could be as effective, because only 50 mm of rainfall could be held before field capacity was reached. Given that cyclones can bring more than double this amount, alternative measures to control excess rainfall must be put in place. If water was harvested into a depression, this may prevent the uncontrolled escape of water over the sides, but lead to pooling, deep drainage, the collapse of subsoil voids and vertical tunnelling into the dump, ultimately increasing the threat of acid-mine drainage. Ironically, water-logging may even occur for plants in the middle of the depression, but

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others on the fringe will have a longer-lasting resource. Alternatively, slight elevation in the middle of the top section may allow for safe shedding of water if, and only if slope angles of the sides are very mild e.g.,  $\leq 12^\circ$ . This does not need to increase the footprint of the dump if greater height is created, and the proportion of the flat area is reduced. Such a reduction in slope angles would reduce runoff and allow steady shedding of water via subsurface flow through the cover layer. This slow descent of moisture should provide an ongoing source of water for plants if cover soils depths  $>0.5$  m or ideally  $>1$  m are provided. On slopes, as on the flat top, deeper soils will support greater vegetation cover, which will in turn shield soil surface from rain impact and ultimately limit erosion at the local scale.

#### *Concluding remarks*

This study highlights the importance of considering ecophysiological attributes for diagnosing problems associated with mine-site rehabilitation. This approach offers valuable information for both mining companies in assisting with rehabilitation design (e.g., construction of suitable soil profiles and slope angles, selection of plant species), and government regulatory bodies in terms of monitoring and quantification of rehabilitation progress. It is hoped that the outcomes and recommendations from this research will improve rehabilitation strategies and lead to the development of well vegetated, stable, non-polluting landforms at this and other mine sites throughout arid Australia and arid regions worldwide.

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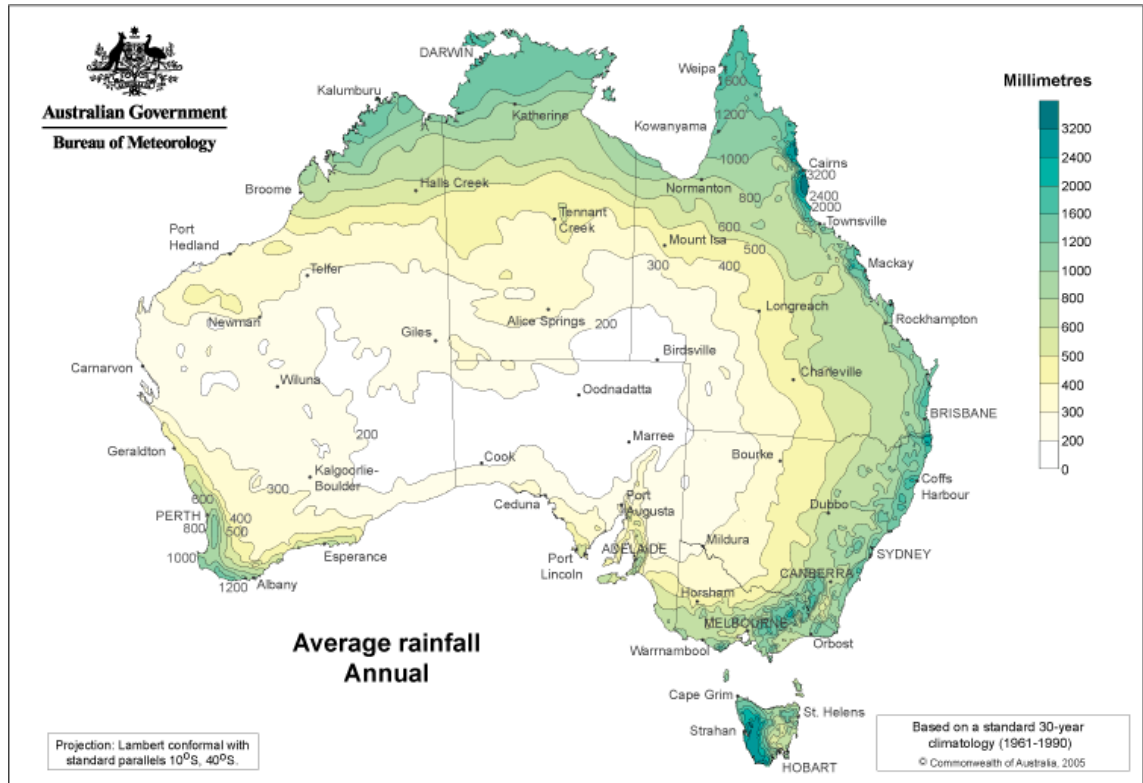
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## Appendix I

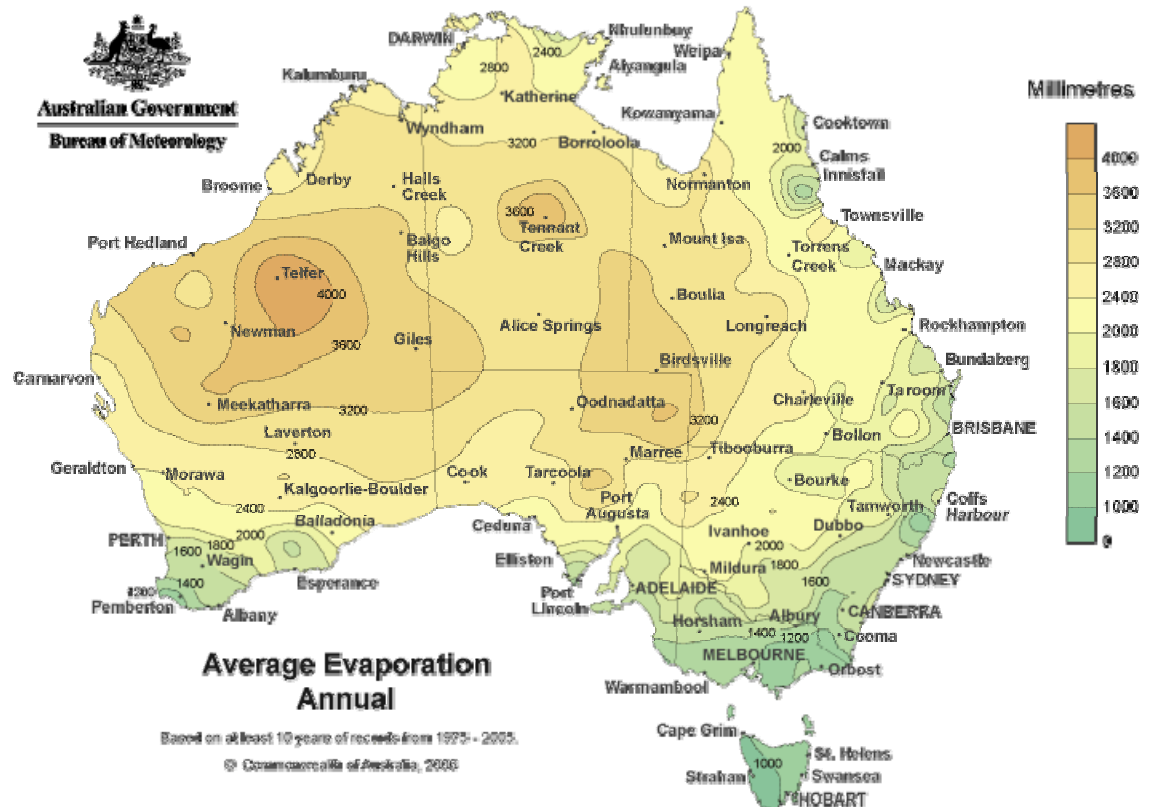
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**Figure I.1** Average annual rainfall throughout Australia. This study was conducted near Telfer in north-western Australia where rainfall is ~330 mm per year (Bureau of Meteorology 2009).



**Figure I.2** Average annual pan evaporation throughout Australia. The study sites near Telfer display evaporation rates ~4000 mm per year (Bureau of Meteorology 2009).

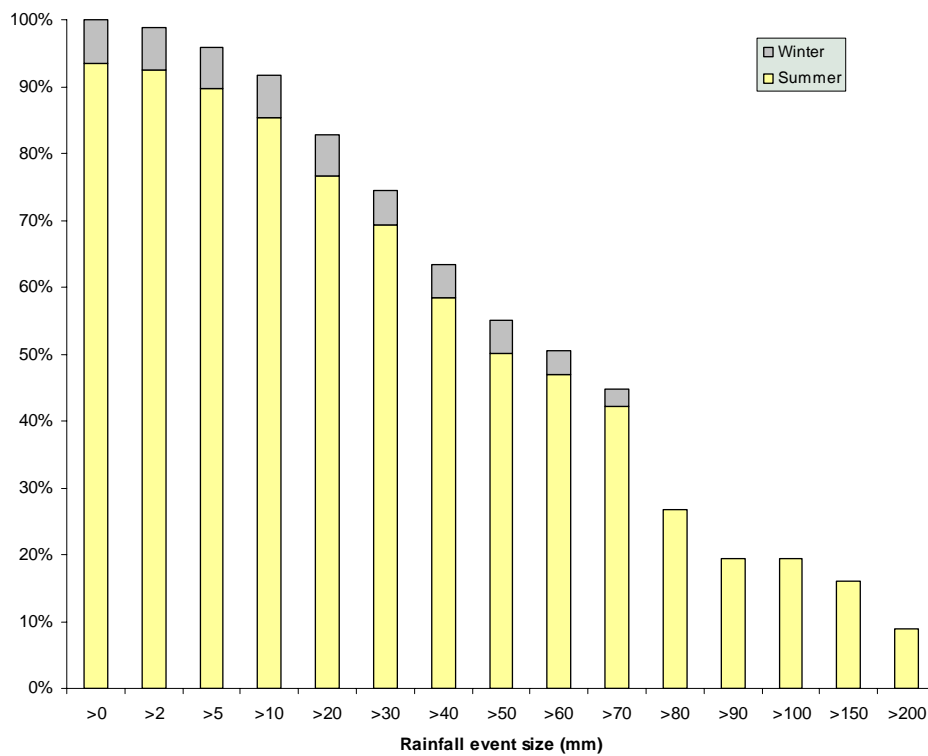


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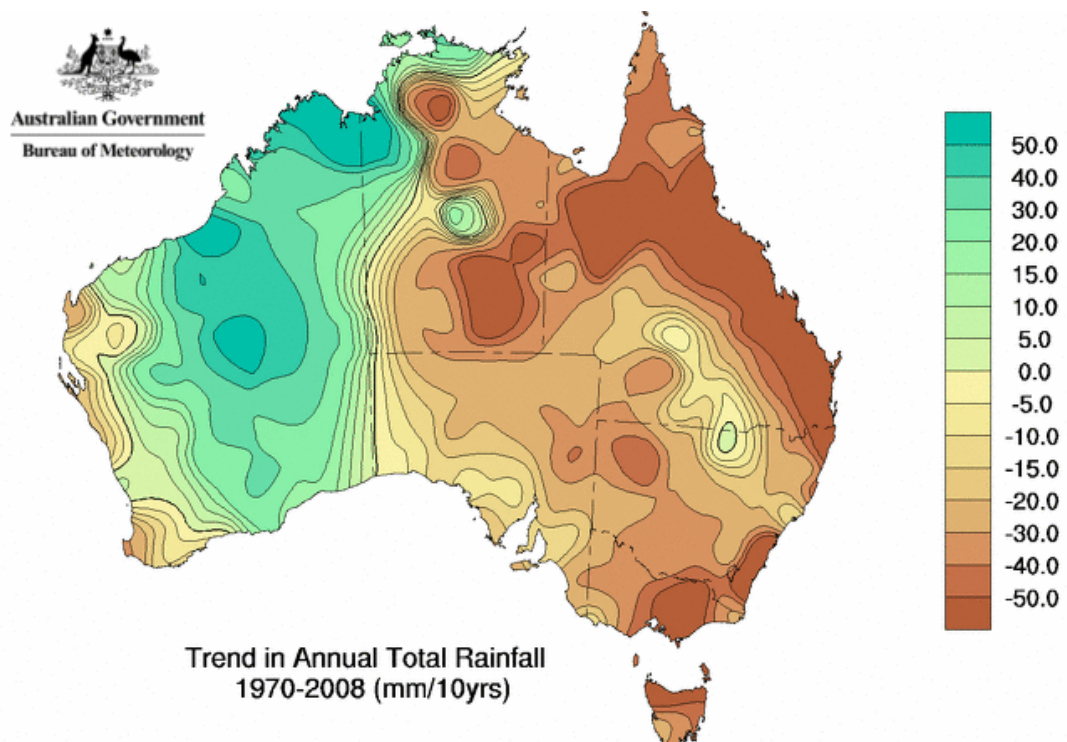
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**Figure I.3** Size classes of rainfall events (4-day clusters) for the Great Sandy Desert study area separated into summer (November – April) and winter (May – October) six-months periods. Data presented for the field work period (2000 and 2006)(Bureau of Meteorology (2006).



**Figure I.4** Rainfall trends throughout Australia between 1970 and 2008. Note that north-western Australia, has been getting wetter over this time, whilst the remainder of Australia has been getting drier. The increase in rainfall where the study sites are located has been due to the greater intensity of summer cyclones (Bureau of Meteorology 2009).



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**Thank you**