Water sourcing by riparian trees along ephemeral riverbeds

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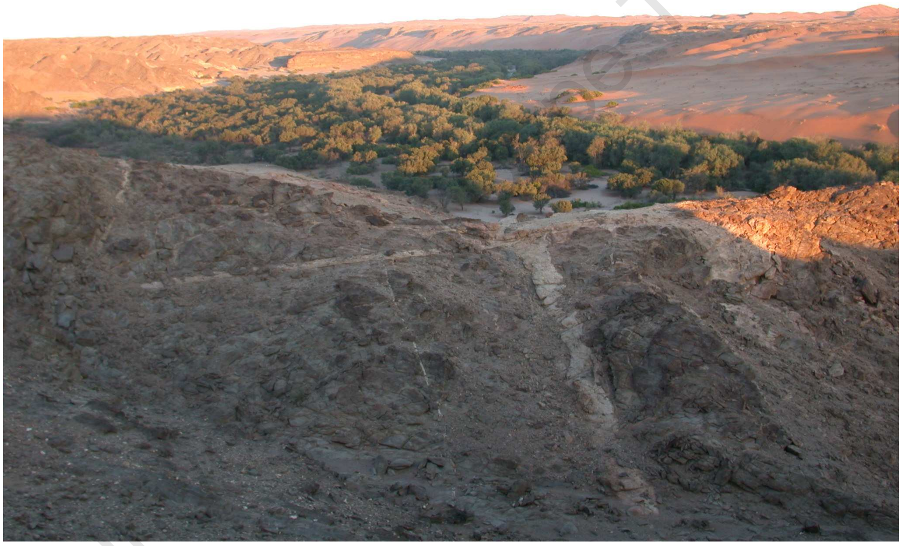

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Front page: Sunset view of the Kuiseb River upstream of Gobabeb

An meine Eltern und Keira, habt Dank

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ABSTRACT

In arid southern Africa, many rivers are ephemeral, and surface flow occurs for less than 10% of the year. Floods, which occur erratically, recharge groundwater resources on which riverine vegetation depends. Trees and shrubs are the most common life forms along these river systems, because surface flows are too erratic for aquatic organisms to flourish. There is concern that alterations to the current water regime of ephemeral rivers will affect the distribution of riparian vegetation as trees provide valuable fodder, shade, firewood and construction material in otherwise inhospitable surroundings. Climate change, population growth and development needs all place growing pressure on these water-limited ecosystems. Careful catchment management is essential to meet human water needs without jeopardising the ecosystems. This is easier said than done however, as ephemeral river ecology and functioning are hardly understood. Their unpredictable hydrology, strong groundwater association, often remote location and the presence of large terrestrial life forms make ephemeral rivers difficult to understand and current 'Environmental water allocation' methods for wetter systems are unsuitable. Alternative methods are being developed, but to date they still have a strong emphasis on aquatic life forms and riparian vegetation is still insufficiently addressed. This study provides an ecophysiological perspective on the water sources and drought tolerance levels of four key riparian tree species in Southern Africa. The aim is to contribute to an improved understanding of the interrelationships between river flow, groundwater and use of water by trees.

Stable Hydrogen and Oxygen isotope results show that the three key species along the Kuiseb River (*Acacia erioloba*, *Faidherbia albida* and *Tamarix usneoides*) do not take up any water from the regularly occurring fog events. Instead, they depend on a seasonally fluctuating mix of shallow and deep soil moisture as well as groundwater. All these water sources rely on regular recharge from floods. It suggests that reductions in flood frequency and especially in magnitude and duration will reduce groundwater recharge and affect species productivity and survival.

It was investigated why A. erioloba, growing in the presence of the alien *Prosopis glandulosa*, show high mortality rates. The study used stable ^{2}H, ^{18}O and ^{13}C isotopes, xylem pressure potentials and percentage canopy dieback to conclude that within the riparian zone, the two species depend on the same water sources and that indigenous *A. erioloba* are

significantly more water stressed when growing alongside *P. glandulosa*. Further inland *A. erioloba* is entirely groundwater dependent while *P. glandulosa* seasonally switches between water sources. This resource partitioning is advantageous for A. erioloba, which does not display the same levels of water stress as in the riparian zone.

An investigation into the physiological structure, including wood density, xylem vessel diameters and xylem vulnerability to cavitation for all four species showed that *A. erioloba* was structurally the most drought tolerant. This finding corresponded well with its high survival rate in the 1980s Namib drought. In the Kalahari, however, it is still outcompeted by *P. glandulosa*, suggesting that the invasive species has a competitive edge over *A. erioloba* that goes beyond xylem structure. *P. glandulosa* and *T. usneoides* are similar in structure. *F. albida* is structurally the most vulnerable of the species, supporting the high mortality rates observed in the 1980's.

Water sourcing using stable Hydrogen and Oxygen isotopes, xylem structure and phenology were compared for three *A. erioloba* stands with access to different groundwater depths (4 m, 21 m and 56 m). The aim was to determine whether *A. erioloba* physiology changed proportionally to groundwater depth. Results show that *A. erioloba* structure and phenology do respond proportionally to groundwater depth, suggesting that *A. erioloba* can reach deep groundwater, but that this comes at a cost of increased water stress and reduced vitality. Ttrees depending on deep groundwater may thus be closer to a water-induced survival threshold than those growing with access to shallower groundwater. Catchment managers should carefully weigh up the benefits of new water developments relative to potential losses of this ecologically and economically important species.

As the final objective and synthesis this study aimed to evaluate if any of the studied species could be used as a bioindicator for tree health in relation to water availability. *T. usneoides* was previously observed to be less tolerant to drought conditions than *F. albida* and *A. erioloba*, while this study has shown *F. albida* to be structurally the most vulnerable. Hence no bioindicator could be indentified and it is concluded that the determination of drought tolerance and the identification of one or more bioindicator species for future monitoring is a complex matter that needs to include more structural studies and field documentation during drought.

Ultimately the use of indicator species and investigations into water sourcing as well as drought tolerance studies should inform catchment management and be included in future assessments of environmental water requirements (EWR) methods and river health. This study concludes that several of the methods applied in this study (shoot growth measurements, percentage canopy dieback, wood density, $\delta^{2}H$, $\delta^{18}O$ and $\delta^{13}C$ stable isotopes, xylem pressure potentials and xylem vessel diameters) are worth applying in in a EWR in conjunction with groundwater and flood (volume, duration and height) measurements. This will require a shift from a traditionally aquatic outlook to one that is more inclusive of terrestrial ecology. More interdisciplinary cooperation and lateral thinking between aquatic and terrestrial ecologists is crucial, so that the frequency, magnitude, predictability and duration of floods and associated groundwater recharge are assessed in terms of water needs of woody riparian species as well as the associated terrestrial fauna.

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CHAPTER 1: INTRODUCTION

Future decreases in available water resources are anticipated in both the Namib and the Kalahari Deserts in southern Africa. Climate change models predict a ten to twenty percent drop in annual rainfall (de Wit and Stankiewicz, 2006); Namibia's uranium mining economy is booming (Swiegers, 2008; Pallett, 2008) and iron ore mining in the Kalahari is ongoing (Powell, 2005). Further abstractions of water from river systems are anticipated for agricultural and urban water needs (Brown, 1990; Powell, 2005; Swiegers, 2008; Pallett, 2008). Introduced alien plant species invade river reaches and are believed to cause competition for scarce water resources with indigenous species (Iponga *et al.*, 2008). The present study examines water sourcing and drought tolerance of three indigenous (*Acacia erioloba*, *Faidherbia albida*, *Tamarix usneoides)* and one invasive (*Prosopis glandulosa*) riparian tree species, commonly occurring along the Kuiseb River in the Namib and the Kuruman River in the Kalahari Desert. The study focuses on the relationship between water availability and growth of trees along ephemeral rivers. A better understanding of the water use of riparian species is essential for sustainable catchment management of ephemeral rivers in arid parts of Southern Africa.

DEFINING EPHEMERAL RIVERS

The aquatic and terrestrial community structure of river ecosystems is primarily shaped by the flow regime (Jacobson, 1997; O'Keefe, 2000). Hence, rivers are frequently classified on a scale of flood days per annum (Poff and Ward, 1990; Jacobson, 1997). There are some discrepancies among the international classifications that have been applied in a Southern African context (Rossouw *et al*. 2005; Moser, 2006). Some classify rivers as perennial (100% flow), semi-permanent (> 75% flow), intermittent streams (10 – 25% flow), and ephemeral (< 10% flow) (Hedman and Osterkamp, 1982; Jacobson, 1997; Boulton *et al.*, 2000). The South African classification differs in terms of flow days per annum and in terminology, so that perennial rivers have 100% flow, semi-permanent rivers have no flow 1% – 25% per annum, ephemeral river have no flow 26% - 75% of year and episodic rivers have no flow for more than 76% of the year (Rossouw *et al*. 2005). The Kuiseb and Kuruman Rivers investigated for this study both flow for less than 10% of the year and are termed 'ephemeral', as stipulated by Hedman and Osterkamp (1982), Jacobson (1997) and Boulton *et al.* (2000). According to the South African classification both rivers would be termed 'episodic'.

Ephemeral rivers typically have highly variable runoff that depends on sporadic, localised and extremely variable precipitation in all or part of the catchment (Jacobson, 1997). As a flood travels downstream after a storm event, the flood volume gradually decreases (transmission losses) because of infiltration into the channel and floodplain sediments, recharging groundwater (Jacobson *et al.*,1995; Lerner, 2003; Seely *et al.*, 2003; Dahan *et al.*, 2008). The amount of groundwater recharge depends particularly on flood duration, but also on magnitude and frequency (Jacobson, 1997; Dahan *et al.*, 2008). Recharge is also affected by riverbed characteristics (Lerner, 2003). Uneven bedrock that underlies river channel sediment forms depressions interspersed with outcrops along a river channel. During floods these depressions fill with infiltrated water and the outcrops keep the groundwater in place in the alluvium long after the flood has passed (Dahan, 2007; Todd and Hoffman, 2007). The flood pulse is the principal driving force responsible for the existence, productivity and interactions of major river biotas (Junk *et al.*, 1989). While some argue that typically short and unpredictable flood pulses in arid river systems disturb the existing biota (Junk *et al.*, 1989), others argue that disturbance of this kind promotes adaptability (Walker *et al.*, 1995). In line with the latter argument the greatest disturbance to ephemeral river systems would be the absence of flood pulses. Reduced flood pulses would reduce groundwater recharge impacting directly on groundwater-dependent lifeforms, such as riparian vegetation (Jacobson, 1997; Moser, 2006).

There are distinct differences in the biotas associated with perennial and ephemeral rivers. The intermittent flow conditions of ephemeral rivers do not allow the same diversity of aquatic and semi-aquatic plants and animals to establish, as are usually found in perennial rivers (Davies *et al.*, 1993; Kemper and Boucher, 2000; Darwall *et al.*, 2009). Trees and shrubs along riparian corridors are the most obvious and permanently established life forms associated with ephemeral river systems (Jacobson *et al.*, 1995; Kingsford, 2000). These riparian corridors include the stream channel and that terrestrial portion from the high water mark to the uplands where floods, elevated water tables and the soil’s ability to hold water all influence vegetation (Naiman *et al.*, 1993). Riparian corridors are considered the most diverse, dynamic and complex biophysical habitats on the terrestrial part of the earth (Naiman *et al.*, 1993). Despite their small land cover, riparian zones are seasonally or permanently inhabited by a large proportion of the vertebrates of an area, indicating their high habitat value, especially in arid areas (Cohn, 2005). Not only wildlife, but also livestock and humans value riparian plants along rivers for shade, food and resources such as wood and building materials (Jacobson *et al.*, 1995; Moser and Henschel, 2004). The current crisis in Zimbabwe has highlighted the importance of riparian corridors for human survival, as many citizens have subsisted on goods and services along the Limpopo corridor since the collapse of the country's national service provision (Colvin, 2009 *pers. com.*). Such dependence on goods and services provided by healthy river ecosystems has to be considered especially in arid and developing countries (Kingsford, 2000; King and Brown, 2006).

Over 1 billion people subsist in arid areas that cover 47% of the Earth's surface (Middleton and Thomas, 1997), giving ephemeral rivers a higher *per capita* importance than their volume of water would suggest (Seely *et al.,* 2003). These rivers are often the only water source in arid areas and the associated, reliable alluvial aquifers allow for permanent settlement (Dahan *et al.*, 2008). In Namibia, for example, 90% of the population depends on water from ephemeral systems (Jacobson *et al.,* 1995; Namibia Water Resources Management Review [NWRMR], 2000; Moser, 2006). Ephemeral rivers support nature reserves and tourism, livestock farming, irrigation, mining and whole industrial urban centers (Jacobson *et al.,* 1995; Heyns *et al.,* 1998). Rivers in arid areas are frequently dammed or diverted, or have water abstracted via boreholes (Heyns *et al.*, 1998; Kingsford, 2000). These dams and diversions reduce flood volume and flood frequency, impacting directly on water quality, alluvial aquifer recharge and all lifeforms dependant on alluvial groundwater (Brown and King, 2002; Kingsford, 2000; O'Keefe, 2000). Careful management is essential to ensure that both human and ecological water needs are met. Unfortunately, conventional water resource management practices worldwide have typically fallen short in this regard and river ecosystems continue to be degraded (MacKay and Moloi, 2003). A lack of protection, climate change, rapid population growth, urbanization and development put increasing pressure on ephemeral systems that could ultimately lead to land degradation and desertification (Jacobson *et al.*, 1995; Jacobson, 1997; Seely *et al.*, 2003; Moser, 2006; Basson, 2009).

THE 'ECOLOGICAL RESERVE' IN THE CONTEXT OF EPHEMERAL RIVERS

Dry countries such as Namibia and South Africa have recently taken progressive legislative stances that advocate the necessity for the sustainable development of water resources (South African National Water Act (36 of 1998); NWRMR, 2000). In line with the new Namibian Water Resource Management Act (2004), three basin management committees have established in ephemeral catchments, which allow for joint decision-making among stakeholders (such as commercial and communal farmers, mining companies and town municipalities) with regards to basin resource management. South Africa's Water Act (1998, No 36) protects environmental water needs by recognising the 'ecological reserve', which is a proportion of water of an acceptable quality that remains in every river to ensure ecological functioning. Under the Act protection includes surface as well as groundwater, protecting both aquatic ecosystems and aquifer dependent terrestrial ecosystems (Colvin *et al.,* 2007). Accordingly, environmental water requirements (EWR) are used as an approach to determine the reserve for each significant water body, taking into account the quantity and quality of water needed for ecosystem conservation and resource protection (Ractliffe and King, 1997; King *et al.,* 2000; MacKay and Moloy, 2002; Tharme, 2003). South Africa has developed its own EWR methods. Based on a growing understanding of aquatic ecology, hydrology, hydraulics, geomorphology and recently also riparian plant inventories, South Africa has designed the Building Block Methodology (BBM), the Downstream Response to Imposed Flow Transformations (DRIFT) and the Flow-Stressor Response (FSR) (King *et al.,* 2000; King, 2004; Kleynhans and Louw, 2008). All of these EWR methods are tailored to the drier and unpredictable settings of South Africa and are used for South Africa's perennial and seasonal rivers.

These methods are not appropriate for ephemeral systems however (Rossouw *et al.,* 2005). The importance of hydraulics in perennial systems plays a reduced role in ephemeral ones. In ephemeral rivers hydrology is so variable that only good, long term data would enable adequate interpretation (Davies *et al.*, 1993; King *et al.*, 2000). Unfortunately such data is rarely available due to the inaccessibility of most ephemeral rivers, too few and badly equipped monitoring stations and regular equipment damage through siltation and jamming debris (McMahon, 1979; Jacobson, 1997). Groundwater plays a major role in ephemeral systems, but its quantity and recharge are notoriously difficult to assess. Hence, it has only recently been incorporated into perennial EWR methods (Lerner, 2003). The strong focus on macroinvertebrates and fish of the existing EWR methods is unsuitable for ephemeral systems, which support very few aquatic organisms but have a prominent terrestrial riparian vegetation instead. Assessments of riparian vegetation in existing EWR methods consist of inventories that include plant location, cover, phenology, structure, abundance and plant/substrata relationship (King *et al.*, 2000; Kemper, 2001; Kleynhans *et al.*, 2007). These data provide a sound ecosystem perspective for riparian vegetation, but species-specific knowledge about life cycles, functioning and water requirements is lacking (King *et al.,* 2000). This knowledge gap is biggest along ephemeral rivers, because aquatic scientists have largely ignored them and because terrestrial ecologists have examined the riparian vegetation without consideration to the influence of fluvial processes or the requirements of individual species (Jacobson, 1997).

The knowledge gap around ephemeral rivers currently make the determination of sustainable water abstraction rates and the development of sustainable management strategies near impossible. This shortcoming is now being addressed in South Africa, where research is under way to formulate EWR methods for non-perennial rivers (Rossouw *et al.,* 2005; Seaman *et al.,* 2009). The new methods still have an aquatic focus (on temporary pools) and the processes determining riparian vegetation structure still needs to be included as a main challenge and focus area.

OVERVIEW OF APPROACHES FOR DETERMINING SPECIES-SPECIFIC PLANT-WATER RELATIONSHIPS IN RIPARIAN ZONES

There is a strong interconnection between a river's natural flow regime and the composition and traits of its riparian species (Merritt *et al.,* 2009). Riparian species disperse, reproduce and survive in response to frequency, magnitude, duration, seasonality and predictability of river flow (Mahoney and Rood 1998; Moser, 2006; Merritt *et al.,* 2009). River flow influences other environmental attributes important for riparian plant growth, such as groundwater recharge, nutrient deposition, sediment transport and substrate deposition (Merritt *et al.,* 2009). This cause-and-effect relationship between a species in relation to its most influential environmental attributes needs to be understood in order to successfully specify environmental water requirements (Merritt *et al.,* 2009). Attributes of water availability, such as surface flow and groundwater level, need to be understood in relation to plant water sourcing, water needs and drought tolerance thresholds (Tabacchi *et al.,* 2000; Hou *et al.,* 2007; Merritt *et al.,* 2009). To date, however, this knowledge is limited.

Plant physiological responses to altered water availability can occur over short time spans, but can have long-term effects for the morphology and health of the individual plant (Smith *et al.,* 1998; Merritt *et al.,* 2009). Plants may undergo water stress in response to changes in solar radiation, rising temperature and decreasing soil moisture in a time span of hours. This can affect stomatal conductance, transpiration, leaf internal CO_2 concentration, carbon isotope discrimination (an index of water use efficiency and time integrated carbon assimilation) and xylem pressure potentials (Pockman and Sperry, 2000; Merritt *et al.,* 2009).

Other plant attributes have been identified to express longer term responses to reduced water availability, including leaf abscission and leaf death (Merritt *et al.,* 2009), increased leaf thickness and reduced leaf size (Rood *et al.,* 2003), reduced shoot and stem growth (Stromberg and Patten, 1996; Scott *et al.,* 1999; Rood *et al.*, 2003), decreased vessel diameters (February and Manders, 1999; Schume *et al.,* 2004) and increased wood density (Jacobsen *et al.*, 2007). Severe water stress may lead to xylem cavitation and branch dieback, or the death of entire trees (Tyree *et al.,* 1994; Scott *et al.,* 1999; Merritt *et al.,* 2009).

Complementary to all the measurement of all these responses, stable oxygen and hydrogen isotope ratios have been used to determine the actual water source of plants, that may differ among seasons, species and age groups (Dawson and Ehleringer, 1991; Ehleringer and Dawson, 1992; Adar *et al.*, 1995; Horton *et al.,* 2003).

All these kinds of measurements have led to a thorough understanding of water relations in some riparian genera indigenous to the USA (*Prosopis*, *Salix* and *Populus*) (Stromberg and Patten, 1996; Snyder and Williams, 2000; Stromberg, 2001; Rood *et al.,* 2003; Stromberg *et al.,* 2007) as well as invasive genera (*Tamarix*) (Busch *et al.,* 1992; Pockman and Sperry, 2000; Horton and Clark, 2001). The methods were used to develop thresholds of groundwater depletion for riparian species through measuring the onset and consequences of chronic water stress (Scott *et al.,* 1999; Cooper *et al.,* 2003; Merritt *et al.,* 2009). Interspecific comparisons of plant attributes among indigenous and invasive species have helped to better understand competitive advantages under altered water regimes (Nilsson and Berggren, 2000; Horton *et al.,* 2001a,b; 2003). Measurements have also informed catchment management and successful rehabilitation of degraded riparian zones (Stromberg and Patten, 1996; Willms *et al.,* 1998; Stromberg, 2001; Rood *et al.,* 2003; Stromberg *et al.,* 2007).

Studies in the United States have explored the concept of identifying indicator species that represent key compositions and features within the riparian landscape (Stromberg *et al.,* 1996). The objective was to identify the water needs and responses to water availability of key indicator species, to summarise and predict the water needs of entire groups and riverine communities. This concept was expanded by Merritt *et al.* (2009), who propose to classify riparian species into different ‘riparian vegetation response guilds’, that address similarities in ‘life history’, ‘reproductive strategy’, ‘morphology, ‘fluvial disturbance’ and ‘water balance’. Merritt *et al.* (2009) argue that the application of response guilds would help scientists and managers to understand the possible changes in vegetation attributes in general, but practical terms. Ultimately this classification could aid to successfully model and predict the likelihood of plant changes in response to projected changes in flows (Merritt *et al.*, 2009).

PAST RESEARCH ON EPHEMERAL RIPARIAN PLANT WATER RELATIONSHIPS IN THE NAMIB AND KALAHARI DESERTS

In theory and in legal terms, South African riparian vegetation is one of the best-protected in the world. In South Africa groundwater dependent ecosystems are protected by the Water Act to have adequate water access (Colvin *et al.*, 2002). This inherently includes the riparian vegetation along ephemeral rivers that depends on groundwater and its recurrent recharge. Scientists have made efforts to ‘mainstream’ the concept and importance of groundwater-tree interactions in South Africa, resulting in the compilation of manuals for ecophysiological methods and their application (Colvin *et al.*, 2002; 2007). In practice, however, there has been very limited implementation. One study attempted to predict evapotranspiration rates by riparian vegetation under different river flow and meteorological conditions for the Sabie River (Birkhead *et al.*, 1997). Their results confirmed the importance of maintained base flows in this historically perennial river. They recommended the use of growth increment measurements and leaf area indexes as useful early warning measurements to prevent riparian mortality from drought stress. Another study looked at floodplain forests on the Luvhuvhu River, determining water relations using δ^2H and δ^{13}C isotope ratios as well as xylem pressure potentials (Botha, 2001). Trees along the Luvhuvhu River were found to have sufficient access to water at the time of the study. Southern African rivers also face the rapid establishment of alien invasive plants along riparian corridors (Brown *et al.*, 1985; Coates-Palgrave, 1983; Brown and Gubb, 1986; Impson *et al.*, 1999; le Maitre, 1999; Curtis and Mannheimer, 2005). Invaded riparian strips show reduced biodiversity (Dean *et al.*, 2002) and the densely growing invasives are eradicated by the ‘Working for Water’ Programme in South Africa in an effort to conserve biodiversity and water resources (le Maitre, 1999; Reinecke *et al.*, 2008). Alien trees, among them species of the genera *Prosopis* and *Acacia*, have been observed to outcompete indigenous species, leading to a die-off of the original plant assemblages (Robertson and Woodborne, 2002; Reinecke *et al.*, 2008). Most commonly competition for water is believed to be the cause, but nutrient competition in nutrient poor soils is another possible reason (le Maitre, 1999; Robertson and Woodborne, 2002; Colvin *et al*. 2007). Research on individual species, interspecies competition for water and plant water needs remain sparse in South Africa. Consequently, riparian plant water needs at the species-level have not found integration into EWR methods.

Namibia and other SADC countries lack the exemplary legal structure and internally developed EWR methods of South Africa, but nonetheless, arid countries like Namibia have long observational records of riparian vegetation responses to water availability. The riparian forests along the Namib Desert rivers are termed ‘linear oases’, reflecting intrinsic value of these rivers to humans and animals (Jacobson *et al.*, 1995). Trees, including *Faidherbia albida*, *Acacia erioloba* and *Tamarix usneoides*, are keystone species within these ecosystems (Jacobson *et al.*, 1995; Dean *et al.*, 1999; Moser, 2006). The value of the trees was recognised in Namibia when mining developments requested large groundwater abstractions from the ephemeral Kuiseb River in the 1970s. Concern about the effects of reduced groundwater availability on the riparian vegetation led to long-term monitoring in the Kuiseb River and neighbouring systems, relating vegetation health (foliage cover and tree mortality rates) and seedling recruitment to flood frequency and groundwater table fluctuations (Bate and Walker, 1980; Ward and Breen, 1983; Huntley, 1985; Rössing, 2003; Moser, 2006). A transpiration model was used for a one-kilometre stretch of Kuiseb woodland. It estimated that this stretch would transpire 2.02 x $10^5 m^3$ of water annually, which is 19% of the area’s total alluvial aquifer volume (Bate and Walker, 1993). A floodless period from 1979 to 1984 in the lower Kuiseb led to a three-metre groundwater table drop, resulting in an average 62% mortality for *F. albida*, 29% for *A. erioloba* and 24% for *T. usneoides* (Theron *et al.*, 1985). Survival rates were found to differ among age groups (Ward and Breen, 1983), showing that interspecific and age group differences exist with regard to adaptability to flood frequency and groundwater fluctuations. As a result, Rössing Uranium Mine conducts long term monitoring of groundwater levels and foliage cover of riparian vegetation in currently pumped river reaches of the Khan River (Rössing 2003, *unpublished report*). In Namibia the research has led to the adoption of management plans, but there is scope for more species-specific research, explaining the physiological reasons behind the previously observed mortalities.

AIMS OF THIS STUDY

South Africa has very little research on water needs of riparian plant species, nor are they readily integrated into catchment management plans. Comparatively, Namibia has done more extensive research in the Kuiseb and Swakop River catchments and has translated research into the wise management of mine water use (Ward and Breen, 1983; Theron *et al.*, 1985; Rössing 2003, *unpublished report*; Moser, 2006). Regionally however, research falls short of a species specific understanding of riparian trees to drought, water table decline and water sourcing. Hence the overarching aim of this thesis is to investigate water sourcing and drought tolerance of some of the most common riparian tree species along ephemeral rivers of the Namib and Kalahari Deserts. Four specific research questions are addressed as the objectives.

The objective of Chapter 3 is to determine the water sources of three common Namib species and three age groups (seedling, juvenile, adult). Stable oxygen and hydrogen isotope ratios are used to determine the sources of plant water, as documented by Dawson and Ehleringer, (1991), Ehleringer and Dawson, (1992), Adar *et al*. (1995), Horton *et al.* (2003) and Quereteja *et al.* (2007). The application of this method has been limited in Southern Africa to date (Botha, 2001; February *et al.*, 2007a,b; Obakeng, 2007) and its inclusion in this study was essential to examine the sources of plant water.

Studies in the Kalahari have shown that the presence of alien species increases mortality rates among indigenous species and a competition for water is suspected (Robertson and Woodborne, 2002, *unpublished*). The unpublished work of Robertson and Woodborne (2002) used one method (δ^{13}C testing from seasonal tree rings), to determine a long term water availability history and to conclude that interspecific water competition occurs. Tree ring research in Southern Africa is complicated by the absence of definite inaction periods of trees and the validity of only using δ^{13}C tree ring tests without other supporting methods can thus be criticised. Hence the conclusion of Robertson and Woodborne (2002) is re-tested in Chapter 4, using a selection of methods. The aim is to test whether the presence of the densely spreading alien plant (*Prosopis glandulosa*) leads to increased water stress among an indigenous species (*Acacia erioloba*) in Southern Africa. Stable δ^{2}H and δ^{18}O isotope ratios are used to determine plant water sources. Leaf δ^{13}C isotope ratios are compared to determine water use efficiency, similar to Robertson and Woodborne (2002). I also use xylem pressure potentials to test for water stress, as this method has previously been used on *A. erioloba* in the Namib (Ward and Breen, 1983). I also quantify percentage canopy dieback, because dieback it is the most obvious symptom observed in *A. erioloba* when growing in proximity of *Prosopis* spp. (*pers. obs.*).

Records and observations prior to this thesis have shown that species differ in drought tolerance levels (Ward and Breen, 1983; Huntley, 1985; Theron *et al.,* 1985). In Chapter 5 I determine if anatomical differences explain differences in drought tolerance between species. The hydraulic architecture of the three Namib and two Kalahari species is compared to determine if structural differences can explain varying levels of observed drought tolerance. Xylem cavitation resistance is a key measure for drought tolerance (Hacke *et al.,* 2000; Pockman and Sperry, 2000; Maherali *et al.,* 2004). The method is work-intensive and difficult to employ in remote areas, but it was chosen due to its limited application in riparian vegetation of Southern Africa to date (Swift *et al.,* 2008) and its potential for predictive results. Xylem vessel diameters adapt to water availability (February *et al.,* 1995), rainfall (February, 1994) and groundwater levels (Schume *et al.,* 2004). They also differ among species with varying levels of cavitation resistance (Hacke *et al.,* 2000). This measure has been applied for riparian species in the USA (Schume *et al.,* 2004), hence its inclusion in this study. Wood density is a rapid measure that integrates many xylem traits related to water stress tolerance and has been suggested to predict the impact of climate change on shrubs (Jacobsen *et al.,* 2007) and of species vulnerability to drought (Hacke *et al.,* 2000; Schume *et al.,* 2004). The method has previously been used in fynbos in South Africa (Jacobsen *et al.,* 2007), in a riparian setting in the USA (Schume *et al.,* 2004) as well as in the Sonoran Desert (Hacke *et al.,* 2000). The simplicity and speed of this method make it potentially valuable as a rapid tool in river health assessments and hence it was included in Chapter 5.

A particularly relevant relationship along ephemeral rivers is the dependence of riparian vegetation on the groundwater table (Hou *et al.,* 2007). Some vegetation/groundwater monitoring is occurring in Namibia (Rössing, 2003, *unpublished report*) as well as in South Africa along the Shingwedzi River in the Kruger National Park (Colvin, 2009, *pers. com.*). Several studies in the USA have investigated this relationship for individual species (Stromberg *et al.,* 1992; Horton *et al.,* 2001a). In Chapter 6 the physiological adaptations of riparian *Acacia erioloba* to three different groundwater depths (4 m, 21 m, 56 m) are studied, in an attempt to infer what responses to water stress can be anticipated with future groundwater declines. As in previous chapters, xylem pressure potentials, canopy dieback, vessel diameter, stable δ^2H, δ^{18}O and δ^{13}C isotope ratios are used and correlated against water table depth. Shoot growth and specific leaf area are additional methods used in this Chapter. Stem diameter growth in relation to water availability has previously been assessed in a South

African study (February *et al.*, 2007b) and is included in a riparian setting here. Shoot growth has successfully been assessed relative to river flow before (Willms *et al.*, 1998; Amlin and Rood, 2003) and this study compares it to groundwater depth along the dry Kuiseb and Kuruman Rivers. Specific leaf area was included because it was shown to decrease for *Prosopis velutina* under conditions of groundwater decline (Stromberg *et al.,* 1992) and because it is a good indicator for longer term changes in available water (Rood *et al.*, 2003).

The synthesis (Chapter 7) addresses the potential of using individual species as bioindicators, as suggested by Stromberg *et al.* (1996) and Merritt *et al.* (2009). Furthermore the usefulness of the applied methods is evaluated in terms of their usefulness in arid Southern African EWR initiatives and future application for catchment management practices.

CHAPTER SUMMARY

This introductory chapter introduced the questions that are addressed in this study. The first section set the work within the context of ephemeral rivers, their functioning and catchment management challenges. Thereafter the existing Environmental Water Requirement methods were introduced and discussed in relation to Ephemeral River functioning. The third section gave an overview of studies on riparian plant water requirements at the species level. The fourth section provided an overview of research on riparian vegetation in the ephemeral rivers of the Namib and Kalahari. The study aims were subsequently introduced and the choice of methods validated. This study has been prompted by growing pressure on ephemeral ecosystems, the inapplicability of existing EWR methods to determine their water needs and the key role that terrestrial riparian vegetation plays in ephemeral ecosystem functioning.

The thesis is divided into an introductory section (Chapters 1 and 2), setting the backdrop to ephemeral systems, EWR’s in Southern African systems, site and species descriptions. The data is presented in Chapters 3 to 6 and their details are summarised in Table 1.1. Chapter 3 focuses on the water sourcing patterns of three common Namib species and three age groups. Chapter 4 covers competition for water between the indigenous *A. erioloba* and alien *Prosopis glandulosa* in the Kalahari. In Chapter 5 the hydraulic architecture of four species is compared to see if any significant structural differences can explain varying levels of drought tolerance. In Chapter 6 the physiological adaptations of riparian *Acacia erioloba* to three different groundwater depths are studied, in an attempt to infer what responses to water stress can be anticipated with future groundwater level drops. Chapter 7 is a synthesis of the data chapters, discussing the value of the methods used in relation to EWR initiatives in Southern Africa and addressing the potential of using any of the studied species as a bioindicator.

Table 1.1: Summary of objectives, study sites, species and number of specimen for each of the four data chapters

Chapter	**Objective**	**Sites**	**Species**	**# Specimen**
3	To determine water sourcing of three common riparian species at three ages (seedling, juvenile, adult)	Gobabeb	*A. erioloba,* *F. albida,* *T. usneoides*	6 samples of each species
4	To test if the presence of *Prosopis glandulosa* leads to increased water stress for a key indigenous species (*Acacia erioloba*)	Gannavlakte	*A. erioloba,* *P. glandulosa*	6 samples of each species s
5	To determine if any significant physiological differences among species can explain varying levels of observed drought tolerance	Gobabeb, Gannavlakte	*A. erioloba,* *F. albida,* *T. usneoides* *P. glandulosa*	6 samples of each species
6	To investigate physiological adaptations of riparian *Acacia erioloba* to shallow (4 m), medium (21 m) and deep (56 m) groundwater	Gobabeb, Swartbank, Gannavlakte	*A. erioloba*	6 samples of each species

CHAPTER 2: SITE DESCRIPTIONS

The South-westerly parts of Southern Africa are dry, with low and highly variable rainfall. The two most prominent arid areas are the Namib and Kalahari deserts. The Namib is a hyperarid desert with annual rainfall averaging between 15mm and 100mm (Seely, 1987). The Kalahari, with annual rainfall of 150mm to 450mm is an arid savanna, although some have classified it as a semi arid desert (van Rooyen and van Rooyen, 1998). Both areas lack surface water, making them largely inhospitable (Verhagen, 1985). Rivers in both deserts are mostly ephemeral, in that runoff events occur for no more than a few hours or days and flood frequency varies between several times a year to once in a decade (Jacobson *et al.,* 1995; Heyns *et al.,* 1998). Rare floods recharge groundwater stores in the river alluvium (Seely, 1987; Jacobson, 1997; Dahan *et al.,* 2008) and trees and shrubs are the most prominent lifeforms along the rivers (Theron *et al*. 1980; Huntley, 1985; Jacobson *et al.*, 1995; van Rooyen and van Rooyen, 1998, Colvin *et al*., 2002). The riverine vegetation offers fodder and refuge for desert-dwelling animals and livestock farming. The easily accessible groundwater resources are used for agricultural and industrial purposes, such as farming along the Kuruman River in the Kalahari (Verhagen, 1985) and industries in towns like Walvis Bay at the Kuiseb mouth in the Namib (Huntley, 1985; Seely, 1987; Jacobson *et al.,* 1995; Moser, 2006).

Research took place at three study sites, two of which were located along the Kuiseb River in the Namib Desert (Gobabeb and Swartbank) and one along the Kuruman River (Farm Gannavlakte) in the Kalahari (Fig. 2.1).

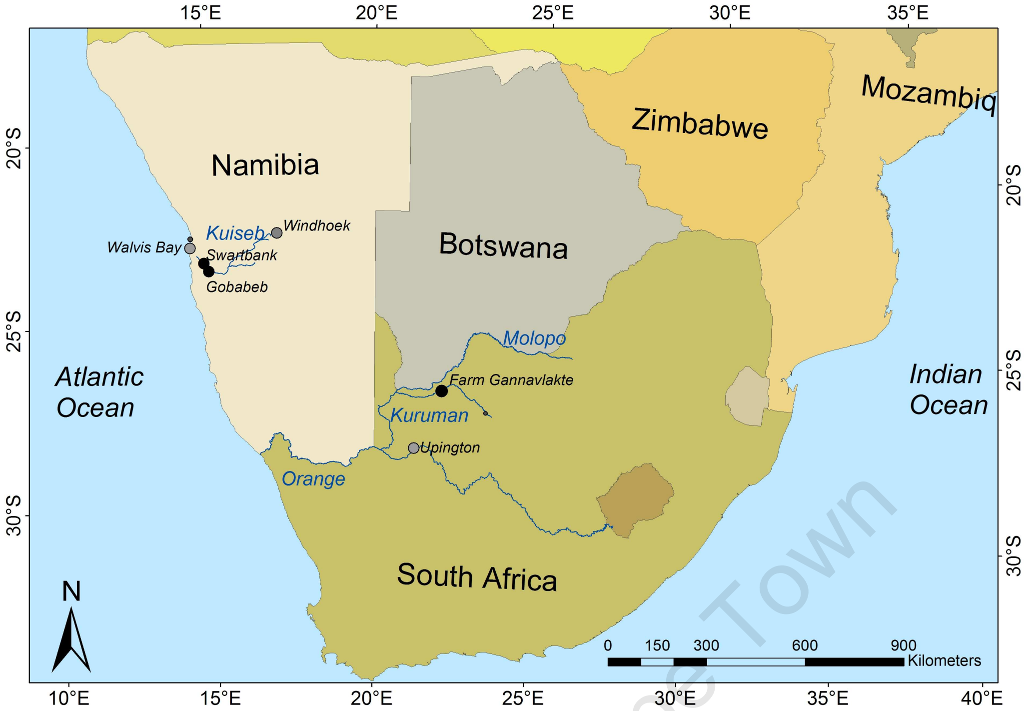


Figure 2.1: Map of Southern Africa depicting the Kuiseb and Kuruman Rivers as well as the location of the three study sites Gobabeb, Swartbank and Farm Gannavlakte

CENTRAL NAMIB AND KUISEB RIVER

The Namib Desert is a relatively narrow strip no more than 200 kilometres wide, stretching from the Olifants River in South Africa north to San Nicolau in Angola (Seely, 1987). Several westward flowing ephemeral rivers cross the Namib on their way to the Atlantic Ocean. One such river is the Kuiseb in the Central Namib (Seely, 1987; Jacobson *et al.*, 1995).

The ephemeral Kuiseb River in Namibia drains a catchment of approximately 15 500 km^2, rising in central Namibia and flowing west across the Namib Desert into an estuary south of Walvis Bay (Bate and Walker 1993; Huntley, 1985). The Kuiseb exhibits an enormous environmental gradient, in terms of both topography and rainfall (Moser, 2006). From the headwaters near Windhoek at an elevation of 2081 metres, the Kuiseb River flows 560 kilometres to the coast (Jacobson, 1997). On its way it firstly traverses about 230 kilometres of a bedrock highlands zone (Khomas Hochland) with mainly mica-schists and highland savanna vegetation. It then rapidly drops about 1000 metres in altitude at the western escarpment where semi/desert – savanna transition vegetation begins. At the footslopes of the escarpment the Kuiseb has incised through a calcrete fanglomerate into underlying bedrock (Marker, 1977). This area is also known as the Kuiseb Canyon (~130 km) and the Gaub River enters the Kuiseb in this area. Below the Canyon the Kuiseb divides the northern Namib gravelplains from the southern wandering dune field. Large flood events hinder the mobile sand dunes from wandering north (Huntley, 1985). From Gobabeb to Rooibank the river crosses a shallow valley section with deep alluvial sands and some bedrock outcrops. These ~120 kilometres are characterised by prolific stands of riparian woodland, consisting of *Faidherbia albida*, *Acacia erioloba*, *Tamarix usneoides, Euclea pseudebenus, Salvadora persica*, *Ficus sycomoris* and *Acanthosicyos horridus*. Over the last ~30 kilometres to the coast the river expands into a wide meandering delta with indistinct channels and low dunes. Some shrublike trees occur as well as several species of halophyte, including *Tamarix usneoides*, *Salsola* spp. and *Lycium* spp. (Theron *et al.*, 1980; Huntley, 1985).

The river course follows a declining rainfall gradient averaging about 400mm per annum in the headwaters and decreasing to less than 20 mm per annum along the coast (Huntley, 1985). Mean potential evaporation rates are extremely high throughout the catchment: 3200mm/a in the upper catchment and 2600 mm/a near the coast (Heyns *et al.,* 1998). The highlands receive summer rainfall from strong convective rainfall events from the Indian Ocean (Logan, 1960). As the clouds travel over the African continent, they continually lose moisture, resulting in decreased precipitation towards the west. In addition, winds from the South Atlantic anticyclonal high-pressure system directly influence the cold Benguela current in the Atlantic. They blow inland from the south-west, creating an inversion layer with cold, moister air close to the ground while the air coming off the escarpment from the east warms and rises above it. The inversion layer restricts turbulences necessary for cloud formation and rainfall. This stable inversion is reversed on rare occasions in summer, resulting in individual rainfall events (Seely, 1987). The southwesterly wind frequently carries cold and heavy fog, formed over the Atlantic, inland for over 60 kilometres. This fog is an important moisture source for a variety of life forms in the Namib (Seely, 1987). Up to fourteen litres of water have been collected off a one-square metre net in a single fog event on the Swartbank mountain, showing that fog is a considerable moisture source (Henschel, 2005, *pers. com*). Precipitation falling in the upper catchment is the main source of floods in the Kuiseb River and surface flow contributions occur only rarely from the lower catchment (Stengel, 1964; Moser, 2006). Floods typically occur between December and April.

The Kuiseb River has four operational gauging stations along its entire length, providing at least fifteen years of flow records (Jacobson, 1997; Moser, 2006). Typical for the Namibian westward flowing rivers, the Kuiseb shows a curvilinear relationship between flow characteristics and distance downstream (Jacobson, 1997; Moser, 2006). From the headwaters to the escarpment flow volume increases to a maximum of 12.0 Mm^3/a at the Kuiseb/Gaub confluence. From there it declines steadily in the lower reaches to 1.45 Mm^3 at Gobabeb (Namibia Water Resources Management Review, 2000). Increasing aridity and substrate differences are responsible for this phenomenon. The upper catchment is rocky with shallow soils, where lots of runoff is generated. The Kuiseb aggrades in its lower reaches, forming deep alluvial floors into which surface flows rapidly infiltrate (Huntley, 1985). Floods rarely reach the Atlantic and only seventeen such occasions have been recorded since 1837 (Stengel, 1964; Moser, 2006). Flood duration also follows a curvilinear relationship. Between 1962 and 2006 upper catchment floods occurred for an average 3.7 days, increasing to 11.1 days at the Kuiseb/Gaub confluence and declining to 8.1 days at Gobabeb and 2.2 days at Rooibank. A linear decline occurs in the number of floods per annum, with an average 7.9 upper catchment floods per year (Friedenau) and only 0.9 floods at Rooibank (Jacobson, 1997; Moser, 2006).

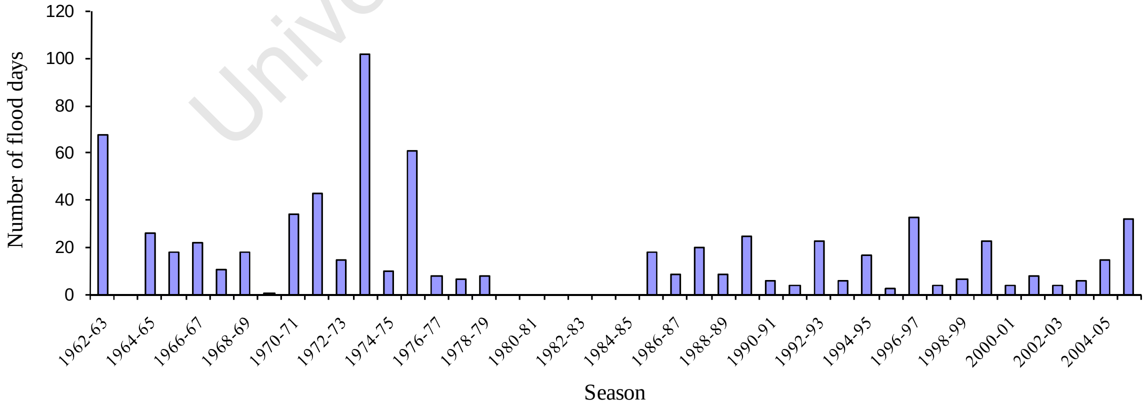


Figure 2.2: Gobabeb flood records, 1962-2006. Total number of days with surface flow recorded per flood season (October-April) (Source: Gobabeb Training and Research Centre; Moser, 2006)

The Kuiseb catchment supports around 25 000 people, of which some live on the 109 commercial livestock farms in the upper catchment. Countless small farm dams are constructed in this area in order to augment the farmers' water resources (Jacobson *et al.*, 1995). The Kuiseb has one large state dam (the Friedenau Dam, capacity 6.33Mm^3) in its upper reaches (Namibia Water Resources Management Review, 2000). The canyon and woodland areas fall in the Namib Naukluft Park, where game dwells along the 'linear oasis' and the Topnaar community farms with livestock and harvests plants from the woodland area (Jacobson *et al.*, 1995). The Gobabeb Training and Research Station is located 56 kilometres from the coast. Here, research on the Namib and the Kuiseb River has been ongoing since 1962 (Lancaster *et al.*, 1984). Water in this area is provided from boreholes and hand-dug wells (Jacobson *et al.*, 1995). Within the last 30 kilometres from the coast wellfields at Swartbank and Rooibank contain over 53 boreholes, supplying an average annual 7.78Mm^3 of water to the towns of Walvisbay and Swakopmund (Christelis and Struckmeier, 2001).

Two study sites were chosen within the riverine woodland area of the Kuiseb River (Fig. 2.3). Site 1 is at the Gobabeb Training and Research Centre (GTRC) (23º33'726 S – 15º02'112 E), and site 2 is at the Swartbank well-field (23º18'212 S – 14º45'672 E).

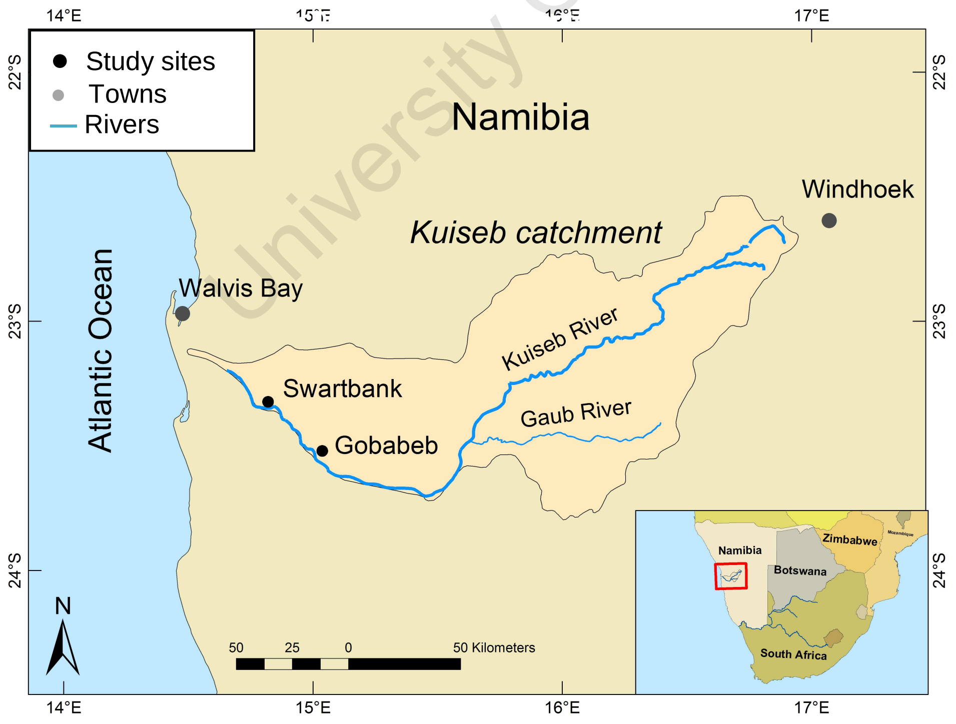


Figure 2.3: Map of the Kuiseb River catchments showing the location of the two study sites Swartbank and Gobabeb

Gobabeb

The average annual maximum and minimum temperatures for Gobabeb are 30.5ºC and 13.2ºC respectively. For the period of June 2004 to May 2006 the hottest month was February and the coldest month was August. Average annual rainfall at Gobabeb is 21 millimetres. It falls in sporadic rainfall events, as depicted in Fig. 2.4. Rainfall in 2006 was unusually good.

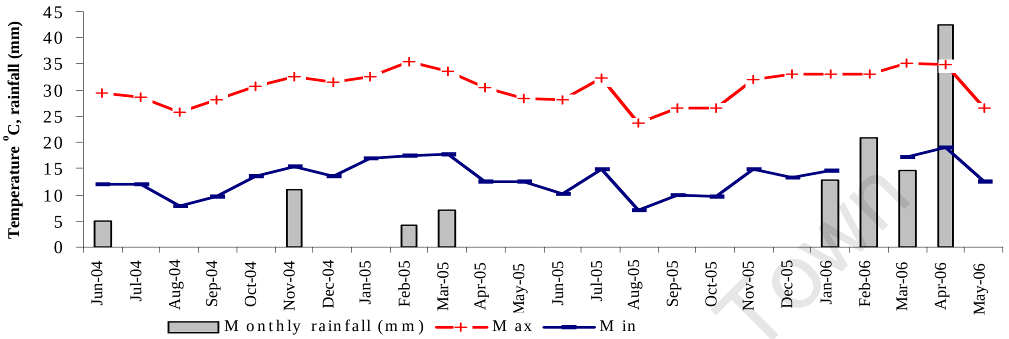


Figure 2.4: Average minimum and maximum air temperatures (ºC) and monthly rainfall values (mm) at Gobabeb from June 2004 to May 2006 (data courtesy GTRC)

Fog from the Atlantic Ocean travels inland to Gobabeb on 38 to 60 days per annum, providing a regular source of moisture and average annual fog precipitation of 31 millimetres (Lancaster *et al.*, 1984). Apart from fog, dew regularly occurs overnight, contributing to raised humidity levels each morning (average 46% humidity) (Henschel, 2005, *pers. com*). That moisture dries out during the day to a mere average of 17%. Fig. 2.5 below shows monthly dawn and midday relative humidity values as well as number of fog days per month. The discrepancy between fog occurrence and humidity levels is attributed to dew, which occurs separately from fog.

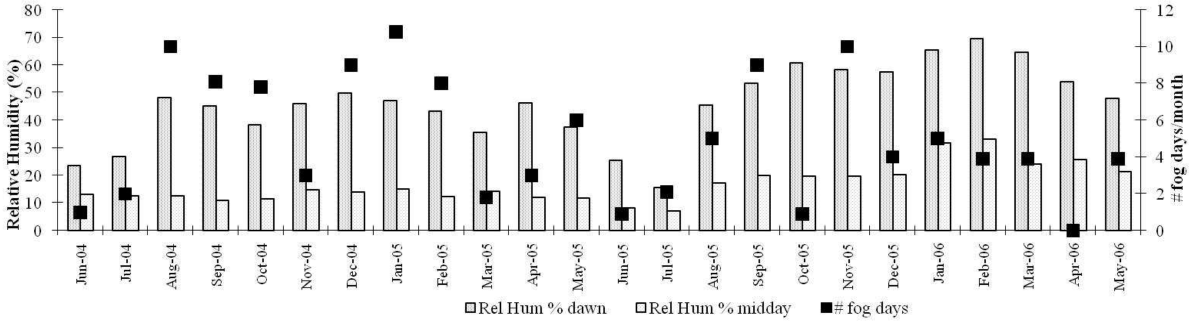


Figure 2.5: Average relative humidity % at dawn and midday and number of fog days per month at Gobabeb from June 2004 to May 2006.

Around Gobabeb the groundwater table fluctuates between four and fourteen metres from the surface of the Kuiseb River (Fig. 2.6). A ten-year overview of groundwater levels at a Gobabeb borehole shows how recharge occurred mainly during the large floods of 1997 and 2000, which flowed for 33 and 23 days respectively (see Figure 2.2). Smaller floods did not significantly recharge groundwater, and the water table steadily declined between major flood events.

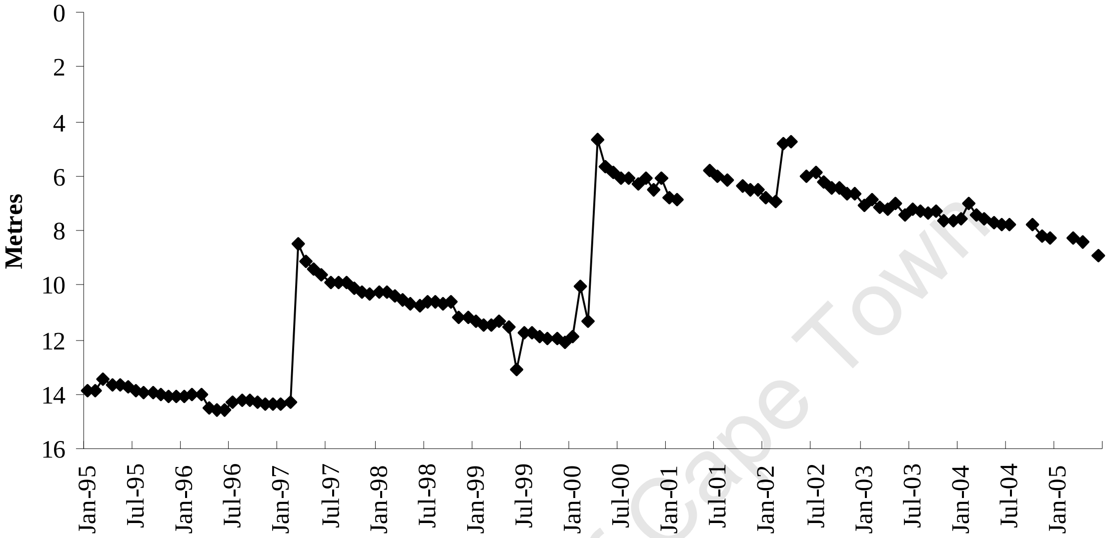


Figure 2.6: Ten year overview of water levels (m) at Gobabeb (borehole # 35016, data courtesy GTRC)

During the study period from June 2004 to March 2006 the Kuiseb flowed past Gobabeb ten times, sometimes several times in one month (February 2005, January 2006 and February 2006). Detailed groundwater levels from June 2004 to March 2006 are depicted in Chapters 3 (Fig. 3.1) and 6 (Fig. 6.2).

Around Gobabeb the well-developed *F. albida* population grows close to the main river channel and some individuals occur in the main channel (Theron *et al.*, 1985; Jacobson *et al.*, 1995; Jacobson, 1997). Individuals of *Acacia erioloba* occur along the main channel and this species dominates the broader floodplains. Young *Tamarix usneoides* stands grow close to the active river channel, while older large stands and individual trees occur across the floodplain and on the dunes along the southern slopes. Individuals of *Euclea pseudebenus* grow interspersed in the woodlands and thickets of *Salvadora persica* grow among and over other tree species from the channel to the river edges. Few non-woody perennials occur, except for the alien herb and shrub species *Datura innoxia*, *Datura stramonium*, *Nicotiana glauca and Ricinus communis*.

Swartbank

At Swartbank the floodplain becomes a broad, braided channel. The Namib sand sea borders the south bank of the river. Considerable volumes of floodwater seep south into the dunes during flood events (Huntley, 1985). Within the river channel the sandy alluvium is underlain by a bedrock compartment, into which water recharges during flood events. A wellfield was established at Swartbank in 1974 to supply the growing water demand of Swakopmund and Rössing Uranium Mine (Christelis and Struckmeier, 2001). Currently Swartbank's groundwater table lies at around 20 metres, steadily declining from the original water level at around seven metres before pumping in 1974 (Moser, 2006) (Fig 2.7).

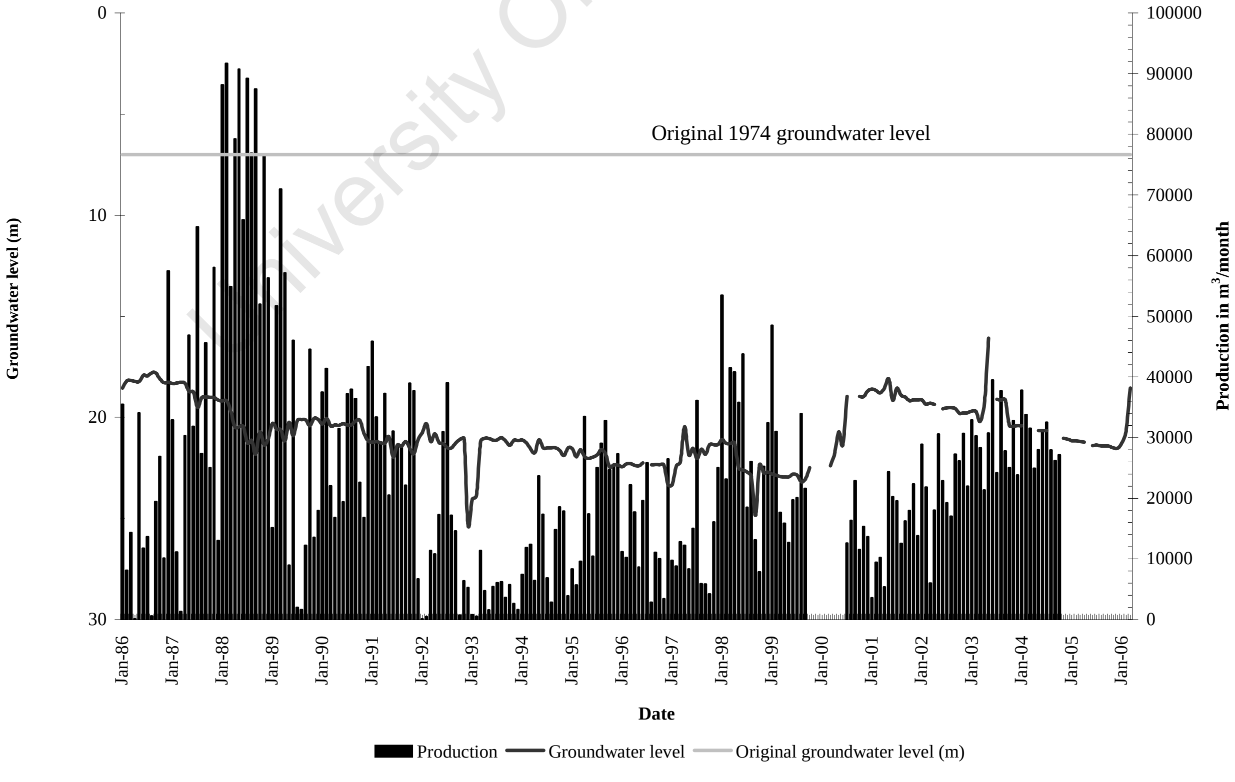


Figure 2.7: Groundwater level at a Swartbank borehole, monthly abstraction figures, recommended abstraction level and original groundwater level (m) from January 1986 to September 2004 (data courtesy NamWater)

The area around Swartbank is uninhabited and hence the amount of weather data is not as well documented as at Gobabeb. An automatic weather station was erected at Swartbank in 1999 and was stolen in 2003 (Henschel, 2006, *pers. com*) and data collection has not resumed since. Below (Fig. 2.8) are the maximum, minimum temperatures and dawn and midday relative humidity values from that automatic weather station. There are no counts of fog days per month. Rain fell twice during the recording period, in September 1999 (0.2 mm) and in March 2000 (18 mm).

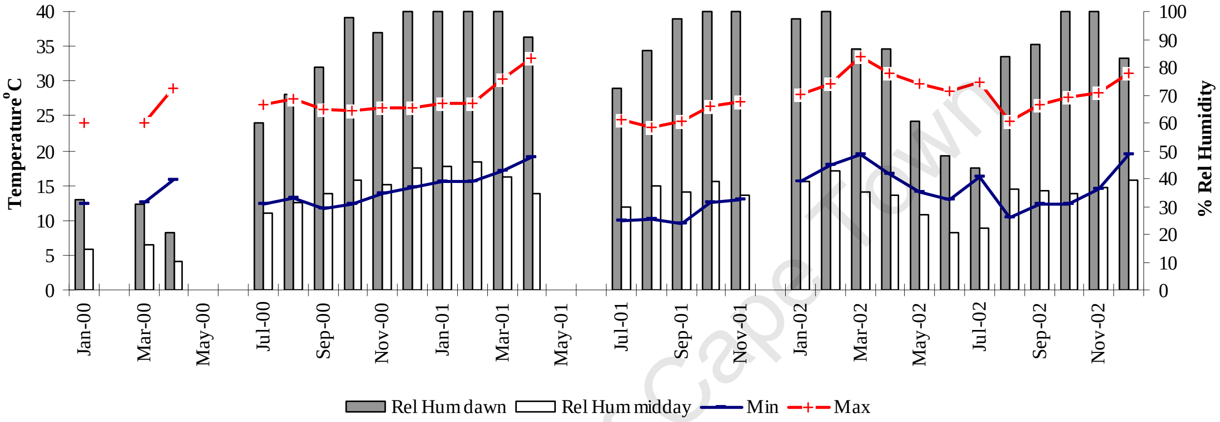


Figure 2.8: Maximum and minimum average monthly temperature (°C) and dawn and midday relative humidity (%) for Swartbank from January 2000 to December 2002.

At Swartbank the vegetation thins out across the wide floodplain. Both *F. albida* and *A. erioloba* grow as individual trees and there is little recruitment. Only a few individuals of *S. persica* and *E. pseudebenus* occur and *T. usneoides* is absent (*pers. obs.*). Non-woody perennial vegetation, including *Cladoraphis spinosa*, *Pechuel-loeschea leubnitziae*, *Acanthosicyos horridus* and alien herbaceous species like *Datura innoxia*, *Datura stramonium*, *Nicotiana glauca and Ricinus communis* covers the wide floodplain (Seely *et al.*, 1987; Theron *et al.*, 1985; Moser, 2006).

SOUTHERN KALAHARI AND KURUMAN RIVER

The Kalahari Basin (Fig. 2.9) extends from the mountains in central Namibia and Angola in the west to the highlands of Zimbabwe in the east. It covers the area between the Orange River in South Africa and watersheds in the Democratic Republic of Congo in the north. The southern Kalahari in South Africa is covered by up to 100 metre deep, reddish-brown to greyish-white aeolian Kalahari sand (Meyer *et al.*, 1985). The area is classified mainly as Gordonia Duneveld (Mucina and Rutherford, 2006), resembling a matrix consisting of grassland, vegetated dunes and dry riverbeds. The ephemeral Kuruman and Molopo Rivers traverse the area in an east-west direction. They are historical tributaries to the Orange River.

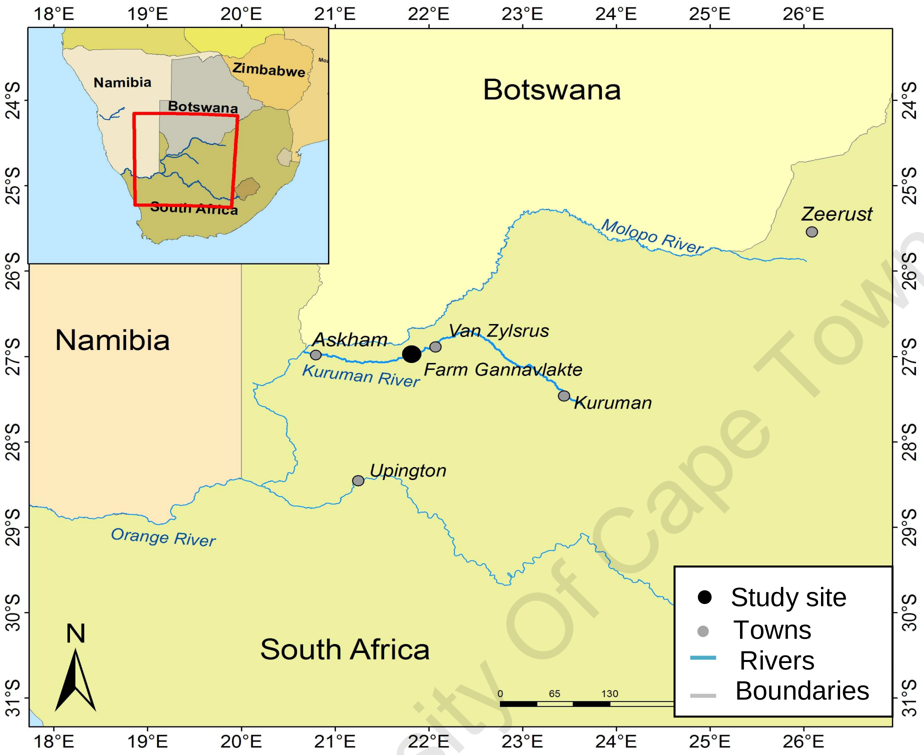


Figure 2.9: Map of Kuruman River showing the location of the farm Gannavlakte in the Kalahari where the study was conducted.

The headwaters of the Kuruman River lie at the town of Kuruman itself. It flows first into a north-westerly direction for about 100 kilometres, after which it turns west past Van Zylsrus for about 200 kilometres before joining the Molopo just west of Askham. The surface elevation declines steadily from about 1050 metres above sea level to 850 metres in the west (Verhagen, 1985). The area is covered with Aeolian sands that are underlain by superficial silcretes and calcretes of the Cenozoic Kalahari Group (Mucina and Rutherford, 2006). The river edges consist of pink to white compact sands and calcrete outcrops (van Rooyen *et al.*, 2001). The riverbed typically consists of finer silt soils than those of the surrounding area, as water carries organic material, minerals and other alluvial components into the lower lying riverbeds (van der Walt and le Riche, 1999). The landscape is shaped by parallel dunes about

3 to 8 metres high, which are vegetated by *Stipagrostis amabilis*, *Acacia heamatoxylon* and *Acacia mellifera* (Mucina and Rutherford, 2006). The interdune plains are dominated by *Rhigozum trichotomum*. The river fringes are lined with riverine woodland, consisting primarily of *Acacia erioloba* and other species such as *Acacia haematoxylon*, *Acacia mellifera*, *Boscia albitrunca*, *Ziziphus mucronata*, *Rhigozum trichotomum* and the invasive *Prosopis* (van Rooyen *et al.,* 2001).

The area receives summer rainfall, 80% of which occurs between October and March (van Rooyen *et al.,* 2001). The Kuruman follows a decreasing rainfall gradient from about 500 mm per annum at Zeerust to less than 150 mm close to Upington (Tyson and Crimp, 1998). Rainfall is highly variable from year to year with wet and dry spells each occurring for up to nine years. It is in the wet spells that unusually high rainfall events may result in river flow along the Kuruman. Four gauging stations have measured flow data in the headwaters around the town of Kuruman since 1960. The data suggests that headwater tributaries flow almost every year, but these flows rarely reach Van Zylsrus. Anecdotal evidence suggests that the Kuruman River has flowed in all or parts of its middle and lower reaches about ten times in the last 116 years (Meyer *et al.*, 1985; Ross-Gillespie, 2004, *pers. com.*; Meyer, 2007, *pers. com.*). The evidence is scant and hard to interpret, because it is often unknown whether the river flowed along its entire length or if a flood was a localised event (Table 2.1). No data are available for flood volumes or duration.

Table 2.1: Flood records for the middle (Gannavlakte) and lower Kuruman River reaches (confluence with Molopo). Flood events from 1970's onwards coincide with exceptionally good Kuiseb River floods (see Table 2.1)

Year	Where observed
1891	Near Molopo confluence
1892	Near Molopo confluence
1896	Near Molopo confluence
1920	Near Molopo confluence
	?
1973	Gannavlakte – no records downstream
1974	Near Molopo confluence
1975	Between Gannavlakte & confluence, also at Gannavlakte
1976	Near Molopo confluence – no flood record at Gannavlakte
1996	Gannavlake – no records downstream
2005	Between Gannavlakte & confluence – no flood record at Gannavlakte

Groundwater levels along the river are higher than away from the river, suggesting that occasional flood events recharge groundwater along the river (Meyer *et al.*, 1985; Verhagen, 1985). Rainfall recharges groundwater away from the river, creating brackish waters as the percolating water travels through unsaturated Kalahari Sand zones (Verhagen, 1985).

The Southern Kalahari is sparsely populated, with sheep and game farming as the main activities. Farmers depend completely on groundwater resources, which are frequently insufficient, or too brackish for livestock farming. Water is often piped from the Kuruman River over kilometres, to provide watering posts with adequate fresh water (Verhagen, 1985). The riverine woodlands along the river makes up a small percentage of the landscape, yet provides essential grazing, shelter and shade for most animal life in the area, as they seasonally move to and from the river (van Rooyen *et al.*, 2001).

Farm Gannavlakte

Farm Gannavlakte (26º57’578 S- 21º50’234 E) in the middle reaches of the Kuruman River is located 17 km south of the South Africa-Botswana border and 30 km west of the small settlement of Van Zylsrus in the Northern Cape. Gannavlakte and the neighbouring farm are owned by Cambridge University and are used as a wildlife sanctuary and a base for research on Meerkat. The average annual rainfall from 2003 to 2006 was 290 mm and average annual minimum and maximum temperatures were 13.2 ºC and 31.3 ºC respectively (Fig 2.10).

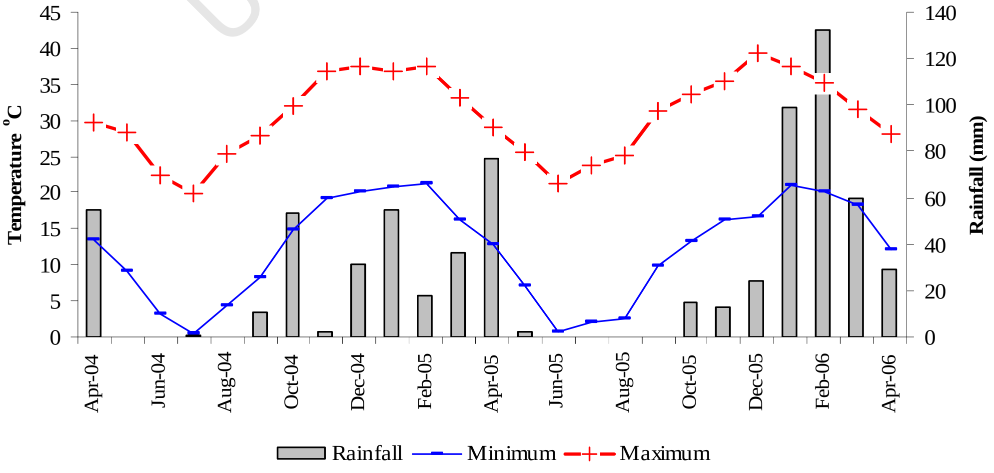


Figure 2.10: Average monthly rainfall as well as average minimum and maximum temperatures at Farm Gannavlakte on the Kuruman River (April 2004 – April 2006).

The three nearest boreholes (in a 5 kilometre radius) have a known groundwater depth of 27, 40 and 80 metres respectively (Ross-Gillepie, 2004, *pers. com.*) and the average depth of the closest 32 boreholes is 56 metres (Department of Water Affairs records).

The riverbanks at Gannavlakte are vegetated primarily by *Acacia erioloba*, *Rhizogum trichotomum* and *Acacia mellifera*. Inside the river channel there are smaller stands of *Ziziphus mucronata*. Individual *Boscia albitrunca*, *Acacia hebeclada* and *Acacia haematoxylon* occur on the river fringes. Alien invasive *Prosopis* spp. are common inside and along the river channel. Between 2002 and 2006 the Department of Water Affairs (Working for Water Programme) cleared *Prosopis* spp. from parts of the river, but some seedlings have re-established themselves since.

SPECIES INTRODUCTION

Four tree species were chosen for this study. They are the indigenous *Faidherbia albida*, *Acacia erioloba*, *Tamarix usneoides* and the invasive *Prosopis glandulosa.*

Faidherbia albida

Faidherbia albida (Del.) A. Chev. (1934) (Family Fabaceae, Subfamily Mimosoideae) is widely distributed over dry areas of Africa, from Senegal to Egypt, from Somalia to the east coast of South Africa and along the western catchments of Namibia. It is found in woodland, wooded grassland and in riverine fringe forests (Coates Palgrave, 1983). In east and southern Africa it is mainly found along watercourses on sandy alluvium. Its optimum growth occurs in areas with annual rainfall of 500 to 800 mm (Centre Technique Forestier Tropical, 1989) but along Namibian ephemeral rivers *F. albida* depends successfully on groundwater resources (Jacobson *et al.*, 1995; Moser, 2006). The tree has a strong and fast growing taproot to secure permanent water access (Bate and Walker, 1980) and it can root to 40 metres depth (Centre Technique Forestier Tropical, 1989; Dupuy and Dreyfuss, 1992). Roots of young seedlings grow between 0.9 and 1.3 centimetres a day (Moser, 2006).

F. albida occurs as a solitary tree or in dense stands along most westward flowing ephemeral rivers of Namibia, including the Kuiseb River (Jacobson *et al.*, 1995). Around Gobabeb, *F. albida* predominates along the riverbanks immediately adjacent to the river channel and occasional large trees occur inside the channel. At Swartbank large individual specimen occur on the floodplains, but at neither sites are any found on the outer, dune-covered river fringes. It is speculated that it cannot survive on the river fringes due to reduced water availability (Theron *et al.*, 1980; Jacobson *et al.*, 1995).

F. albida can reach heights of up to 31 metres and it has a lifespan of 70 to 90 years (Centre Technique Forestier Tropical, 1989). Its bark is rough and dark brown when mature and but white-green when young and branches are characteristically zigzag in shape. The thorns are straight, paired and around two centimetres long (Coates-Palgrave, 1983). The flowers are creamy-white spikes up to 14 centimetres long, occurring mainly in July and August. The leaves are compound and bipinnate with three to ten pairs of pinnae, bearing six to 23 leaflets each (ibid.). Leaflet size varies with age (*pers. obs.*) and water availability (Craven and Marais, 1986) from 2.5 to 12mm long and 0.7 to 5mm wide (Centre Technique Forestier Tropical, 1989). Contrary to other species *F. albida* sheds its leaves at the onset of the rainy season from December to March, and produces new ones from July to September (Curtis and Mannheimer, 2005). This contraseasonal leafing pattern is believed to be a cause of anaerobic soil conditions for roots in the wet season, which enforces a resting period for trees (Centre Technique Forestier Tropical, 1989). Van Wyk *et al.* (1985) found that *F. albida* in the Kuiseb only shed part of its leaves in the wet season, unlike trees in other regions. The tree is known to shed its leaves in times of water stress, too (Centre Technique Forestier Tropical, 1989). The pod is large (25x5cm), orange brown, indehiscent and curled. Pod fall occurs three months after flowering during the dry season (November to January), making it a valuable food source in the dry season. The seeds are brown, 10 mm x 6 mm and can remain viable for several years (Moser, 2006). The seeds germinate easily under favourable wet conditions, but only seedlings, washed up high enough onto the sandbank after a larger peak flood are likely to establish themselves (Barnes, 2001). Others are washed away with the next flood (Jacobson, 1997; Moser, 2006).

In 1987 *F. albida* was rated as one of the five most important (then) acacias in Africa, (Barnes *et al.,* 1997) and it is a protected species in South Africa (Coates Palgrave, 1983). Farmers throughout Africa value the tree for its soil enhancing properties, and its presence in agricultural fields improves crop yields (Dangasuk *et al.*, 2001; Dupuy *et al.*, 1992). Nutrient accumulation is not visible under trees along the Namibian rivers and it is believed that regular flood events evenly distribute the nutrients along the riverbed (Abrams *et al.*, 1997). *F albida's* pods and foliage are nutritious livestock fodder, providing 6-7MJ/kg as compared to 2.8MJ/kg of dry grasses (Centre Technique Forestier Tropical, 1989). One large tree can produce as much as 180-200kg of pods, equating to a value of N$585 in pod sales or N$599 in goat production (Moser, 2006). The gum, roots, pods, leaves and bark of the tree have medicinal uses (Craven *et al.,* 1986; van Wyk *et al.*, 1997) and the wood is used for building and carving (Centre Technique Forestier Tropical, 1989; Jacobson *et al.,* 1995).

Acacia erioloba

Acacia erioloba E. Mey., Comm. 1: 171 (1836) (Family Fabaceae, Subfamily Mimosoideae) is another one of the five key African acacia species, protected in South Africa by the National Forests Act of 1941 (Coates Palgrave, 1983; Powell, 2005). Despite this, their numbers have been on a steady decline through commercial firewood and pod collection, alien plant invasion, mining, dam construction and herbicide use all contribute to its decline (Powell, 2005).

It occurs solely in southern Africa, over a wide rainfall gradient from 40 to 900mm/annum. Its distribution is not determined by rainfall, but rather by the presence of wind-blown Kalahari sands and in drier areas also by the availability of groundwater (Barnes *et al.,* 1997). In arid areas, its seedlings germinate rapidly after rare rainfall or flood events, using the temporary soil moisture to send a taproot down (1.2 to 1.5 cm/day) to a permanent water source (Moser, 2006). After that it is independent of rainfall and can live for up to 300 years (Barnes, 2001). It is known for its deep rooting ability with cited records of roots found at 60 and 70 metres in the Kalahari (Canadell *et al.*, 1996; Obakeng, 2007). Due to its deep root system, it extends further into the deserts than any other tree (Barnes *et al*., 1997). It is frost tolerant and can handle degrees of water salinity (van der Walt *et al.,* 1999). It is found in arid woodlands, stony or sandy areas, but it develops best on deep alluvial sands in valleys, waterwashes and riverbeds (Milton, 1991). Just like *F. albida*, it is prominent throughout the Kalahari and along Namibia's ephemeral rivers (Theron *et al.*, 1985).

Depending on its surroundings *A. erioloba* can vary in height from a straggly shrub of two metres high, to a stately tree of sixteen metres with a wide, spreading crown. Old bark is very furrowed and grey to blackish brown, while young bark is shiny and reddish brown. It has pairs of strong, straight spines, up to six centimetres long. Flowers are bright golden-yellow balls, occurring at different times, depending on location (Curtis and Mannheimer, 2005). In the Kuiseb flowers occur on trees from June until April, but peak flowering time is from

November to January (van Wyk *et al.,* 1985). In the Kalahari *A. erioloba* is one of the first tree species to flower in spring (September) (van der Walt *et al.,* 1999). Leaves are compound, with two to five pairs of pinnae, each bearing eight to fifteen pairs of leaflets (4 to 13mm long and 1 to 4 mm wide) (Coates-Palgrave, 1983). Leaflet size varies with water availability (Barnes *et al.,* 1997). *A. erioloba* is evergreen with a slight drop in leaves in dry winter months (August) (Curtis and Mannheimer, 2005). The fruit is a large, grey, velvety, thick and ear shaped pod (11 by 5cm). The indehiscent pod bears dark brown seeds (8 to 14 by 7 to 10mm) (Barnes *et al.,* 1997), which germinate readily once they have passed through the gut of game and livestock. Trees start to flower after ten years of age (Barnes *et al*., 1997) or once they have reached a height of three metres in the Kuiseb (van Wyk *et al.,* 1985). At about twenty years of age, trees regularly produce large pod crops (Barnes *et al.,* 1997).

Milton and Dean (1995) suggest that *A. erioloba* is an ecological keystone species in those areas where no other large trees can grow. When mature, it acts as an island, providing scarce services and resources in places like the Kalahari and the Namib, including shade, shelter, nesting sites, lookout posts and specialized prey items. The use of *A. erioloba* trees by birds, game and other animal species such as the tree rat (*Thallomys*) concentrate nutrients under the trees, resulting in distinctive plant communities under the canopy (Milton *et al.,* 1995; Barnes *et al.,* 1997). More palatable species of grass and fleshy-fruited shrubs such as *Searsia* and *Grewia* species are common (Barnes *et al.,* 1997).

A. erioloba pods, shoots and leaves are readily eaten by game and livestock and pods are said to increase milk yield in cows (Coates-Palgrave, 1983). A large *A. erioloba* tree yields on average 200 kg of pods per annum, which is equivalent to a Namibian market value of ~ N$ 200 from pod sales or about N$ 700 from goat production (Moser, 2006). Barnes *et al.* (1997) have found published values for the high crude protein content of pods (10-16%) and foliage (up to 17% protein). The gum is edible and its hard wood is used for firewood, building material and fenceposts. The seeds can be used as a coffee substitute and the crushed pods can be eaten as porridge. Its gum, bark and roots are used medicinally (Barnes *et al.,* 1997).

Tamarix usneoides

The genus *Tamaricaceae* has some 90 species that are found from Europe to North China. *Tamarix usneoides* E Meyer ex Bunge (Family Tamaricacae) is common along the arid western parts of South Africa and western and southern Namibia. Its occurrence extends into

North Africa and Iran. It is a small to medium-sized tree, usually between three to seven metres tall, reaching a maximum height of ten metres (Curtis and Mannheimer, 2005). It is almost exclusively associated with dry riverbeds, brackish wetlands and shorelines (Coates-Palgrave, 1983), where it typically grows in dense tree stands of mixed heights. It is an indicator of shallow and often saline groundwater (Curtis and Mannheimer, 2005). Trees can be buried by sand after flood events, resprouting from old stems and lateral roots (Craven and Marais, 1986). Its leaves are very small, overlapping and scale-like (1x0.5mm) along branchlets. Both branchlets and leaves are grey-green in colour and photosynthesising. Flowers occur throughout the year in small, white, feathery sprays (ibid.). Wind-dispersed seeds are produced in low numbers all year round.

Tamaricaceae are salt exuding halophytes (Waisel, 1972). Leaves get wet almost every night from dew or fog and dry out over the course of the day, covered with salt crystals that help to reduce transpiration rates. A considerable amount of dew and fog water drips onto the soil in the mornings, where it is believed to be an additional water source for the trees (Waisel, 1960). Xu *et al.* (2007) however did not find any active root zone in the top 30 centimetres of soil under *T. ramosissima* that might suggest surface water uptake. Tests on water absorption by *Tamarix aphilla* leaves showed that the species does take up very limited amounts of water through its leaves when it is very stressed and subjected to huge amounts of atmospheric moisture. It is not clear how the process of leaf water uptake occurs. Waisel (1960) proposes that such leaf water uptake has survival value under conditions of great water stress, but it does not meet the overall plant water need. The primary water source for *Tamarix aphilla* in Israel and *T. ramosissima* in Asia remains soil and groundwater (Adar *et al.*, 1995; Xu *et al.*, 2007). They have been found to have dual root system with maximal rooting depth of 16 metres (Adar *et al.*, 1995).

In the United States *Tamarix chinensis* (saltcedar), originally from Asia, is the most widespread alien invasive along riverbanks of western USA (Cohn, 2005). *T. chinensis* require less soil moisture than indigenous vegetation and continue growing thick stands in the absence of large flood events (Cohn, 2005), thus altering the riverine ecosystems. There are efforts to eradicate the species due to its high water consumption and invasive nature.

In Namibia, *Tamarix usneoides* is used as livestock browse, wind breaks and firewood (Coates-Palgrave, 1983). In North Africa the exuded salt is harvested for table salt, but the

Namibian salt is considered inedible (Curtis and Mannheimer, 2005). In Israel *Tamarix aphilla* is used for dune stabilisation and timber (Adar *et al.*, 1995). In the Middle East the species *Tamarix mannifera* is attacked by a small insect, causing a white powder to fall from bored holes in the stem. This is the ‘manna’ eaten by Bedouins in the area and is said to be the manna that fed the children of Israel (Coates-Palgrave, 1983; Craven *et al.,* 1986). Many different insects are associated with *T. usneoides* and different galls are frequently visible on the foliage (Craven *et al.,* 1986).

Prosopis glandulosa

The genus *Prosopis* (Family Fabaceae, Subfamily Mimosoideae) consists of 44 species, which mostly occur in the central and southern parts of America. At least six of these, including *Prosopis glandulosa* Torrey var., *P. chinensis* Molina, *P. velutina* Wotoon and *P. pubescens* have been introduced to South Africa and Namibia around the 1800’s as shade, fodder and fuel trees (Harding, 1987; Impson *et al.*, 1999; le Maitre, 1999). The species have since spread widely throughout the southern parts of Namibia (Curtis *et al.,* 2005), covering at least 180 000ha of North-western South Africa (Coates-Palgrave, 1985). Due to hybridisation, species identification has become difficult (Impson *et al.,* 1999). This study took care to identify and use *P. glandulosa* throughout the study, but accidental selection of hybrids cannot be excluded. *P. glandulosa* is mostly found along rivers, well points, cattle posts and homesteads. They establish particularly well in deep soils with alluvial aquifers. Periodic flood events, livestock and game distribute its seeds. Seeds can also establish successfully under their adult trees, forming dense, impenetrable, monospecific thickets (Brown *et al.,* 1985; Brown *et al.,* 1986; Curtis and Mannheimer, 2005). Le Maitre (1999) calculated that the tree doubled its distribution area every five years, transforming open land into a dense thicket in ten to twenty-four years.

In Namibia, Curtis and Mannheimer (2005) recorded most trees in the 3-8m height class. *P. glandulosa* is a multistemmed tree with a spreading canopy and pairs of very strong spines, rather than thorns. Leaves have one pair of pinnae, with 7 to 18 leaflets per pinnae. Leaflets are dark green and widely spaced (10-50mm by 20-40mm) (van Wyk *et al.,* 1997). The tree is drought - deciduous, dropping most of its leaves in the dry season. The flowers are golden-yellow spikes, appearing mostly in October. The fruit is a flattened pod (100-250mm long) with seeds embedded in floury tissue. One tree produces between 90 to 140 kilograms of pods from January to March (Harding, 1987; van Wyk *et al.*, 1997; Curtis and Mannheimer, 2005).

Biodiversity studies indicate that species richness in *Prosopis* spp. woodlands is significantly lower than in indigenous vegetation. A great reduction in bird species was observed between indigenous *Acacia karroo* woodland and invasive *Prosopis* spp. woodland (Dean *et al.,* 2002). The *Prosopis* spp. woodland had comparatively little herbaceous understorey cover. A marked reduction in ant species was observed between an undisturbed riparian *A. erioloba* stand and a dense *P.glandulosa* stand along the Kuruman River (*pers. obs*.). A recent observation of *A. erioloba* mortality along parts of the Kuruman River where *Prosopis* spp. are invading, suggests that the indigenous vegetation is out competed for water (le Maitre, 1999; Robertson *et al.,* 2002). There is growing concern of *Prosopis* spp. impacting on agricultural land productivity and on scarce groundwater resources (le Maitre, 1999). Le Maitre's (1999) literature review on *Prosopis* states that the tree has high transpiration rates when it has free access to water, either from surface water or groundwater. Catchment management plans support the eradication of *Prosopis* spp. species along rivers, as the trees are considered inefficient water users, with an estimated annual water use of 997m^3 per densely invaded hectare (le Maitre, 1999). The Working for Water Project in South Africa employs people throughout South Africa to eradicate alien invasive plants along river channels, in an effort to conserve water resources, protect natural biodiversity and create much-needed jobs (Department of Water Affairs and Forestry, 1997). *Prosopis* spp. are the main alien invasives being cleared out along ephemeral rivers in the Northern Cape. As a bio control measure, three seed-feeding bruchid beetles from the south-western USA have been released in South Africa in order to reduce the number of viable seeds produced every year (Impson *et al.,* 1999).

Farmers have valued the tree for its shade and fodder and have actively spread it in Namibia and South Africa in the past (Harding, 1987). The seeds are highly nutritious and have a similar protein value as soybeans (Harding, 1987). The wood is very hard and workable, but the multistemmed growth form limits the applications and its best uses in Southern Africa are as firewood or charcoal (Harding, 1987).

In South Africa, the spread of alien trees such as *Prosopis* spp. is a well-recognised biotic factor that can destabilise river ecosystems (O'Keefe, 2000). *Prosopis* spp. are the main invaders of ephemeral rivers in Namibia and South Africa (Coates-Palgrave, 1983). Their reputation as high water users and their overt outcompeting of indigenous riparian vegetation make it interesting to include *P. glandulosa* in this study.

CHAPTER 3: THE RELATIONSHIP BETWEEN FOG, FLOODS, GROUNDWATER AND TREE GROWTH ALONG THE LOWER KUISEB RIVER IN THE HYPERARID NAMIB

INTRODUCTION

In southern Africa studies have shown that increased flood intervals and receding groundwater tables result in increased tree mortality with mortality rates differing between species and age classes (Ward and Breen, 1983; O'Connor, 2001). With increasing anthropogenic demand for the utilisation of the aquifer in the lower reaches of the Namibian Kuiseb River there has been some concern for the potential effects this demand may have on the lowering of the groundwater table and a potential consequence in a changed vegetation structure (Huntley 1985).

At my study site near Gobabeb in the western half of the Namib Desert rainfall is extremely low averaging between 0 and 12 mm a year (Henschel and Seely, 2008). Fog events are, however, more frequent, occurring on average 60 – 200 days of the year (Shanyengana *et al*., 2002). These fog events provide a predictable source of water for biota in the Namib (Seely, 1979; Louw and Seely, 1980). Throughout the world, research has demonstrated that where there are frequent fog events, trees have adapted to intercept and utilise the moisture from these events (Cavelier and Goldstein, 1989; Cavelier *et al.,* 1996; Gabriel and Jauze, 2008; Simonin *et al.,* 2009). In the Namib Desert trees are confined to the banks of ephemeral rivers such as the Kuiseb. In this chapter I determine the extent to which different age groups of these trees are able to utilise the locally available water sources, including soil water, groundwater as well as fog water.

A number of studies have shown that the stable Hydrogen and Oxygen isotope ratios of xylem water may be used to demonstrate the water source of a plant (Busch *et al.,* 1992; Evans and Ehleringer, 1994; Schwinning and Ehleringer, 2001; February *et al.,* 2007a,b). The method is based on the assumption that water extracted from the non photosynthesising tissue of plants will have the same isotope ratio as the source water (White *et al.,* 1985). I use the stable isotope ratios of water extracted from plant xylem to estimate the water source for seedling, juvenile and adult stages of three common tree species (*Acacia erioloba*, *Tamarix usneoides* and *Faidherbia albida*), growing in the lower Kuiseb River near Gobabeb. The aim is to improve the understanding of the relationship between fog, floods, groundwater and tree water uptake along river courses in hyperarid regions. Such an understanding is important for the protection of riparian areas throughout the world as abstraction and dewatering continue to threaten riparian systems (Stromberg *et al.*, 1996).

METHODS

Study site

The study was conducted at the Gobabeb Training and Research Centre (23º33’726 S – 15º02’112 E) in the area classified as riverine woodland of the lower Kuiseb River (Huntley 1985). The average minimum and maximum temperatures for Gobabeb during the two-year study period were 13.2 ºC and 30.5 ºC respectively. The site falls within the hyperarid central Namib zone with erratic, average annual rainfall of 27 mm (Lancaster *et al.*, 1984). Fog is generated over the cold up welled water of the Atlantic Benguela current and is the most reliable and regular moisture source for the area, occurring on average for 38 days of the year (Lancaster *et al.*, 1984).

At Gobabeb the lower reaches of the Kuiseb River form a divide between gravel plains to the north consisting of granites, gneisses, schist’s and quartzite’s (Bao *et al.*, 2001) and a wandering dune sea to the south. The active river channel is less than one hundred metres wide at the study site with a depth of 4-5 m to the water table and at around 8 m on the floodplain (Fig. 3.1). It is the alluvium on the floodplain that supports the riparian vegetation. Dominant riparian species are *Acacia erioloba*, *Faidherbia albida*, *Tamarix usneoides*, *Euclea pseudebenus*, *Salvadora persica*, *Acanthosicyos horrida* as well as invasive herbaceous species such as *Nicotiana glauca*, *Rhicinus communis* and *Datura* spp. (Theron *et al.*, 1985). The riverbed consists of several granite bedrock compartments filled with sand and alluvium. Flood events, generated in the higher rainfall upper catchment (400 mm/a) 400 km to the Northeast, move downstream as flash floods that wash away northward moving dune sand while recharging the alluvial aquifers (Ward and von Brunn, 1985; Dahan *et al.*, 2007). During the course of this study (June 2004 to March 2006) no flood events occurred in the Kuiseb at Gobabeb.

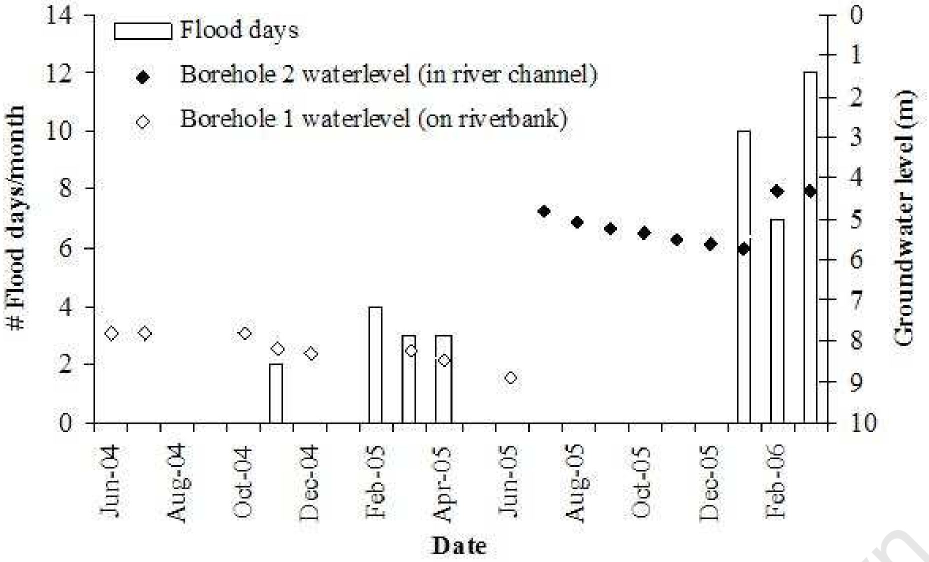


Figure 3.1: Monthly groundwater levels (below ground level) and number of flood days from June 2004 to March 2006 at Gobabeb. The datalogger in borehole 1 (on the river bank) broke in June 2005 and further data was obtained from a freshly drilled monitoring borehole in the river channel where groundwater is closer to the surface (borehole 2, courtesy WADE project).

Stable Hydrogen and Oxygen isotope analysis

I identified three age classes (adult, juvenile and seedling) of the three most common tree species (*Acacia erioloba*, *Faidherbia albida* and *Tamarix usneoides)* at our study site. All of the adults established after a flood in 1974 and were growing within 50 m of the active river channel. All juveniles established after the 2000-2001 floods and were located within 30 m of the active river channel. There were no *T. usnoides* seedlings while *A. erioloba* and *F. albida* seedlings emerged inside the active river channel after the February 2004 and April 2005 floods. Six trees of each species and age class were randomly selected for the study within a 500 m long and 100 m wide section of the riparian zone at Gobabeb.

Twig (c.a. 50 mm x 10 mm) samples from each of the six trees from each size class were collected on six separate occasions for stable isotope analysis. These collections were made six times, twice in the dry season (June 2004 & June 2005), the late dry season (Nov. 2004 & Dec 2005) and the late flood season (Mar 2005 & Apr 2006). In the active river channel a soil auger was used to extract soil samples every 50 cm to a depth of 4 m after flood events in Nov 2004, April 2005 and March 2006 and in June 2004, June 2005 and Dec 2005. In Nov

2004 two cores were also extracted from the elevated floodplain outside the active river channel.

From June 2004 to March 2006 fog and groundwater were collected monthly. A fog collector was constructed by mounting a 40 x 50 cm rectangle of 80% shade cloth vertically between two upright poles. Fog condensed on the cloth ran into a gutter and was diverted into a 25 litre container. A layer of silicon oil inside the container prevented evaporation. Groundwater was collected monthly directly from the borehole supplying Gobabeb with water (borehole 1, Fig. 3.1) while rain and floodwater were sampled during rain and flood events.

Twig samples of non-suberized wood were collected for juvenile and adult trees. The roots of seedlings were sampled in Nov 2004 and 2005 as there was insufficient above ground non-photosynthesising material. An early flood in November 2004 washed half of the seedlings away reducing the number of seedlings available for collection.

The twig and root samples were collected directly into borosilicate tubes (Kimax – Kimble, New Jersey, USA) which were then directly inserted onto a cryogenic vacuum extraction line to separate the water for isotope analysis. A ten gram sub sample of the soil was transferred into borosilicate tubes for extraction. After extraction the water samples were analysed for $^{2}H/H$ ratios using a variation of the zinc closed tube reduction method (Coleman *et al.*, 1982), while $^{18}O/^{16}O$ were obtained using the CO_2 equilibrium method of Socki *et al*. (1992). Isotopic ratios of both $^{2}H/H$ in H_2 and $^{18}O/^{16}O$ in CO_2 were determined using a Thermo Delta Plus XP Mass Spectrometer (Hamburg, Germany) at the University of Cape Town. Internal UCT standards were run to calibrate my results relative to Standard Mean Ocean Water (V-SMOW) and to correct for reference gas drift. The deviation from V-SMOW is denoted by the term δ and results are expressed as parts per mil (‰) through the equation:

$$\delta^{xx}E = (R_{sample}/R_{standard}) - 1 \times 1000$$

Where $\delta^{xx}E$ is the respective element (^{2}H, ^{18}O), ^{xx} is the mass of the heavier isotope in the abundance ratio, and R_{sample} and $R_{standard}$ are the ratios of the heavy to light isotope of sample and standard respectively (Dawson *et al.*, 2002). The analytical uncertainty is approximately 2 ‰ for $\delta^{2}H$ and 0.2 ‰ for $\delta^{18}O$.

All statistical analyses were conducted using Statistica 8.0. Standard correlations were performed between different isotopic source water values. One-way ANOVA's followed by Tukey post hoc tests were done to detect any significant differences ($p < 0.05$) among tree species and age groups. Kruskall Wallis nonparametric tests were used to determine significant differences between trees and source waters. Student t-tests were performed to compare soil profiles.

Water source modelling

The proportion of fog, shallow soil, deep soil and groundwater utilised by trees was modelled using the IsoSource mixing model (Phillips and Gregg, 2003). I chose this model over all others because I was only interested in modelling tree utilisation of three potential water sources with only two isotopes (Hydrogen and Oxygen), and because it is user-friendly. I applied the model to estimate the percentage contribution of each water source to the three age classes of the different species. The IsoSource mixing model provides ranges of feasible contributions for each individual source. These can often be quite broad, hence an additional non-isotopic constraint was applied on the model to further reduce the range of feasible contributions of each source (Phillips and Gregg, 2003; Phillips *et al.,* 2005; Quereteja *et al*., 2007). Fog was significantly different in $\delta^{18}O$ and $\delta^{2}H$ to tree water, and was hence not a main water source to trees. Consequently, only numerically feasible solutions were included in the modelling solutions in which the percentage of fog contribution was smaller than contributions from groundwater, shallow and deep soil water.

RESULTS

Plant source water

Meteoric waters follow a Rayleigh distillation process that results in a linear relationship between $\delta^{18}O$ and $\delta^{2}H$ for water samples worldwide (Craig, 1961; Gat, 1996). This relationship is termed the global meteoric water line (GMWL) (Craig 1961). I construct our own local meteoric water line (LMWL) for the Gobabeb area using flood, local rain and fog water ($\delta^{2}H = 7.2 * \delta^{18}O – 0.6$ ‰; Fig. 2). As the majority of our water samples are subject to free evaporative processes, these plot below the global meteoric water line with a slope of less than 8 (Gat, 1996; February *et al.,* 2007b). The fog is separated in delta space on this plot from groundwater, which is superimposed on the plot (Fig. 3.2). The early, smaller flood waters show more evaporative enrichment than the larger, late season flood waters that are high and long enough to recharge the aquifer (Fig. 3.1 and 3.2).

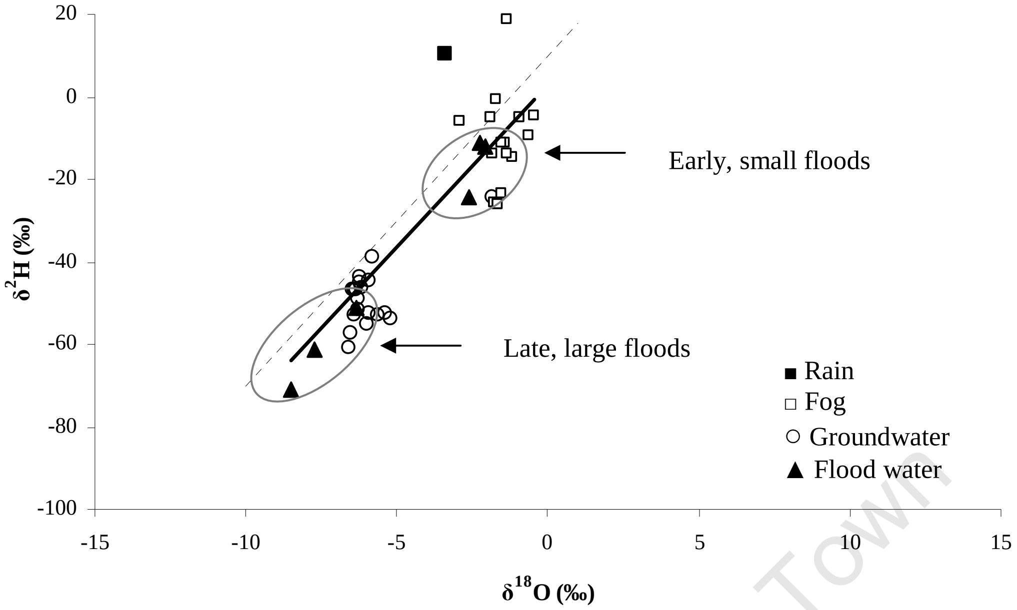


Figure 3.2: Local meteoric water line ▬ for the lower Kuiseb River, including fog, floodwater and one rainfall event. Groundwater values ○ and the global meteoric water line - - - are superimposed.

The isotope ratios of soil water in the wet season are significantly correlated with floodwater isotope ratios ($r^2 = 0.39$; $p = 0.01$; $n = 22$). Also, the soil isotope profile in the flood season is homogenous, with no significant differences in isotope ratios for soil water at different depths ($F_{8,22} = 0.37$, $p = 0.9$; Fig. 3.3).

In the dry season however there is a wide range in soil water isotope ratios with significant differences between shallow, enriched waters (0-100 cm; $\delta^{18}O = -2.9 \pm 1.8$ SE) and deep, more depleted waters (150-400 cm; $\delta^{18}O = -7.3 \pm 0.4$ SE) ($p = 0.001$; Fig. 3.3).

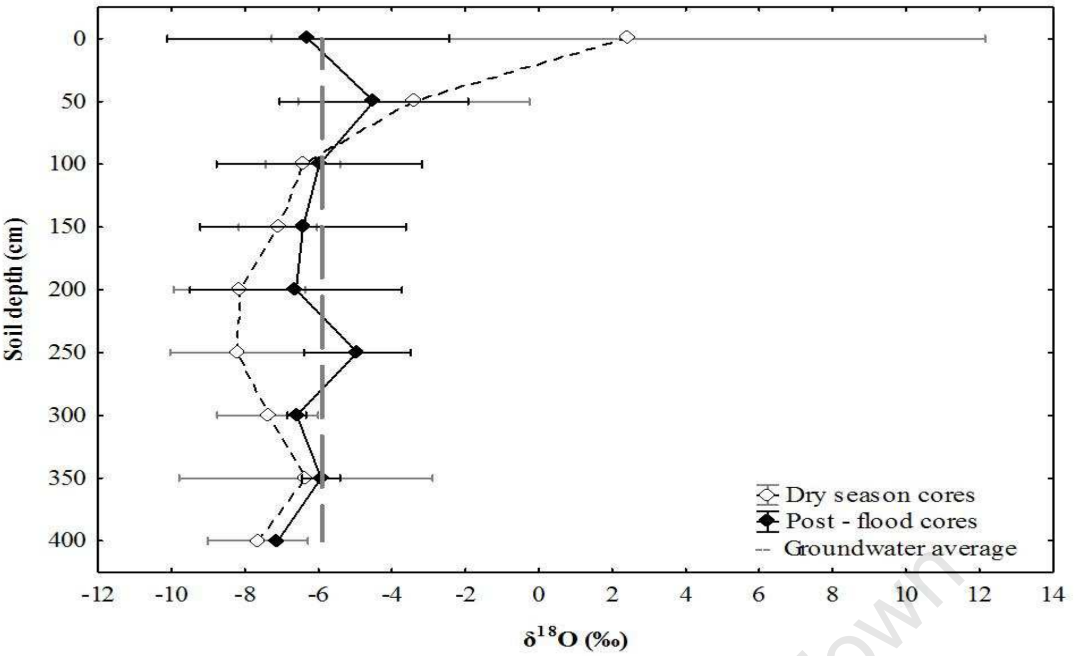


Figure 3.3: Average δ^{18}O ratios of soil water in the dry season (June 2004, November 2004 floodplains, December 2005) and immediately after floods (November 2004 river channel, April 2005 and March 2006) in relation to groundwater (δ^{18}O = -5.9 ‰).

Xylem water isotope ratios

All *A. erioloba* isotope ratios were at all times significantly different from fog water ($p < 0.001$). There are no significant seasonal (wet - dry) differences in stable isotope ratios for xylem water of *Acacia erioloba*. There are, however, significant age class differences in isotope ratios of the xylem water of adult and juvenile trees ($p = 0.02$) in the wet season. The isotope ratios of wet season adult *A. erioloba* xylem water are very similar to deep soil water δ^{18}O values while the isotope ratios for juvenile plants are similar to that of shallow soil water and groundwater but significantly differ from fog and deep soil water ($p < 0.01$) (Fig.3.4).

The isotope ratios for xylem water of adult *A. erioloba* in the dry season are intermediate between groundwater and soil water. Dry season juvenile water isotope ratios are similar to shallow soil water (0-100 cm) and significantly different from groundwater ($p = 0.006$) and deep soil water ($p < 0.001$). I only collected seedlings for isotope analysis in the dry season. These results show that the isotope ratios for seedlings are very similar to deep soil water δ^{18}O values and significantly different from that of fog water ($p < 0.002$).

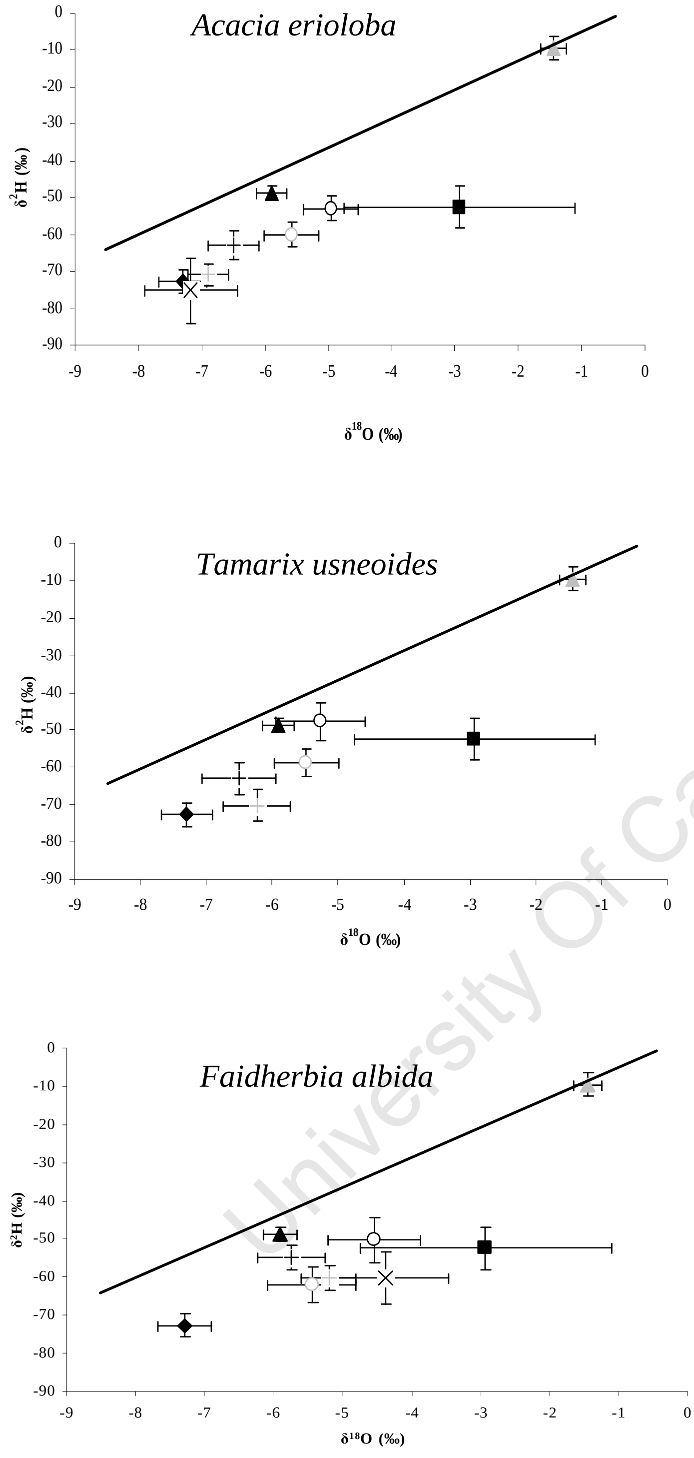


Figure 3.4: Average δ^{18}O versus δ^2H values from adult wet season (+) and dry season (+), juvenile wet (○) and dry (○) and seedling (×) specimen for (a) *A. erioloba*, (b) *T. usneoides* and (c) *F. albida*. Seedlings were not plotted for *T. usneoides*. All age groups are plotted against the LMWL (—), groundwater (▲), fog (▲), shallow (■) and deep (♦) soil water.

There are no significant seasonal (wet – dry) or age group differences in xylem water isotope ratios for *Tamarix usneoides* and all tree water ratios are significantly different from fog ($p < 0.001$). Isotope ratios of xylem water from adult *T. usneoides* differ significantly from shallow soil water ($p = 0.04$) and are intermediate between deep soil water and groundwater in both seasons (Fig.3.4). The results for xylem water of juvenile *T. usneoides* is intermediate between groundwater and shallow soil water, differing significantly from deep soil water for both seasons ($p \leq 0.01$).

There are no significant differences in xylem water isotope ratios between *F. albida* seedlings, juveniles and adults. All are, however, significantly different from fog ($p < 0.001$) and deep soil water ($p \leq 0.01$). Dry season juvenile and seedling *F. albida* plot within the range of shallow soil water isotope ratios (Fig. 3.4) and they are both significantly different from the isotope ratios of groundwater ($p \leq 0.02$).

Linear modelling

I use the IsoSource linear mixing model (Phillips and Greg, 2003) to further quantify proportional source water contributions for the three species used in this study. No results could be obtained for wet season adult *T. usneoides* or the seedlings of *A. erioloba* and *F. albida* through the model, because they all lay outside the polygon that is formed by the $\delta^{18}O$ and $\delta^{2}H$ values of the four source waters. The model can only calculate possible water use for tree values that fall within the polygon (Phillips and Greg, 2003). Values outside the polygon are assumed to have other contributions.

Table 3.1: Proportions of feasible water sources (%) for the different tree species and ages. Average source proportions are shown in bold, as well as the range (1 and 99%) of minimum and maximum source proportions.

	Groundwater (4m) $\delta^{18}O$ = -5.9 ‰ $\delta^{2}H$ = -48.6 ‰	Shallow soil (0 – 1m) $\delta^{18}O$ = -3.8 ‰ $\delta^{2}H$ = -51.9 ‰	Deep soil (1.5 – 3 m) $\delta^{18}O$ = -7.3 ‰ $\delta^{2}H$ = -65.9 ‰	Fog water $\delta^{18}O$ = -1.5 ‰ $\delta^{2}H$ = -9.5 ‰
A. erioloba adult wet	**2 %** (0 – 6%)	**7 %** (4 – 11%)	**90 %** (88 – 93%)	**1 %** (0 – 3%)
A. erioloba adult dry	**30 %** (24 – 36%)	**6 %** (3 – 10%)	**62 %** (58 – 65%)	**2 %** (0 – 4%)
A. erioloba juvenile wet	**19 %** (10 – 29%)	**28 %** (22 – 33%)	**49 %** (42 – 58%)	**4 %** (0 – 9%)
A. erioloba juvenile dry	**42 %** (29 – 54%)	**34 %** (28 – 40%)	**20 %** (11 – 28%)	**5 %** (0 – 10%)
A. erioloba seedling	Not possible to calculate, lies outside of the source water polygon			
T. usneoides adult wet	Not possible to calculate, lies outside of the source water polygon			
T. usneoides adult dry	**19 %** (16 – 22%)	**17 %** (15 – 19%)	**63 %** (61 – 66%)	**1 %** (0 – 3%)
T. usneoides juvenile wet	**22 % (**11 – 34%)	**27 %** (21 – 33%)	**45 %** (37 – 56%)	**5 %** (0 – 11%)
T. usneoides juvenile dry	**74 %** (65 – 82%)	**14 %** (9 – 18%)	**5 %** (0 – 12%)	**7 %** (4 – 11%)
F. albida adult wet	**12 %** (6 – 18%)	**41 %** (37 – 46%)	**45 %** (41 – 50%)	**2 %** (0 – 5%)
F. albida adult dry	**52 %** (42 – 62%)	**13 %** (9 – 19%)	**30 %** (23 – 38%)	**4 %** (0 – 9%)
F. albida juvenile wet	**9 %** 5 – 15%)	**36 %** (33 – 40%)	**52 %** (49 – 56%)	**2 %** (0 – 4%)
F. albida juvenile dry	**73 %** (65 – 80%)	**15 %** (14 – 17%)	**8 %** (4 – 14%)	**3 %** (0 – 6%)
F. albida seedling	Not possible to calculate, lies outside of the source water polygon			

Water source proportions were calculated with the IsoSource model (http://www.epa.gov/wed/pages/models.htm; Phillips and Gregg, 2003). Only numerically feasible solutions were chosen in which source waters, found to be significantly different in $\delta^{18}O$ and $\delta^{2}H$ to the respective tree age and species, were smaller than the contribution from the other three water sources.

The results of our model show that none of the tree species in this study use fog water (Table 3.1). Rather, all of the trees are reliant on a seasonally fluctuating combination of groundwater, shallow soil and deep soil water. All these three sources directly depend on Kuiseb aquifer recharge through regular large floods. Adult *T. usneoides* and *A. erioloba* rely largely on deep soil water year - round. Juvenile *A. erioloba* and *T. usneoides* use the three source waters in very similar proportions over time, with juvenile *T. usneoides* being mostly groundwater dependent (65 – 82%, mean 74%) in the dry season. Juvenile and adult *F. albida* behave similarly, being more shallow and deep soil water dependent in the wet season, becoming predominantly groundwater dependent in the dry season.

DISCUSSION

The results of our model (Table 3.1) show that all of the trees are reliant on a seasonally fluctuating combination of groundwater, shallow soil water and deep soil water. None of the tree species in this study use fog water regardless of age class even though fog events may contain considerable (0.1 – 1.01 m^{-2} day^{-1}) amounts of water (Henschel and Seely, 2008). In hyperarid areas such as at our study site the occurrence of fog plays an important role in the water economy of many organisms. This is indeed the case for many species in the Namib (Henschel and Seely, 2008), except for the riparian trees.

Adult *T. usneoides* and *A. erioloba* rely largely on deep soil water. Juvenile *A. erioloba* and *T. usneoides* use the three source waters in very similar proportions over time, being mostly groundwater dependent in the dry season and largely deep soil water dependent in the wet season. Juvenile and adult *F. albida* depend on both shallow and deep soil water in the wet season, becoming predominantly groundwater dependent in the dry season. These shifts in water uptake are also supported in other research, suggesting that riparian trees have much more flexible water uptake patterns than previously expected (Snyder *et al.*'s 1997, Glen and Nagler 2005).

The soil and groundwater sources directly depend on Kuiseb aquifer recharge that occurs during floods in the wet season (November to April), as indicated in Figure 3.2 and by other recent studies (Dahan *et al.*, 2008). These flood events have flowed past Gobabeb on average 33 days per year from 1963 to 1976 and 10 days per year from 1977 to 2006 (Mizuno, 2010). The regularity of the floods are such that none of the tree species in this study have adapted physiologically to utilise fog water. Over a ten year period recharge of the groundwater was primarily due to the large floods of 1997 and 2000, which flowed for 33 and 23 days respectively (data from 1995-2005, borehole # 35016, courtesy Gobabeb Training and Research Centre). Smaller floods did not significantly recharge groundwater, with the water table steadily declining between large flood events.

As a result of a drought in the upper reaches of the catchment from 1980 to 1984 there was no recharge of the aquifer in the Kuiseb and water levels dropped by between 2 and 6 metres (Hattle, 1985). My study trees are so reliant on this regular recharge that drought related deaths accounted for 24% of the *T. usneoides*, 29% of the *A. erioloba* and 62% of the *F. albida* (Theron *et al.,* 1985). Previous vegetation studies in the Kuiseb speculated that the observed mortality patterns among species and age groups were related to differences in rooting structure and depth of water uptake (Ward and Breen, 1983). The isotope results suggest that the observed mortality rates are not directly related to rooting depth, as all three species use the same water sources, even if in slightly different proportions (Table 3.1). *A. erioloba* is the only species showing significant differences in water use between age groups (Fig. 3.4). During the 1980's drought, higher mortality rates were observed for *A. erioloba* specimen with a circumference of less than 50 cm (Theron *et al*., 1985). It is the only case in which historic drought mortality records coincide with isotopic evidence for differences in water uptake. However, it is not concluded that this is an indication for different rooting depths for *A. erioloba* age groups, as there may also be other physiological explanations that are not part of this Chapter's research focus. There has been very little research on the physiological traits associated with drought for *A. erioloba* and *F. albida* with no studies on *T. usneoides*. What little there has been are in agreement with these figures showing that *Tamarix ramosissima* is drought tolerant (Glen and Nagler, 2005), *A. erioloba* avoids droughts through deep rooting (Obakeng, 2007; Lubczynski, 2009) while *F.albida* cannot survive beyond the river fringes due to reduced water availability (Theron *et al.,* 1980; Jacobson *et al.,* 1995) and they are drought sensitive (Ward and Breen, 1983; O'Connor, 2001). The physiological traits of the species will be examined in greater detail in Chapter 5.

Future predictions point towards increased water abstraction (Swiegers, 2008; Pallett, 2008) and global climate change (de Wit and Stankiewicz, 2006) in the Namib and most arid parts of Southern Africa. To maintain the structural integrity of this landscape for future generations it is vitally important that conservation efforts are directed toward maintaining regular and especially large flood events in the ephemeral rivers. Without such recharge events and with aquifer declines beyond any natural fluctuations, the vegetation structure along ephemeral rivers such as the Kuiseb will be seriously threatened, as all of the trees and all age classes in this study demonstrate a reliance on regular flood recharge of either the aquifer or soil moisture.

CHAPTER 4: DOES THE ALIEN INVASIVE *PROSOPIS* OUTCOMPETE THE INDIGENOUS *ACACIA ERIOLOBA* FOR WATER ACCESS ALONG EPHEMERAL RIVERBANKS?

INTRODUCTION

Prosopis glandulosa var. *torreyana* is one of the main invaders of drainage lines in semi-arid and arid areas of Namibia and South Africa, where it forms dense, impenetrable thickets (Coates-Palgrave, 1983; Impson *et al.,* 1999). *Prosopis* species were introduced to South Africa and Namibia around the turn of the 20th century as a source of fodder for cattle and sheep, as well as shade and firewood (Brown and Gubb, 1986; Impson *et al.*, 1999). Since then, at least four species (*P. glandulosa* var. *glandulosa*, *Prosopis glandulosa* var. *torreyana, Prosopis velutina, Prosopis chilensis*) have hybridised and naturalised, spreading in semi-arid and arid regions of the subcontinent (Coates-Palgrave, 1983; Impson *et al.*, 1999). Prolific seed production and high germination rates result in its rapid spread along riparian corridors (Shiferaw *et al.,* 2004). *Prosopis* species in South Africa are estimated to use 1000 m^3 of water annually per densely overgrown hectare (le Maitre, 1999). In an effort to conserve water resources, catchment management plans support the eradication of *Prosopis* spp. along rivers. A government initiated ‘Working for Water’ Programme is actively engaged in removing *Prosopis* spp. from drainage lines in the Northern Cape region of South Africa.

The need to eradicate *Prosopis* spp. from riparian corridors in arid systems is not only determined by water conservation. In the Namib and Kalahari Deserts *A. erioloba* is one of the main tree species occurring in and beyond riparian woodlands (Ward and Breen, 1983; Jacobson *et al.,* 1995; van Rooyen and van Rooyen, 1998; Dean *et al.*, 1999; van Rooyen *et al.,* 2001; Seymour and Huyser, 2008). When mature, it acts as an island, providing shade, shelter, nesting sites and lookout posts for animals (Milton and Dean, 1995; Dean *et al.*, 1999; Powell, 2005; Eccard *et al.*, 2006). The use of *A. erioloba* by birds, game and rodents concentrates nutrients under the canopy of these trees, resulting in distinctive and more palatable plant communities (Milton and Dean, 1995; Barnes *et al.*, 1997; Dean *et al.*, 1999; Eccard *et al.,* 2006). It is considered a keystone species, as it persists in arid areas where no other large trees can grow (Milton and Dean, 1995; Barnes *et al.,* 1997). It has been suggested that *A. erioloba* needs to be recognized and protected for its keystone function in ephemeral river corridors (Colvin *et al.*, 2007).

A. erioloba mortality increases as *Prosopis* species densities increase (Robertson and Woodborne, 2002; *pers. obs*.). A number of studies have suggested that that *Prosopis* species outcompete *A. erioloba* for water (le Maitre, 1999; Robertson and Woodborne, 2002; Colvin *et al*., 2007). It has also been suggested that that *Prosopis* species are able to withstand high levels of water stress, (Nilsen *et al.,* 1983; Nilsen *et al.,* 1984; Hultine *et al.,* 2005), have extremely fast root growth as well as a dual root system. The dual roots allow for a very deep tap root (maximum 53 metres) (Stromberg *et al.,* 1992), as well as extensive lateral root development (Nilsen *et al.,* 1983; Stromberg *et al.,* 1992; le Maitre, 1999; Robertson and Woodborne, 2000). This dual root system allows *Prosopis* species to rapidly switch between groundwater in the dry season and shallow soil water in wet season (Snyder *et al.,* 1998), optimising the use of available water and nutrient uptake. The opportunistic water uptake with the dual root system is believed to give *Prosopis sp*. a water sourcing advantage over *A. erioloba* (le Maitre, 1999; Robertson and Woodborne, 2002; Colvin *et al*., 2007). A similar dual root system, root growth and water sourcing strategy has been observed for *Tamarix* spp. invading river corridors in the USA (Busch *et al.,* 1992; Dawson and Pate, 1996; Sala *et al.,* 1996; Horton and Clark, 2001).

In this chapter I test the hypothesis that indigenous riparian species experiences increased water stress in areas densely overgrown *Prosopis sp*. I conduct a case-study of this hypothesis by examining plant tree density measurements, percentage canopy dieback, plant water source and moisture stress. I do this along the ephemeral Kuruman River in the Northern Cape Province of South Africa.

METHODS

Site description

The study was conducted in the southern Kalahari on the farm Gannavlakte (26º57’578 S-21º50’234 E). The farm is a fieldstation for the Cambridge University Meerkat Project, located 17 kilometres south of the South Africa-Botswana border and 30 kilometres west of van Zylsrus in the Northern Cape Province. Gannavlakte lies along the middle reaches of the ephemeral Kuruman River, a historic tributary to the Orange river. The climate of the area is characterised by hot, wet summers and cold, dry winters. Mean annual rainfall for the last decade is 280 millimetres, with an average of 80% of the rain falling between October and March (van Rooyen *et al.,* 2001). The average minimum and maximum temperatures are 13.2ºC and 31.3ºC respectively. The area is largely covered with Aeolian sand underlain by superficial silcretes and calcretes of the Cenozoic Kalahari Group (Mucina and Rutherford, 2006). The river edges consist of pink to white compact sands and calcrete outcrops (van Rooyen *et al.,* 2001). The riverbed typically consists of finer silt soils in comparison to the surrounding area, as rare flood and annual rainwater carries organic material, minerals and other alluvial components into the lower lying riverbeds (van der Walt and le Riche, 1999). The average groundwater depth along the Kuruman River is 65 metres (DWAF borehole records) and in the only unused borehole available near Van Zylsrus the water table was measured with a piezometer (Diver: Eijkelkamp/van Essen, Netherlands), fluctuating between 54.2 and 57.8 metres from March 2005 until January 2007 (Figure 4.1).

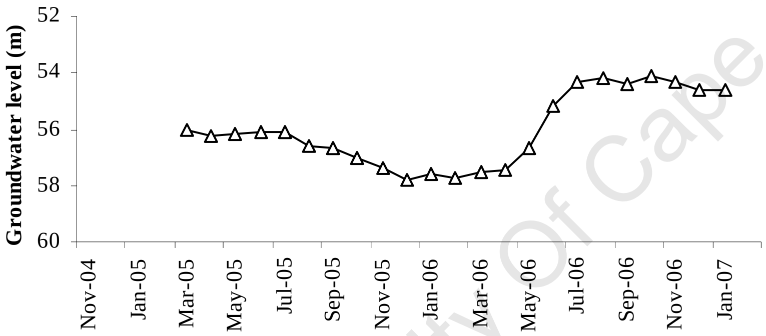


Figure 4.1: Groundwater level (metres) at Van Zylsrus from March 2005 to January 2007.

The area is arid savanna, classified by Mucina and Rutherford (2006) as Gordonia duneveld. The river fringes are lined with riparian woodland, consisting primarily of *Acacia erioloba, Acacia haematoxylon*, *Acacia mellifera*, *Boscia albitrunca*, *Ziziphus mucronata*, *Rhigozum trichotomum* and the invasive *Prosopis glandulosa* (van Rooyen and van Rooyen, 1998; Mucina and Rutherford, 2006).

Data collection

Before 2002 the river along half of the farm was cleared of *P. glandulosa*, while the other half remained overgrown. The clearing was done as part of the Working for Water Programme, an initiative of the national Department of Water Affairs that aims to control alien plants through a combination of manual clearing, chemical control and biological control (River Health Programme, 2001). Four plots were layed out for the study. Each plot was 20 metres wide and 100 metres long. The invaded plots were densely overgrown with *Prosopis* spp. while there were no *Prosopis* spp. in the cleared plots. One of each was layed out along the riverbank while the other two cleared and invaded ones were layed out 300m inland from the river (Figure 4.2). In each plot six mature specimens of *A. erioloba* were identified and clearly labelled and in each of the invaded quadrants an additional six mature specimen of *P. glandulosa* were identified and marked. The labelled trees were sampled to determine significant differences among sites (riparian vs inland, invaded vs cleared) in water source, water stress, mortality and water use efficiency.

Samples were collected from April 2004 to April 2007 on six separate occasions during the hot and dry (November/December), hot and wet (March/April) and cold and dry (June/July) seasons.

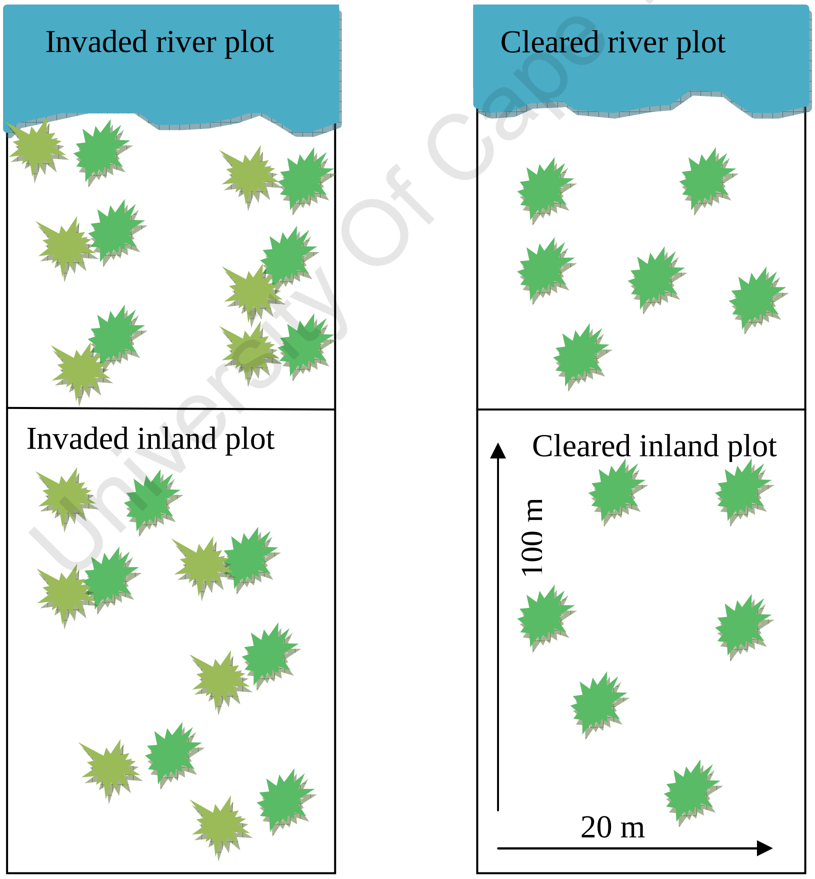


Figure 4.2: Diagrammatic representation of the four plots used in this study, all with stands of *A. erioloba* (dark green). Two were overgrown while two had been cleared of *P. glandulosa* (olive green).

Vegetation structure and vitality

Tree density

Tree density was determined for cleared as well as invaded areas on the farm. The objective was to show differences in tree density between cleared and invaded areas. For this purpose six transects were established, three transects in cleared and three in invaded areas. Each transect was 5 metres wide and 300 metres long, moving inland diagonally from the river. All along each transect mature trees were identified and recorded.

Percentage canopy dieback

Recent canopy dieback is an integrative measure of plant physiological condition (Horton *et al.,* 2001b). Canopy dieback is frequently reported as a physiological response to water stress (Stromberg *et al.,* 1992; Horton *et al.,* 2001b; Rood *et al.,* 2003). In April 2007 two observers scored canopy dieback on all *A. erioloba* trees at each site, estimating the percentage of dead material on each tree in comparison to foliage. Scores were made in 10% increments, with 0% dieback being very healthy and 100% dieback equating to a dead tree. The score average was recorded as the percentage canopy dieback for each tree.

Water source

Stable Oxygen and Hydrogen isotope ratios

The method has been described in detail in Chapter 3. In this chapter I use stable hydrogen and oxygen isotope ratios to determine the source waters of *A. erioloba* and *P. glandulosa* in all four plots.

On all six fieldtrips from April 2004 until November 2005 non-photosynthesising twigs (0.5 – 1 cm wide and 6 – 7 cm long) were collected at dawn from *A. erioloba* and *P. glandulosa* in each plot. Twigs were cut and immediately placed into a sealed borosilicate tube (Kimax – Kimble, New Jersey, USA), placed into a cooler box and frozen as soon as possible. Groundwater was collected every fieldtrip from three boreholes, located within a five-kilometre radius of the site. Depth to groundwater in each borehole was 27, 40 and 80 metres depth respectively (Ross-Gillepie, 2004, *pers. com.*). Soil samples at 50 cm were taken in April 2004, when rain had wetted the surface sufficiently to make augering possible. The samples were placed in double plastic bags, wrapped with masking tape and frozen as soon as possible. All rainwater was collected opportunistically from the rain gauge on the farm immediately after every rainfall event. All water was collected in 7ml vacutainers, the airtight lid was wrapped with Parafilm for extra protection from evaporation and samples were stored in a refrigerator.

All twig, soil, ground and rainwater samples were processed at the University of Cape Town (UCT) as described in Chapter 3. All isotopic values were expressed in standard delta notation relative to the V-SMOW (Vienna Standard Mean Ocean Water) standard (Dawson *et al*., 2002).

Plant moisture stress

Leaf stable carbon isotope ratios

Measurements of $\delta^{13}C$ values may usefully contribute to determine water use efficiency, which is the amount of carbon biomass produced per unit of water transpired by the crop (Farquhar *et al.,* 1989). Leaf $\delta^{13}C$ isotope ratios are an indicator of long-term intercellular carbon dioxide concentrations and thus of water use efficiency (WUE) in C_3 plants (Ehleringer and Cooper, 1988). $\delta^{13}C$ values are closely related to stomatal aperture, as carbon isotope ratios are partially determined by the ratio of CO_2 in the leaf intercellular air spaces relative to atmospheric CO_2 ratios (Ehleringer, 1993b). As stomata close when less water is available to the plant, the ratio between intercellular and atmospheric CO_2 increases and more of the heavier isotope from the intercellular CO_2 is used in carbon assimilation, resulting in more enriched $\delta^{13}C$ values (Farquhar *et al.,* 1989; Ehleringer, 1993b; Dawson *et al.,* 2002). Here I use the $\delta^{13}C$ values of both *P. glandulosa* and *A. erioloba* in all four plots to determine differences in plant available water with the clearing of the invasive *P. glandulosa*.

In April 2007 a total of twenty fully expanded, mature leaves were collected from each tree, picking from each cardinal direction. All samples were oven dried at 70˚C for 24 hours, ground to 1mm mesh with a hammer mill and subsampled to two milligrams. Samples were analysed for $^{13}C/^{12}C$ ratios on a Thermo Delta Plus XP Mass Spectrometer (Hamburg, Germany), coupled to a Thermo Finnigan Flash Elemental analyser. $\delta^{13}C/^{12}C$ isotope ratios are expressed relative to the Pee Dee Belemnite marine limestone standard (Craig, 1957).

Xylem Pressure Potentials

Xylem pressure potential (XPP) is a measure of a plants' water status or level of water stress. XPP indicates plant water demand by determining the tension that the water column is under in the plants' xylem tissue. Water is transported in xylem vessels along a negative pressure gradient (tension), from the water absorbing roots to the transpiring leaves of a plant (Tyree and Zimmermann, 2001; Koch *et al.*, 2004). The less water available to the plant, the greater the tension on the water column. XPP is an integrative measure of water availability and the environmental pressures placed on a plant including humidity levels, rainfall and temperature (Scholander, 1965). XPP measured before dawn indicates the water demand when the plant is in equilibrium with its environment, excluding photosynthetic or transpirational demand. XPP's are used here to show differences in water stress between *P. glandulosa* and *A. erioloba* in the four plots.

Predawn and midday XPP's were determined for two late wet seasons (April 2004, March 2005) and two early dry seasons (June 2004 and June 2005) and two late dry seasons (November 2004, November 2005). Predawn and midday XPP's were determined for all labelled trees using distal, healthy twigs in a Scholander pressure chamber (PMS Instrument Company, Corvallis, Oregon, USA).

Data analyses

All data are presented as means, unless otherwise stated. A p-value of $p < 0.05$ was required for significance in all tests. Differences for $\delta^{18}O$, $\delta^{2}H$, $\delta^{13}C$ isotopes and canopy dieback were assessed for statistical significance in Statistica 8.0, using Student T-tests and one-way ANOVA's with Tukey post hoc tests. The data was log transformed when assumptions of heterogeneity of variance and normality were not met. When transformations were unsuccessful, a non-parametric Kruskall-Wallis test was used. A level of significance of $p = 0.05$ was observed for all calculations. Repeated-measures ANOVA were used for predawn and midday XPP in SPSS, version 15.0. and as described in ACITS (1997). Time was used as the within-subjects factor and tree groups as the between-subject factors. The multivariate hypothesis testing approach (Wilks' Lambda test) was used throughout.

RESULTS

Vegetation structure and vitality

Tree density

P. glandulosa density was highest close to the riverbed (Fig 4.3), decreasing markedly with distance from the river. *A. erioloba* density in the cleared and invaded transects are highest immediately adjacent to the river. Cleared transects have another increase in *A. erioloba* at 300 metres from the river.

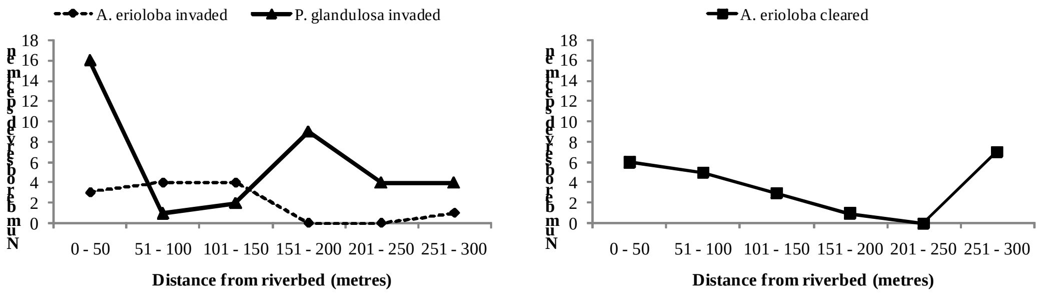


Figure 4.3: Number of mature specimens of *A. erioloba* and *P. glandulosa* trees observed in the (a) invaded and (b) cleared transects

Percentage canopy dieback

There was a significant difference in the amount of dead material on *A. erioloba* ($F_{3,20} = 5.3$, $p = 0.008$ One way ANOVA) between plots (Table 4.2). *A. erioloba* from the invaded river plot had almost twice as much dieback (66.7%) as *A. erioloba* in the other three plots (31.7% to 41.7%).

Table 4.2: Average percentage dead material on *A. erioloba* in the four plots (n = 6 per quadrant), standard error in brackets

Site	**Mean % dieback (±1 SE)**
A. erioloba cleared river	31.7 (7.0)
A. erioloba cleared inland	41.7 (7.7)
A. erioloba invaded river	66.7 (8.7)
A. erioloba invaded inland	31.7 (4.6)

Water source

Stable Oxygen and Hydrogen isotope ratios

Meteoric waters follow a Rayleigh distillation process that results in a linear relationship between $\delta^{18}O$ and $\delta^{2}H$ for water samples worldwide (Craig, 1961; Gat, 1996). This relationship is termed the global meteoric water line (GMWL) at a global scale and a local meteoric water line at the local scale (LMWL) (Craig 1961). The Gannavlakte local meteoric water line (LMWL: $\delta^{2}H = 6.1 * \delta^{18}O + 2.6$ ‰) plots below the global meteoric water line (GMWL), expressed as $\delta^{2}H = 8 * \delta^{18}O + 10$ ‰ (Fig. 4.4). Rainfall isotope values vary considerably ($\delta^{18}O = -6.9$ to 10.02 ‰) with values inversely correlated to rainfall amount ($\delta^{18}O$ $r^2 = 0.54$, $p = 0.0002$). Heavier rainfall events plot closest to groundwater.

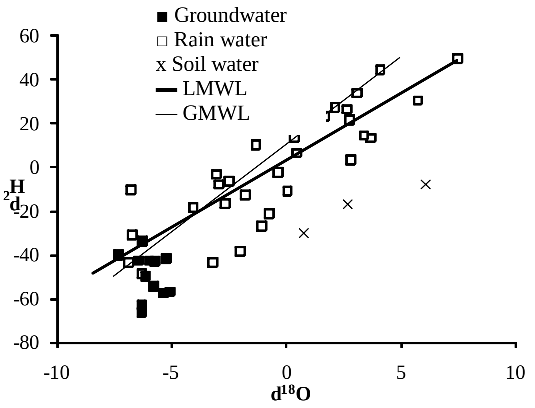


Figure 4.4: The relationship for δ^{18}O and δ^{2}H for all rainfall samples (n=32) from the study showing both the LMWL and GMWL. Soil core results (n=3) and groundwater isotope values (n=12) are superimposed.

The groundwater isotope values are consistent over time and across the three sampling boreholes (Fig 4.4). The three soil core values (0.5 metre depth) show isotopic enrichment, relative to rainfall isotope ratios. These values plot below the LMWL (Fig 4.4).

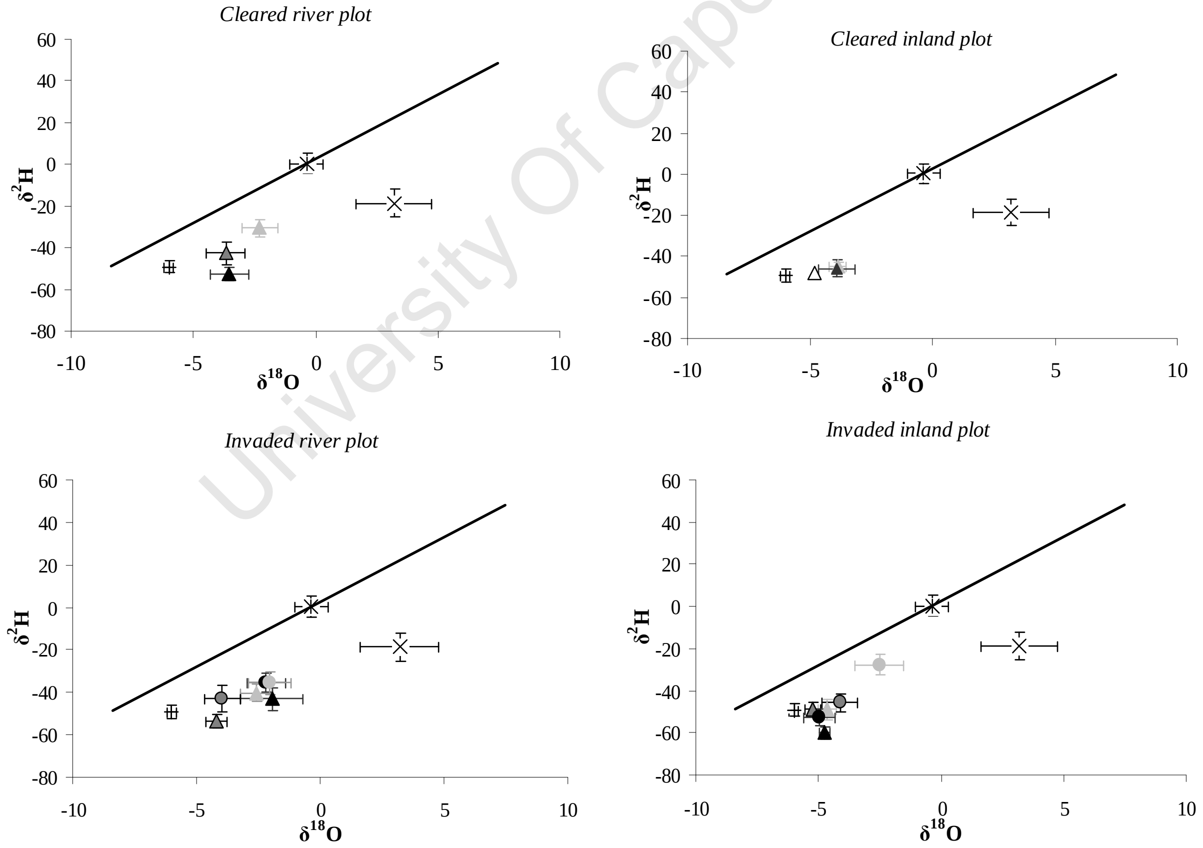


Figure 4.5: Average δ^{18}O and δ^{2}H values (± 1 SE) for source waters and tree waters at each plot. *A. erioloba* are depicted for the dry season (▲), start of the wet season (▲) and end of the wet season (▲) in all four plots. *Prosopis* are depicted in both invaded plots for the dry season (●), start of the wet season (●) and end of the wet season (●). Graphs include the local meteoric water line (—) as well as average soil (×), rain (Ж) and groundwater (+).

All isotope ratios for tree xylem water in the cleared river plot are located below the LMWL and intermediate between rainfall and groundwater (Fig 4.5). At the end of the wet season *A. erioloba* xylem water isotope ratios differ significantly from groundwater (Kruskall-Wallis nonparametric $\delta^{18}O$; $p < 0.001$). No significant differences in xylem water isotope ratios were found with season.

A. erioloba isotope ratios for water at the cleared inland plot (Fig. 4.5) are similar to dry season groundwater values. There are no significant differences in xylem isotope ratios with season.

Both *P. glandulosa* and *A. erioloba* xylem water isotope ratios in the invaded river plot (Fig. 4.5) differ significantly from groundwater in the wet season (Kruskall Wallis nonparametric $\delta^{18}O$; $p \leq 0.02$), but are not significantly different in the dry season.

In the invaded inland plot *A. erioloba* and *P. glandulosa* isotope ratios are similar to groundwater values (Fig. 4.5), except for *P. glandulosa* at the end of the wet season (Kruskall Wallis nonparametric $\delta^{18}O$; $p \leq 0.012$). *P. glandulosa* water isotope ratios at the end of the wet season are significantly different from groundwater and not significantly different from the rain.

Plant moisture stress

Leaf stable carbon isotope ratios

There were significant differences in $\delta^{13}C$ values between plots (One-way ANOVA; $p < 0.001$; Table 1 Appendix). *P. glandulosa* $\delta^{13}C$ isotope ratios are significantly more depleted than *A. erioloba* except in the invaded river plot (-24.99‰). The results for *A. erioloba* show significant differences in $\delta^{13}C$ values between cleared (-26.25‰), invaded (-24.99‰) river plots. There are however no significant differences between cleared and invaded inland plots for *A. erioloba*. There are also no significant differences in $\delta^{13}C$ values for *P. glandulosa* invaded river and inland plots.

Table 4.3: Average δ^{13}C values with standard error (± 1 SE) in brackets and number (N) of specimen sampled for all four plots

Quadrant and species	**δ ^{13}C (‰)**	**N**
A. erioloba cleared river	-26.09 (0.26)	6
A. erioloba cleared inland	-26.25 (0.18)	6
A. erioloba invaded river	-24.99 (0.24)	6
A. erioloba invaded inland	-26.09 (0.29)	6
P. glandulosa invaded river	-24.17 (0.18)	6
P. glandulosa invaded inland	-24.86 (0.33)	6

Xylem pressure potentials

The predawn XPP values for all inland plots are stable across seasons, compared to the river plots (Figure 4.6). The minimum-maximum ranges for inland plots (*A. erioloba* cleared inland -0.88MPa; *P. glandulosa* -0.75 MPa and *A. erioloba* invaded inland – 0.43 MPa) are all smaller than for the river plots (*A. erioloba cleared* river - 0.89 MPa; *P. glandulosa* – 1.52 MPa and *A. erioloba* invaded river – 1.25 MPa).

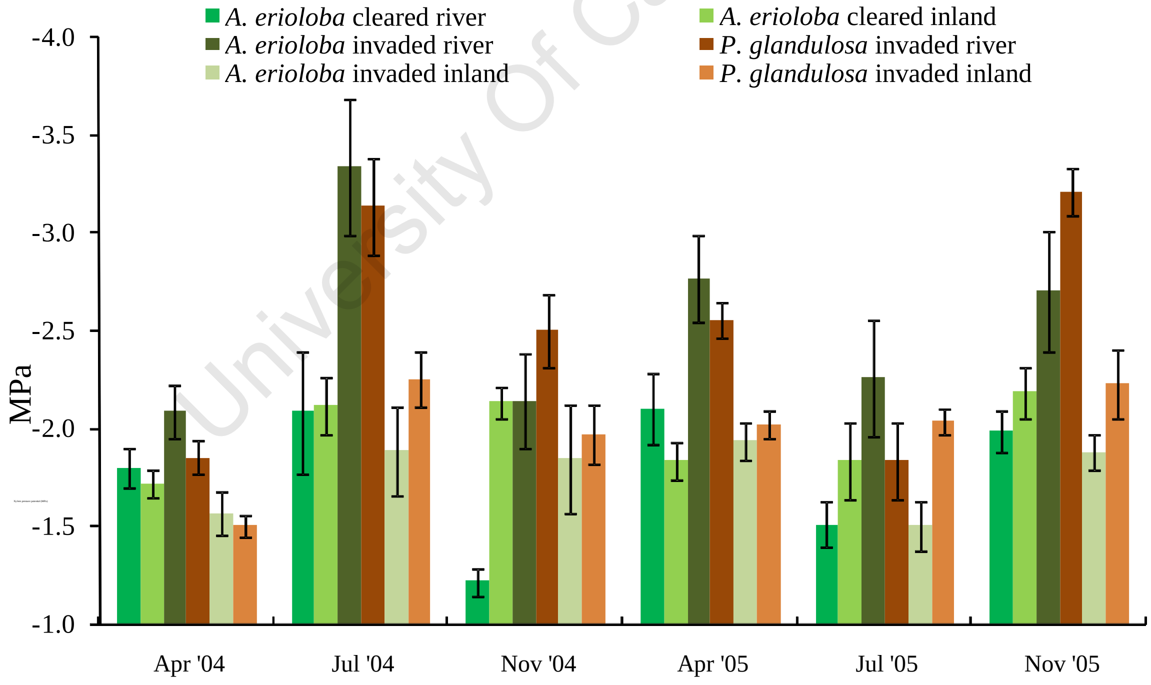


Figure 4.6: Average (n=6) predawn xylem pressure potential (MPa) for cleared river and inland *A. erioloba*, invaded river *A. erioloba* and *P. glandulosa* and for invaded inland *A. erioloba* and *P. glandulosa*. Predawn values from April 2004 late wet season to November 2005 early wet season.

The between-subject test (Repeated measures ANOVA) shows significant differences between tree stands ($F_5 = 10.1$, $p < 0.001$; Tables 2 and 3 Appendix). Both *P. glandulosa* and *A. erioloba* of the invaded river plot have significantly more negative predawn XPP than all other tree groups (Tukey post hoc; $p < 0.001$).

DISCUSSION

My results show that *A. erioloba* is significantly more water stressed in the riparian zone when *P. glandulosa* is present, but not in the invaded areas further inland. The two species use the same water source when growing together in the riparian zone, but water sourcing differs between the two species further inland with *P. glandulosa* using a more shallow water source than *A. erioloba*.

Verhagen (1983) and Meyer *et al.* (1985) both describe how pans and depressions in the riverbed collect water and act as recharge zones. They discussed this in the context of flood events, but my personal observation is that rainwater runoff also accumulates along depressions in the riverbed. Rainwater stands in these depressions for several days, allowing isotopic enrichment through evaporation before infiltration. This is directly reflected in the river plot water isotope results (Figs 4.4, 4.5) and in the isotope ratios of soil water and the xylem water of both *A. erioloba* and *P. glandulosa* in the invaded and cleared river plots. Both species use this shallow water while it is available and increase groundwater use towards the end of the dry season as the shallow soil water supply is depleted. *A. erioloba* and *P. glandulosa* thus have the same water use strategy at the invaded river plot and *A. erioloba* has the same water use strategy at both river plots. Much greater groundwater dependence is observed for *A. erioloba* at both inland plots. The consistent deep rooting and groundwater dependence of inland *A. erioloba* is in agreement with the literature (Obakeng, 2007), while the flexible water uptake of riparian *A. erioloba* is similar to the results in Chapter 3. *P. glandulosa* at the invaded inland plot does consistently make use of directly infiltrating rainwater in the wet season (Fig. 4.5), switching to groundwater at the end of the dry season. This dual water uptake has also been reported for *P. velutina* in the USA (Snyder and Williams, 2003) and is in agreement with the dual root system descriptions of previous studies (Snyder *et al.*, 1998). As a result *P. glandulosa* and *A. erioloba* in the invaded inland plot only share groundwater resources at the end of the dry season. The water source findings are summarised and illustrated in Figure 4.7.

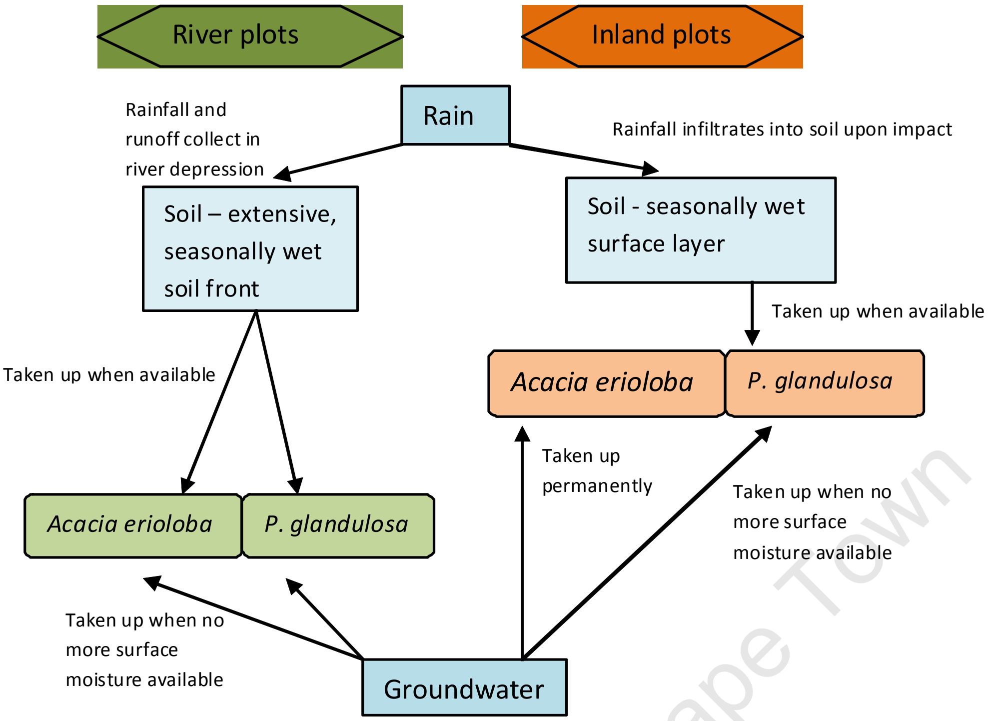


Figure 4.7: Conceptual diagram to summarise and illustrate the research findings and our current assumptions of seasonal water uptake

Desert plants are generally characterised by δ^{13}C values of around -20 to -25‰ (Ehleringer, 1993a; Rundell and Sharifi, 1993). The *A. erioloba* δ^{13}C values for both cleared as well as the invaded inland plots fall just outside the published desert plant δ^{13}C value range with -26.09 to -26.25‰. Two unpublished *A. erioloba* δ^{13}C isotope studies reported values between -25.3‰ and -28.2‰ in the Namib and -22‰ to -27‰ in the Kalahari (Robertson and Woodborne, 2000; Woodborne, 2004 *unpublished report*). The significant differences in leaf δ^{13}C values found between invaded river *A. erioloba* (-24.99‰) and the remaining three plots of this study (Table 4.3) show that *A. erioloba* in that particular plot is under more water stress than any of the other study plots. This directly complements the δ^{18}O and δ^{2}H findings of the invaded river plot that *P. glandulosa* and *A. erioloba* use the same water sources. In Woodborne's unpublished Kalahari study (2000) mortality of *A. erioloba* occurred at around –22.5‰, while *P. glandulosa* still survived at values up to –20.5‰. Based on these earlier results *A. erioloba* in the invaded river plot are approaching a lethal water stress level, which is mirrored by the high canopy dieback (Table 4.2) as well as the significantly higher XPP levels (Fig. 4.6). Hence all measurements, δ^{13}C, canopy dieback and XPP support my hypothesis at the invaded river plot that *A. erioloba* is significantly more stressed. The hypothesis is not correct however for the invaded inland plot, as $\delta^{13}C$, canopy dieback and XPP measurements are similar to the results of *A. erioloba* at the two cleared plots.

The same water uptake, observed for *A. erioloba* in the invaded plots, is also occurring for *A. erioloba* at both control plots (cleared river and inland plot). The results suggest that *A. erioloba* has a natural shift in water source uptake with increasing distance to the river. This uptake pattern does not change in the presence of *P. glandulosa* and it leads to a distinctly similar water uptake at the invaded river plot and a distinctly different one at the invaded inland plot. Similar findings of niche partitioning among species and locations occurred for exclusively riparian species along floodbanks (*Melaleuca argentea*) versus top-bank species (*Corymbia bella*) in Australia (O'Grady *et al.*, 2005). In my study, *P. glandulosa* use the same water resources as the indigenous *A. erioloba* in the riparian corridor of the Kuruman River, while $\delta^{13}C$ values, XPP results and canopy dieback show that this creates significant water stress for *A. erioloba*. It suggests that there is competition for water between the two species within the riparian zone. However, increased water stress for *A. erioloba* in invaded areas does not extend beyond the river fringe. *A. erioloba* switches from dual water uptake in the riparian zone to deep groundwater use inland, while *P. glandulosa* continues its dual water uptake inland, using shallow water when available and switching to groundwater in the dry season. It suggests that the two species coexist at the inland plot by taking up water from different sources. The conclusion of this chapter is that it is very likely that *A. erioloba* dies from water competition with *P. glandulosa* along riparian zones of ephemeral rivers in Southern Africa, but that resource partitioning occurs between the two species further away from the active river channel.

CHAPTER 5: COMPARING HYDRAULIC ARCHITECTURE – DO RIPARIAN SPECIES IN SOUTHERN AFRICAN DESERTS DIFFER IN THEIR TOLERANCE TO REDUCED WATER AVAILABILITY?

INTRODUCTION

At Gobabeb in the Namib, the groundwater table dropped by three metres during a natural drought period from 1979 to 1984. Mortality rates of about 62% for *F. albida*, of 29% for *A. erioloba* and 24% for *T. usneoides* were recorded (Theron *et al.,* 1985). In the Kalahari *A. erioloba* dies off in the presence of *Prosopis* spp., due to increased water stress (Chapter 4). The common observation in both areas is that all riparian tree species are not equally affected by drought. Similarly, reduced water access along rivers in the USA resulted in a shift of species abundance and distribution (Nilsen *et al.,* 1984; Stromberg *et al.,* 1996), suggesting that species do not have the same levels of drought tolerance. Plant adaptation and tolerance to drought is a complex phenomenon that differs among desert phreatophytes (Nilsen *et al.,* 1984) and has been widely investigated among woody species (Franklin *et al.,* 1987; Mencuccini and Comstock, 1997; Hacke *et al.,* 2000; Hacke *et al.,* 2001; Horton *et al.,* 2001b; Sperry *et al.,* 2002; Xu *et al.,* 2007; McDowell *et al.,* 2008). Great rooting depth (Nilsen *et al.,* 1984) and rapid root growth are typical survival methods observed among groundwater-dependent species (Hacke *et al.,* 2000) and these were addressed for Namib and Kalahari trees in Chapters three and four of this thesis. But trees also cope with drought through a number of physiological traits and responses including narrowed vessel diameter, increased wood density and protection from xylem cavitation through stomatal control (Hacke *et al.,* 2000; Sperry *et al.,* 2002; Jacobsen *et al.,* 2007; Li *et al.,* 2009). This chapter contains a comparative study of such hydraulic traits to add insight into levels of drought tolerance among species. I compare some xylem physiology of *A. erioloba*, *F. albida* and *T. usneoides* in the Namib, as well as *A. erioloba* and *P. glandulosa* in the Kalahari, to determine whether there are structural explanations to observed differences in drought tolerance.

Xylem consists of an assemblage of vessels embedded in structurally supporting fibres. Adjacent vessels are connected by pit membranes and pit pores, through which water flows between vessels, thus forming a network of interconnected water transporting conduits (Bailey, 1916; van der Willigen, 1996; Tyree and Zimmermann, 2001). Pits have a bordered structure for support and a large, porous membrane area that allows water movement, but that is impermeable to air when functional (Tyree and Zimmermann, 2001). For a plant, water transport through xylem is necessary to replace water lost during transpiration, preventing desiccation and allowing photosynthesis (Li *et al.*, 2009). The cohesion-tension theory of sap ascent postulates that water is pulled up through xylem vessels along a negative pressure gradient (tension), with transpiration, surface tension and water adhesion to cell walls providing the necessary force to lift water from the soil to the leaves of a plant (Scholander *et al.*, 1961). Tension in the water column, also termed xylem water potential (Ψ, or XPP), increases with transpiration and with decreasing soil water availability (Tyree and Zimmermann, 2001; Koch *et al*., 2004). Drought conditions are associated with long-term increases in Ψ (Lopez *et al.*, 2005). There is strong evidence to suggest that increased Ψ causes cavitation in the xylem conduits by the replacement of functional conduit water with air (Zimmermann, 1983; Sperry and Tyree, 1990; Cochard and Tyree, 1990; Lopez *et al.*, 2005). Such cavitation interrupts water flow, inhibiting the plants ability to transpire and photosynthesise (Li *et al.*, 2009). How much tension xylem vessels can take before they cavitate depends primarily on the pore sizes of the intervessel pit membranes, as claimed by Zimmermann's (1983) air-seeding hypothesis. Numbers of intervessel pits and associated cavitation risks reduce proportionally with vessel size, thus enabling smaller vessels to withstand greater Ψ in dry conditions (Tyree and Sperry, 1989; Hargrave *et al.*, 1994; Tyree and Zimmermann, 2001; Sperry *et al.*, 2006). Vessel diameter does correlate positively with rainfall and has frequently been used to infer levels of drought tolerance (Baas, 1976; Carlquist, 1977; February *et al.*, 1995; Lo Gullo *et al.*, 1995; Hargrave *et al.*, 1994; Hacke *et al.*, 2000; Martinez-Vilalta *et al.*, 2002; Schume *et al.*, 2004). Another factor significantly correlated to drought tolerance is xylem density, which increases with reduced vessel diameter and increased vessel wall thickness (Hacke *et al.*, 2001; Jacobsen *et al.*, 2007).

Along with structural adaptations, plants exhibit varying degrees of stomatal control to avoid damaging levels of Ψ (Sperry *et al.*, 2002). Isohydric plants shut their stomata at threshold Ψ, thus controlling transpiration and inhibiting photosynthesis. Anisohydric plants, on the other hand, keep stomata open and continue to transpire and photosynthesise at the risk of incurring xylem cavitation (Tardieu and Simonneau, 1998).

In this chapter I test the hypothesis that riparian trees exhibit differences in xylem structure and drought tolerance levels. I use commonly occurring riparian trees growing along ephemeral rivers in the arid Southern African areas for that purpose. I determine the vulnerability to cavitation of xylem tissue, average xylem vessel diameter and wood density. Xylem pressure potentials and diurnal depression rates as described in González Rodríguez *et al*. (2000) are applied to determine water stress and to infer levels of stomatal control.

MATERIALS AND METHODS

Study area

The study was conducted at Gobabeb (23º33'726 S – 15º02'112 E) in the Namib Naukluft Park in Namibia and on the farm Gannavlakte (26º57'578 S - 21º50'234 E) just south of the Botswana border in South Africa. Gobabeb is located in the hyperarid parts (average 21 mm/annum) of the Namib, along the lower reaches of the Kuiseb River. An average of 1.45 Mm^3 flows past Gobabeb in one or two annual flood events (Namibian Water Resources Management Review, 2000; Moser, 2006). Gobabeb has an average groundwater depth of four metres and key riparian species around Gobabeb are *Faidherbia albida*, *Acacia erioloba, Tamarix usneoides*, *Euclea pseudebenus* and *Salvadora persica* (Theron *et al.*, 1985; Jacobson *et al.*, 1995; Jacobson, 1997). The average maximum and minimum temperatures for Gobabeb are 30.5ºC and 13.2ºC respectively. Average annual rainfall and fog precipitation at Gobabeb are 27 mm and 31 mm respectively (Lancaster *et al.*, 1984).

Gannavlakte is located along the Kuruman River in the semi-arid Kalahari, classified as Gordonia Duneveld (Mucina and Rutherford, 2006). The river fringes are lined with woody species, consisting primarily of *Acacia erioloba*, *Acacia haematoxylon*, *Acacia mellifera*, *Boscia albitrunca*, *Ziziphus mucronata* and *Rhigozum trichotomum* and the invasive *Prosopis glandulosa* (Dean *et al.*, 1999; van Rooyen *et al.*, 2001). Gannavlakte receives an average summer rainfall of 290 mm (van Rooyen *et al.*, 2001). Average minimum and maximum temperatures are 13.2ºC and 31.3ºC respectively. The Kuruman River last flowed past Gannavlakte in 1996 (Ross-Gillesby, 2004, *pers. com.*) and groundwater levels lie at 56 metres depth. A full description and depiction of the study sites is given in Chapter 2.

The study was conducted from June 2004 to August 2007. Measurements were taken on six adult *A. erioloba*, *F. albida* and *T. usneoides* specimens along a one-kilometre stretch of the Kuiseb River at Gobabeb and six adult *A. erioloba* and *P. glandulosa* specimens along a 100-metre stretch of the Kuruman River that has been densely overgrown with *P.glandulosa*.

Xylem pressure potential

Xylem Pressure Potentials (XPP) were determined for two flood seasons (April 2005, March 2006), two dry and early dry seasons (June 2004 and June 2005) and two late dry seasons (November 2004, December 2005) using a Scholander pressure chamber (PMS Instrument Company, Corvallis, Oregon, USA). Predawn (Ψ_{PD}) and midday XPP's (Ψ_{MD}) were determined for six specimens per species at each location. Distal, healthy twigs were sampled before dawn and again at midday.

The XPP data is first plotted as Ψ_{PD} against Ψ_{MD} and then again as Ψ_{MD} against diurnal depression (Ψ_{MD} - Ψ_{PD}) as set out in Ritchie and Hinckley (1975). Predawn XPP is a reliable indicator of the maximum soil water potential to which the roots of the plant are exposed, as it reflects the equilibrium between soil and plant water potentials in the absence of water flux (Tardieu and Simonneau, 1998; Brodribb and Holbrook, 2005). Plants growing in soil with decreasing water have increasingly negative predawn XPP. Midday XPP reflects soil water potential as well as daily fluctuations following evaporative demand and stomatal opening (Tardieu and Simonneau, 1998). Diurnal depression (Ψ_{MD} - Ψ_{PD}) is a good measure for maximal diurnal stress plants experience and it can be used to identify isohydric or anisohydric plants and it can be used to show a plant's ability to recover from daily water stress. A combination of very negative Ψ_{MD} and a small diurnal depression indicate severe plant water stress (González Rodríguez *et al*., 2000).

Vulnerability to cavitation

Understanding the dynamics of the onset of water conduction failure is of crucial importance for determining drought resistance strategies by plants (Lo Gullo and Salleo, 1991). Vulnerability to drought- induced xylem cavitation can be defined as the relationship between XPP (Ψ) and xylem embolism. This can be expressed as a 'vulnerability curve', which is percentage loss of hydraulic conductance (PLC) plotted against the XPP that induced that loss of conductivity (Ψ) (Tyree and Sperry, 1989; Sperry and Hacke, 2002). A plant vulnerable to water stress reaches complete cavitation at much lower XPP than a resistant one. On the vulnerability curve this will plot as a steeper curve for a sensitive than a more tolerant plant (Pammenter and Vander Willigen, 1998). Vulnerability curves provide graphic information about species' sensitivity to drought, thus allowing easy interspecific comparisons and predictions of how plants will fare in drier conditions (Hacke *et al.*, 2000; Pockman and Sperry, 2000; Martinez-Vilalta *et al.*, 2002). Hacke *et al.* (2000) showed that co-occurring desert species differed in cavitation resistance based on their rooting depth and vegetative phenology. The co-occurring species of this study are all phreatophytes, but they do differ in phenology and their maximum rooting depth. Hence vulnerability curves were drawn up for each species, to show significant differences in cavitation.

The vulnerability curves were constructed from hydraulic measurements, using six to nine samples per species. Straight stems 0.6 to 1.2cm wide were located in the field, and cut off as long as possible (ideally > 100cm) on either side as possible. In very branched and thorny species appropriate branches were rare, thus sampling could not be restricted to tagged specimens. Cut ends of samples were immediately moistened with wet tissue paper and tied up with plastic bags. The whole sample was then wrapped in black plastic bags and clingwrapped as tightly as structure allowed, placed into a coolbox and transported to the laboratory within 24 hours. Here, xylem conductivity was measured using a modification of the protocol described by Sperry *et al.* (1988). Branch sections were cut back with a razor blade under water to 14.2cm. Cutting under water ensured no further embolisms were introduced. To get maximum conductivity k_{max}, stems were connected to a tubing system and flushed for an hour with deionised, degassed, filtered (1.2µm), water (pH 2 HCl) at 150 kPa to remove all embolisms. Hydraulic conductivity (k_{max}) was then measured gravimetrically on each stem segment (Sperry *et al.*, 1988) using a four-point analytical balance (Sartorius). Stems were connected to the system and hydraulic conductivity was calculated as the mass flow rate of water ($g\ s^{-1}$) through the segment divided by the pressure gradient (<1 kPa). Mass increments (read off every ten seconds) were converted into a volumetric measure ($cm^2\ s^{-1}$) taking temperature into account.

After k_{max}, loss in conductivity was determined using the centifuge technique (Alder *et al.*, 1997). Stems were loaded into a custom-fitted centrifuge and spun for four minutes at speeds corresponding to specific XPP's. Between spins stems were placed back into solution for several minutes before measuring k_h. Stems were spun at increasingly higher speeds and remeasured, until k_h equaled zero.

In order to validate the results of the centrifuge method, the flow meter was transported to Gobabeb and branches of *T. usneoides* (n = 4) were bench-dried, using a modification of the protocol as described in Cochard and Tyree (1990). Long branches (~200cm) were cut predawn, wrapped in black plastic bags, the cut stem end was tied into a wet plastic bag and everything was brought back to the field laboratory immediately. Field XPP of the branch was determined with a Scholander pressure chamber and a segment was cut from the branch under water. Both the segment length (~14cm) and width (0.6 – 1.5 cm) remained comparable to the stem dimensions in the centrifuge method. k_{field} was determined and the segment was flushed and re-measured to obtain k_{max}. Meanwhile the branch dried on the bench, permanently covered in black plastic bags to avoid rapid desiccation in the low atmospheric humidity (< 10%). The cut end of the stem was kept wet at all times and excess plant material (> 10 cm) between segment cuts reduced the risk of artificial air embolisms. As soon as branch XPP increased by about –1 Mpa, another segment was cut, measured, flushed and remeasured for k_{max}, until branch k_h equaled zero.

PLC was calculated from $100(1-k_i/k_{max})$, where k_{max} is the maximum conductivity determined after initial flushing and k_i is the respective conductivity at increasing XPP (Tyree and Zimmermann, 2001). Subsequently, a Weibull function was fitted to the data to describe the relationship of percent loss of conductivity and XPP. The function is given as:

$$PLC = 100 – 100 / \exp(-\Psi_{xylem} / b)^{c}$$

Where *b* and *c* are parameters representing the shape and slope of the curve. Parameter *b* indicates XPP (Ψ) at which 63% loss of conductivity is incurred and *c* determines the curve slope at point *b* (Lopez *et al.*, 2005; Li *et al.*, 2009). Xylem pressure potential at 50% (P_{50}) and 95% (P_{95}) loss was calculated, based on the Weibull fit (Table 5.3).

Vessel diameters

Vessel diameter has the largest effect of all on hydraulic conductivity (k_h) (Tyree and Ewers, 1991). According to Poiseuille’s equation, hydraulic conductivity is proportional to the fourth power of the vessel radius (Tyree and Zimmermann, 2001). The contribution of one large vessel, four times the relative size (4) of another (1), will contribute 4^4=256 times the amount of water (Tyree and Ewers, 1991; February, 1994; Tyree and Zimmermann, 2001).

Xylem dimensions have been suggested as being positively related to the vulnerability of xylem to cavitation (Zimmermann, 1983; Tyree and Sperry, 1989; Lo Gullo *et al.*, 1995; Hargrave *et al.*, 1994; Hacke *et al.*, 2000; Tyree and Zimmermann, 2001). Some studies could not confirm this positive relation between species, but they have stated it to be true for vessels within species (Tyree and Dixon, 1986). A general trend in diameter of plant conduits is that of wide conduits occur in wet and moist climates and small ones occur in cold and/or dry environments (February *et al.,* 1995; Gillespie *et al.,* 1998). Measurement of vessel diameter is thus a useful and widely applied method for estimating drought tolerance (Lo Gullo *et al.,* 1995; Hargrave *et al.,* 1994; Hacke *et al.,* 2000; Martinez-Vilalta *et al.,* 2002).

Following hydraulic conductivity measurements, six twigs per species were used to determine the conduit diameter of xylem vessels. Sections (20-30 microns thick) of each twig were cut using a Reichert-Jung base sledge microtome. The sections were stained for ten minutes in safranin red, cleaned with a glycerine/glycerol solution and mounted on glass slides. Wedge-shaped sections, large enough to count 100 vessels (Jacobsen *et al.,* 2007) were photographed (3.2 Megapixel Sony X1R) under a microscope at 40x magnification (Leitz Laborlux K, Germany). Vessel lumen diameter was determined for one hundred vessels per stem, using the computer software Sigma Scan Pro 5.0.

Wood density

Wood density is an indicator of xylem traits that relate to water stress tolerance, such as P_{min}, vessel area and percentage fibre wall (Jacobsen *et al.,* 2007). Wood density has been used to predict the impact of climate change on plants (ibid) and to compare water stress tolerance among desert plants (Hacke *et al.*, 2000). Seven twigs per species were cut in the field (10cm long and 0.7 cm diameter) and transported back to the laboratory frozen. There, they were saturated in degassed water for 24 hours, in order to obtain maximum weight (Jacobsen *et al.,* 2007). Twigs were cut to a length of 2.5 cm and the pith and bark were removed with a razor blade. Wood volume was determined by displacement in a graduated cylinder (Jacobsen *et al.,* 2007). The wood was then oven dried for 24 hours at 75 ºC and the dry weight was determined. Wood density is expressed as g cm^{-3}.

Data Analysis

Differences for xylem pressure potentials, vulnerability curves, vessel diameter and vessel density were assessed for statistical significance using paired t-tests in the case of two samples and one-way ANOVA with Tukey post-hoc tests in the case of multiple samples. The data were log transformed when assumptions of heterogeneity of variance and normality were not met. When transformations were unsuccessful, a non-parametric Kruskall-Wallis test was used. Simple correlations were run between datasets. All data is presented as mean (± 1 SE), unless otherwise noted. A p-value of $p < 0.05$ was required for significance in all tests. Tests were performed in Statistica 8.0.

RESULTS

Xylem Pressure Potentials

Predawn xylem pressure potentials (Ψ_{PD}) are all similar for Gobabeb *A. erioloba*, *F. albida* and *T. usneoides*. Similarly, the Gannavlakte Ψ_{PD} for *P. glandulosa* and *A. erioloba* are similar (Fig. 5.1a). All three Gobabeb trees are significantly less stressed for Ψ_{PD} than the two Gannavlakte trees (Kruskall-Wallis Nonparametric test; $p < 0.001$; Table 4a in Appendix).

The trees growing at Gobabeb plot out separately for Ψ_{MD} and diurnal depression ($\Psi_{MD} - \Psi_{PD}$) from Gannavlakte trees (Fig. 5.1b). Both Gannavlakte *A. erioloba* and *P. glandulosa* are significantly more stressed over midday than *A. erioloba*, *F. albida* and *T. usneoides* at Gobabeb (One way ANOVA; $p < 0.001$; Table 4b in Appendix). Gobabeb *A. erioloba*, *F. albida* and *T. usneoides* all differed significantly from each other in Ψ_{MD} (Tukey post hoc test; $p < 0.001$), with *F. albida* having the least negative Ψ_{MD}. In terms of diurnal depression, Gannavlakte *P. glandulosa* and *A. erioloba* as well as Gobabeb *F. albida* had similar low values (-1.15 to -1.34 Mpa). *T. usneoides* (-1.83 Mpa) had a significantly higher diurnal depression than all other trees (Kruskall Wallis nonparametric; $p \leq 0.02$; Table 4c in Appendix) except Gobabeb *A. erioloba*.

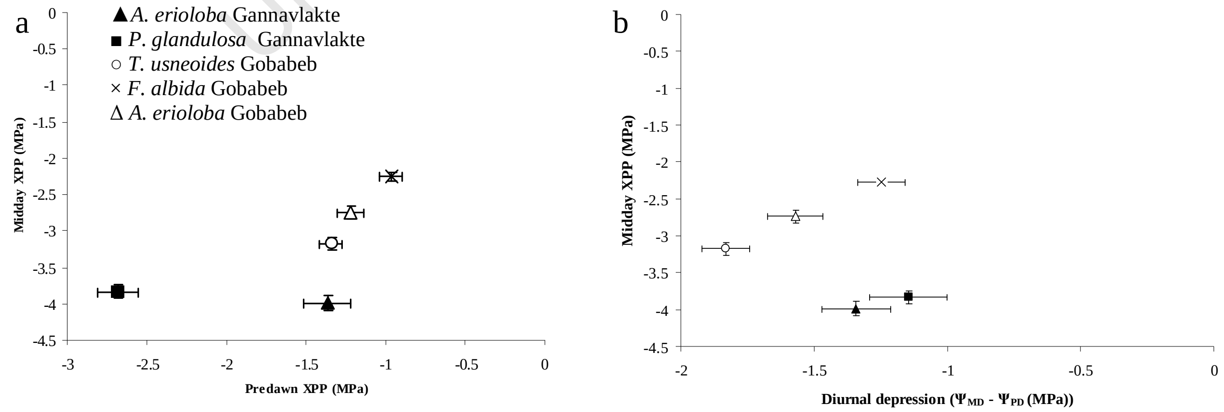


Figure 5.1: Plot of total (a) average predawn xylem pressure potential (Ψ_{PD}) for each tree group against midday xylem pressure potential (Ψ_{MD}) and (b) plot of midday xylem pressure potential (Ψ_{MD}) for each tree group against diurnal depression ($\Psi_{MD} - \Psi_{PD}$)

Vulnerability to cavitation

All vulnerability curves are steep, suggesting very high vulnerability to cavitation. As a comparison with the centrifuge method, an additional four *T. usneoides* samples were bench dried (Fig. 5.2). The two methods produce equally steep curves.

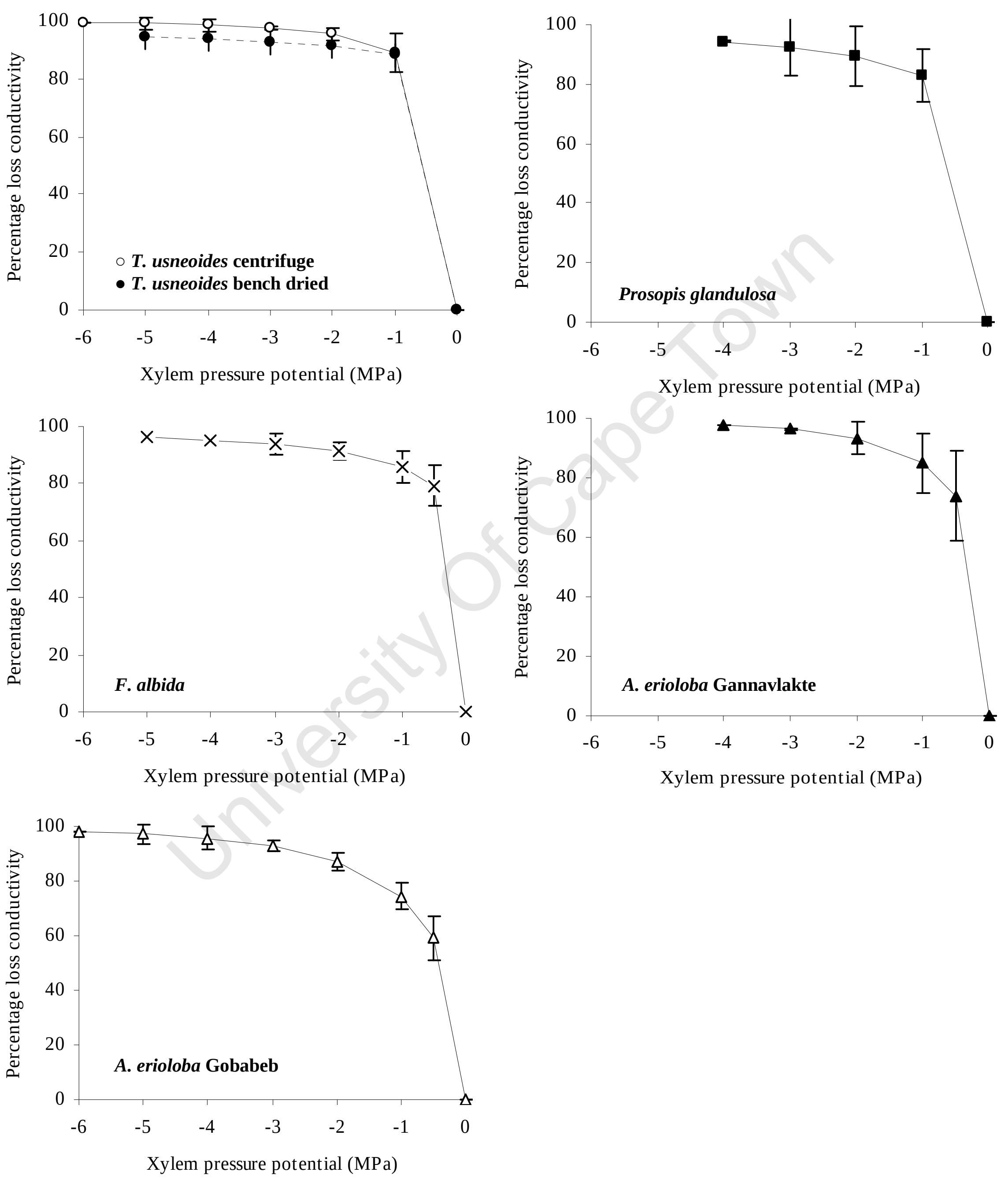


Figure 5.2: Vulnerability of xylem to cavitation for *T. usneoides* (n = 4 centrifuge and n = 4 bench drying), *P. glandulosa* (n=6), *F. albida* (n=7), *A. erioloba* Gannavlakte (n=6) and *A. erioloba* Gobabeb (n=7), presented as % loss of conductivity with decreasing XPP.

The curve shape (Fig. 5.2) and P_{50} values (Table 5.1) show that *A. erioloba* from Gobabeb is marginally more cavitation resistant than the other trees, having the least steep curve and the lowest P_{50} value. This is followed by *A. erioloba* at Gannavlakte, making *A. erioloba* the most cavitation resistant species. The slope steepness and rapid loss of conductivity creates high variation in the P_{95} values, particularly evident between the two *T. usneoides* curves, despite their similar appearance (Table 5.1).

Table 5.1: Xylem pressure potential at 50% and 95% hydraulic conductivity as defined by the Weibull function as well as minimum midday XPP (P_{min})

Species	**n**	P_{50}	P_{95}	***b***	***C***	**Midday P_{min}**
T. usneoides centrifuge	4	-0.08	-1.9	0.18	0.47	-3.5
T. usneoides bench dried	4	-0.01	-6.12	0.02	0.19	-3.5
F. albida	7	-0.03	-3.8	0.12	0.32	-2.4
A. erioloba Gobabeb	7	-0.3	-3.7	0.6	0.6	-3.3
P. glandulosa	6	-0.07	-4.6	0.195	0.35	-4.0
A. erioloba Gannavlakte	6	- 0.13	-2.5	0.28	0.5	-3.9

Vessel diameter

Average vessel diameters differ significantly between species (One way ANOVA analysis $F_{4,25} = 24.4$, $p < 0.001$: Table 5.2). Gannavlakte *A. erioloba* has the smallest xylem vessels, their diameters differing significantly from those of *P. glandulosa*, Gobabeb *A. erioloba* and *F. albida* ($p < 0.02$). *F. albida* has the largest xylem vessels and their diameters differ significantly from Gannavlakte *A. erioloba*, *P. glandulosa* and *T. usneoides* ($p < 0.001$: Table 5.2).

Table 5.2: Average vessel diameter µm (± 1 SE) of (n = 6) stem cross- sections per species. Post-hoc results in Table 5 of Appendix

Species	**Vessel diameter (µm)**
T. usneoides	32.81 (0.39)
F. albida	51.75 (0.85)
A. erioloba Gobabeb	46.05 (0.79)
P. glandulosa	38.08 (0.66)
A. erioloba Gannavlakte	29.00 (0.52)

Mounted stem cross-sections for each of the species (Fig. 5.3) show that all except *P. glandulosa* are diffuse porous, meaning that vessels are spread randomly across the xylem. *P. glandulosa* is drought-deciduous over dry winters (June/July), going dormant by late April and sprouting around September, putting down a new layer of xylem. As a result, it is the only one of the study species with a ring-porous xylem structure (Fig. 5.3b). The two *A. erioloba* cross-sections (a, c) differ significantly in vessel diameter (Table 5.2). Gannavlakte *A. erioloba* (a) has conspicuous bands of lignified cells surrounding its xylem vessels, which the Gobabeb specimen (c) does not display to the same degree (see arrows).

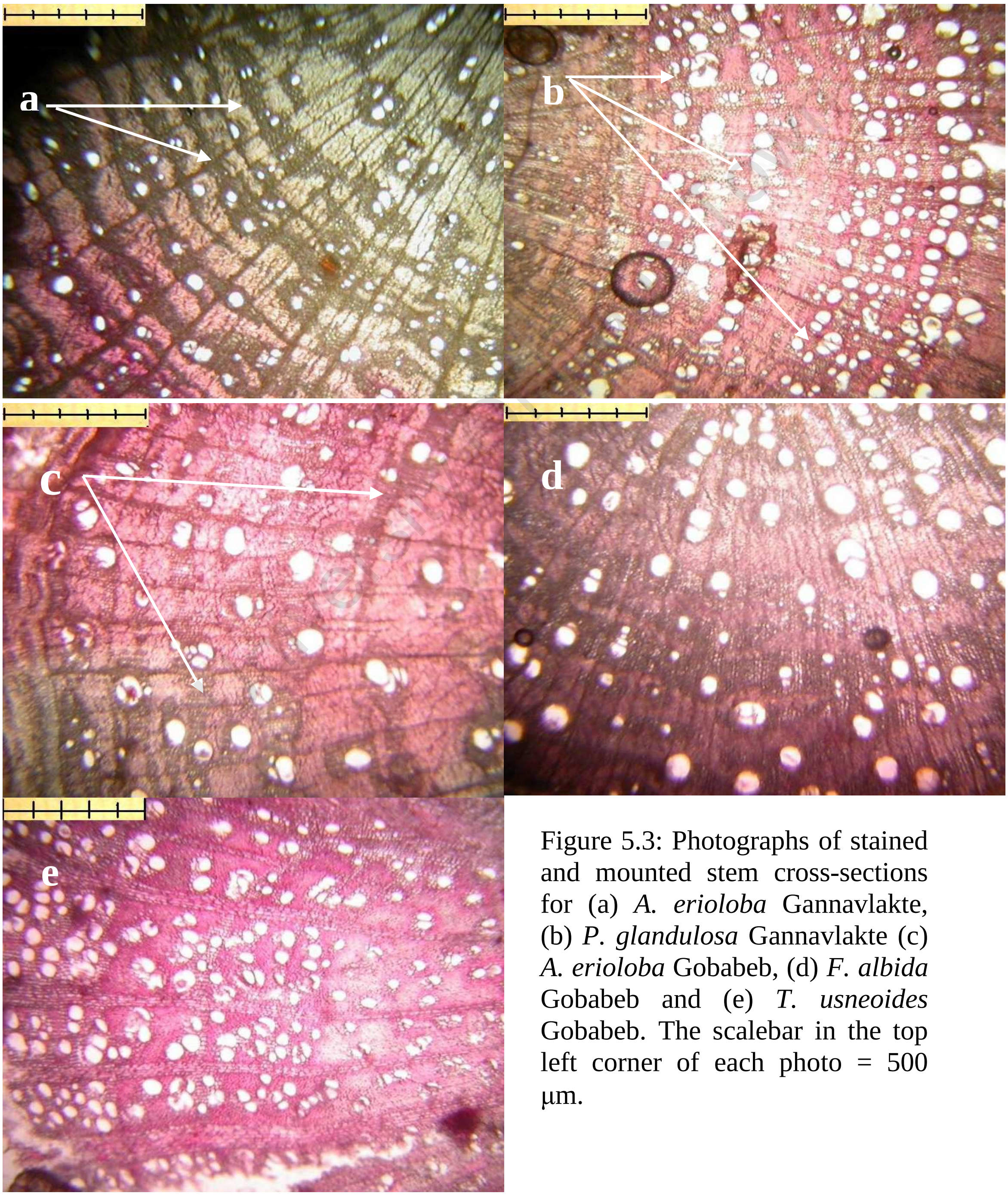


Figure 5.3: Photographs of stained and mounted stem cross-sections for (a) *A. erioloba* Gannavlakte, (b) *P. glandulosa* Gannavlakte (c) *A. erioloba* Gobabeb, (d) *F. albida* Gobabeb and (e) *T. usneoides* Gobabeb. The scalebar in the top left corner of each photo = 500 µm.

Wood density

One way ANOVA results show significant differences in density between species ($F_{4,30}$ = 8.04, $p < 0.001$). *F. albida* wood is significantly less dense than *A. erioloba* wood at Gobabeb (Tukey post-hoc test; $p < 0.001$; details Table 6 Appendix), at Gannavlakte ($p < 0.001$) and *P. glandulosa* ($p = 0.03$). *A. erioloba* has the densest wood of the species. Average wood density for the five species is shown in Table 5.3.

Table 5.3: Average wood density (g cm^{-3}) and standard error (± 1 SE); (n = 7) per species.

Species	**Avg Density gcm^{-3}**
F. albida	0.54 (0.03)
A. erioloba Gobabeb	0.74 (0.03)
T. usneoides	0.64 (0.03)
P. glandulosa	0.68 (0.04)
A. erioloba Gannavlakte	0.77 (0.03)

DISCUSSION

The results of this chapter support the hypothesis, suggesting that trees differ in structure and drought tolerance, supporting the previously observed mortality patterns in both the Namib and Kalahari. During the 1980s drought period in the Namib, the mortality rate for riparian *T. usneoides* was 24%, followed by *A. erioloba* (29%) and *F. albida* (62%) (Theron *et al.,* 1985). At Gannavlakte in the Kalahari, the riparian *A. erioloba* shows increased water stress and mortality in the presence of *P. glandulosa* (Chapter 4).

Vulnerability curves suggest that all four species have a highly vulnerable xylem structure and that they all require a constant supply of water. The trees studied in this thesis show cavitation rates similar to riparian species in the Sonoran Desert (*Populus fremontii*, *Fraxinus velutina*, *Prosopis velutina*) described by Pockman and Sperry (2000). *T. usneoides* vulnerability curves however are far steeper than curves for riparian *Tamarix ramosissima* in the USA (Pockman and Sperry, 2000; Hultine *et al.,* 2005). Within Southern Africa, they are more vulnerable than wetland fynbos species measured in the Cape floristic kingdom (Aston, 2007 *unpublished thesis*). The vulnerability curves show that the xylem of *A. erioloba* at both sites is marginally more cavitation resistant than xylem of the other tree species. Apart from *T. usneoides*, these findings reflect the drought mortality rates recorded in the Namib almost thirty years ago (Theron *et al.*, 1985), but do not explain why *A. erioloba* has increased mortalities in the presence of *P. glandulosa* in riparian zones.

Apart from the vulnerability curves, xylem density results also suggest that *A. erioloba* is structurally best equipped to tolerate drought. Despite variations in vessel diameter between locations, *A. erioloba* wood density was consistently the highest among the investigated species. Barnes *et al.* (1997) described *A. erioloba* wood to be very dense with large vessels. This description fits well with the Gobabeb wood structure, where the large xylem vessels are surrounded by bands of lignified cells (Fig. 5.3c). This lignified cell arrangement strongly suggests that it acts as protection from embolism, resulting in the increased resistance to cavitation observed in the vulnerability curves. Greater wood density, smaller vessel diameters, more pronounced lignified cell bands (Fig. 5.3a) and lower Ψ_{PD} and Ψ_{MD} for *A. erioloba* at Gannavlakte suggest that the species adapts its physiology to drier surroundings. This aspect is discussed in more detail in Chapter 6.

The low Ψ_{MD} for Gannavlakte *A. erioloba* and especially *P. glandulosa* (Fig. 5.1a), paired with the low diurnal depression rates, show that Gannavlakte trees grow in drier conditions than the Namib trees. They are under more water stress during the day than Gobabeb trees with limited overnight recovery from low XPP. *Prosopis glandulosa* is deciduous (Nilsen *et al.*, 1983) and leaf abscission at the end of the wet season allows the species to survive the driest months in dormancy (Fig. 5.3b). Seasonal dormancy is likely to be an important advantage for *Prosopis* over *A. erioloba*, because structurally, *P. glandulosa* is consistently more vulnerable than *A. erioloba* and shows the highest predawn and midday water stress (Fig 5.1a) of all the species. In terms of wood density, vessel diameter and vulnerability to cavitation, *P. glandulosa* is similar to *T. usneoides*. In the U.S.A. *Tamarix* and *Prosopis* species are considered equally drought resistant (Glen and Nagler, 2005).

The results for Xylem pressure potentials show that *T. usneoides* had the most negative Ψ_{MD} values at Gobabeb as well as the overall highest diurnal depression rates (Fig. 5.1b). These results also suggest that the species has limited or no stomatal control to inhibit transpiration during the day. The species is a salt-exuding halophyte (Mace, 1971; Glen and Nagler, 2005). It exudes salt onto the evaporative surface of its stomatal cavities (Mace, 1971), resulting in salt crystal accumulation in and around the cavity. These crystalline accumulations have been linked to reduction in transpiration rate at very high vapour pressure deficits (Mace, 1971), suggesting that the species relies on the clogging of stomata under extreme conditions, rather than actual control of stomatal aperture. The vulnerability curves are exceptionally steep for *T. usneoides* and are in direct opposition with the low (24%) mortality rates in the 1980's. Structurally, *T. usneoides* has small vessel diameters, relatively high wood density and experiences negative P_{min} values. *T. usneoides* is thus structurally adjusted to regularly experience low XPP. The vulnerability curves are the only results that counter the rest of the findings and I speculate that the higher salt concentrations in *T. usneoides* may have influenced the hydraulic conductivity measurements, leading to skewed vulnerability curve results for the species.

The high Ψ_{PD} and Ψ_{MD} values of *F. albida* suggest that the species is isohydric, closing down transpiration to remain above $\Psi_{min\,=}$ -2.4 MPa. It is likely to avoid cavitation by keeping its xylem pressure potentials high and stable. The XPP values for *F. albida* do correspond with results from previous studies (Ward and Breen, 1983; Roupsard *et al.*, 1999; Botha, 2001) and isohydric behaviour was previously noted for *F. albida* along the Levhuvhu River in South Africa (Botha, 2001). *F. albida* also has the largest vessel diameter as well as the lowest wood density, suggesting that it has the most vulnerable xylem structure of the species. Hence stomatal closure is likely its main drought protection mechanism.

I conclude that previously observed mortality patterns in both the Namib (Theron *et al.*, 1985) and Kalahari (Robertson and Woodborne, 2002) can partially be explained by looking at tree xylem structure. *A. erioloba* xylem structure is the most resistant, providing an explanation for its comparatively low mortality rate in the 1980's Namib drought. However, it is still affected by the presence of *P. glandulosa*, which has a seeming competitive edge over *A. erioloba* due to its seasonal dormancy and its flexible water uptake, as discussed in Chapter 4. *P. glandulosa* also has bigger vessels with greater tension on the water column than *A. erioloba*, suggesting that it is taking up more water than *A. erioloba*. *T. usneoides'* relatively resistant xylem structure complements the relatively low mortality rates observed in the 1980's drought. *F. albida* has the most vulnerable xylem structure of the species and this directly complements the observed mortality levels in the 1980's.

CHAPTER 6: *ACACIA ERIOLOBA* (MEYER) AND OPTIMAL ROOTING DEPTH: PHYSIOLOGICAL ADAPTATIONS OCCUR WITH DEEPER WATER TABLES

INTRODUCTION

This chapter pays particular attention to the species *A. erioloba*. Some of the data here are a repetition of data presented for the species at Gobabeb and Gannavlakte in Chapters 3 to 5, but an additional study site is added here and the data is looked at in relation to groundwater depth. It is the change in focus, not the data that provides a novel angle to this chapter.

Acacia erioloba is one of the major tree species of the Namib and Kalahari Desert regions, occurring throughout northern South Africa and most of Namibia and Botswana (Coates-Palgrave, 1983). It is particularly prominent in riparian woodlands along ephemeral riverbeds in both the Kalahari and Namib deserts (Jacobson *et al.*, 1995, Milton and Dean, 1995). *A. erioloba* survives in arid areas due to its deep rooting ability, enabling it to source groundwater and remain unaffected by low rainfall conditions (Ward and Breen, 1983; Bate and Walker, 1993; Canadell *et al.,* 1996; Barnes *et al.*, 1997; van der Walt and le Riche, 1999; Barnes, 2001a; Seymour and Huyser, 2008). The ability to take up water from 70 metres depth has been shown for this species in the Kalahari (Obakeng 2007). Often it is the only species occurring in arid areas and the ecosystem services it provides are disproportionate to its relative abundance (Barnes *et al*., 1997; Eccard *et al*., 2006). Its pods and leaves are a valuable fodder crop for game and livestock (Jacobson *et al*., 1995; Moser, 2006). It is considered a keystone species that is instrumental in maintaining biodiversity patterns and processes (Dean *et al.,* 1999).

There is widespread concern about the conservation of this valuable endemic tree of southern Africa (Ward and Breen, 1983; Theron *et al.,* 1985; Bate and Walker, 1993; Milton and Dean, 1995; Barnes *et al.*, 1997; Dean *et al.,* 1999; Anderson and Anderson, 2001; Barnes, 2001a; Barnes, 2001b; Dean *et al.,* 2002; Powell, 2005; Eccard *et al.,* 2006; Moser, 2006; Seymour, 2007). The species is coming under increased pressure through firewood harvesting (Anderson and Anderson, 2001) and competition for water with both humans and alien vegetation (Rőssing, 2004 *unpublished report*; Powell, 2005; Moustakas *et al.*, 2006). Ninety percent of Namibians depend on ephemeral water sources for their daily water use (Jacobson *et al.*, 1995) and Kalahari livestock farmers rely solely on groundwater resources (Verhagen, 1985). Human groundwater needs in both the Namib and Kalahari thus directly compete with the water requirements of *A. erioloba*. Iron ore mining in the Kalahari (Powell, 2005) and expanding uranium mining in the Namib are additional water intensive practices that may deplete groundwater resources, further reducing available water for *A. erioloba* (Huntley, 1985; Brown, 1990). The rapid and prolific expansion of the alien *Prosopis* species in the Namib and Kalahari is believed to have resulted in more competition (Robertson and Woodborne, 2002; Colvin *et al*., 2007).

A number of studies have demonstrated the ability for deep rooting for *A. erioloba* (Canadell *et al.*, 1996; Obakeng, 2007), but there has been little research on the physiological adaptations to rooting depth for *A. erioloba*. In the USA a number of studies have been conducted on a variety of species, mainly within the family *Salicaceae*. These studies have have shown the relationship between available water and physiological attributes, such as xylem pressure potential, leaf size, xylem vessel diameter, tree height and canopy volume (Stromberg *et al.*, 1992; Sala *et al.*, 1996; Scott *et al.*, 1999; Horton *et al*., 2001a,b; Cooper *et al.*, 2003; Rood *et al.*, 2003; Shrestha *et al.*, 2003; Schume *et al.*, 2004; Cooper *et al*., 2006).

In this chapter I test the hypothesis that trees adapt their physiology with depth to groundwater. For this purpose I look at physiological adaptations of riparian *Acacia erioloba* growing at three different groundwater depths in the Kalahari and the Namib deserts. The study sites are Gobabeb (4 m) and Swartbank (21 m) in the Namib Desert and Gannavlakte (56 m) in the Kalahari. Groundwater was considered the primary difference between these sites.

Apart from groundwater depth, Gobabeb and Swartbank are very similar in rainfall (0 - 12 mm/a) (Henschel and Seely, 2008), fog occurrence (60 – 200 days/a) (Shanyengana *et al*., 2002) and coarse, sandy alluvium. Gannavlakte along the Kuruman receives no fog, but more rainfall (average 290 mm/a). Coarse soils and the presence of dunes in the landscape are similar to the Namib sites. The biggest difference between sites is the annual amount of rainfall, but the Kalahari isotope work (Chapter 4) shows that *A. erioloba* is largely groundwater dependent.

Stable $\delta^{18}O$ and $\delta^{2}H$ isotopes were used to determine the water sources used by trees at each site. $\delta^{13}C$ isotope values and xylem pressure potentials were used to determine water use efficiency and water stress respectively. Xylem vessel diameters, specific leaf area, shoot length, monthly stem growth and canopy dieback were compared between sites. All measured physiological traits were correlated to depth of the water table to ascertain if significant relationships exist.

Tree productivity and health is proportional to available water. The consequence of lost productivity and tree health due to long term drops in water tables need to be considered by catchment managers if *A. erioloba* is to be protected as an ecological and economic keystone species.

MATERIALS AND METHODS

Study area

The study was conducted at Gobabeb (23º33’726 S – 15º02’112 E) and Swartbank (23.18.161 S, 14.45.693 E) in the Namib Naukluft Park in Namibia and on the farm Gannavlakte (26º57’578 S - 21º50’234 E) just south of the Botswana border in South Africa. The first two sites are located in the hyperarid parts (0 – 12 mm/annum) of the Namib (Henschel and Seely, 2008), along the lower reaches of the Kuiseb River. Fog is a major moisture contributor in this area, with fog events occurring on average 60 – 200 days of the year (Shanyengana *et al*., 2002). Gobabeb has an average groundwater depth of four metres, Swartbank 21 metres and Gannavlakte 56 metres. A full description and depiction of the study sites is given in chapter 2 (Fig. 2.1).

Data collection

Six adult *A. erioloba* were randomly selected along the active river channel at all three study sites. Fieldwork was conducted between April 2004 and April 2007 during the late dry (November/December), late wet (March/April) and early dry (June/July) seasons, collecting samples for stable hydrogen and oxygen isotopes, plant moisture stress, xylem pressure potentials, vessel diameters and plant phenology.

Water table depth

The borehole at Gobabeb was approximately 150 metres from the study site, on a two-metre raised embankment which is equivalent of tree elevation above the riverbed. At Gobabeb, the depth to the water table was measured at a borehole supplying water to the Gobabeb Research Station from June 2004 until June 2005, after which the piezometer became dysfunctional. In June 2005 a different project (WADE) drilled a monitoring borehole and their water level data was used from June 2005 until September 2006. At Swartbank the borehole was approximately 200 metres from the study trees inside the active river channel, again roughly at similar height with the study trees. An unused borehole was used to measure depth to the water table at Swartbank from November 2004 until March 2006. Gannavlakte was problematic, as all boreholes in a 5 km radius were in use, making it impossible to measure water depth as a timeseries. The only unused and water-containing borehole for datalogging was found in van Zylsrus, 30 kilometres upstream of the study site, with an average depth of 56 metres. Data from the surrounding boreholes were plotted (Fig 6.1 and Table 6.1) to show that average depth to the water table from the 32 closest boreholes is also at 56 metres (Department of Water Affairs records). The measured water depth at van Zylsrus was therefore considered representative of average groundwater depth in the area. The Gannavlakte piezometer and Barometer (Diver and Baro Diver: Eijkelkamp/van Essen, Netherlands) were fitted into the van Zylsrus borehole in April 2005 until April 2006.

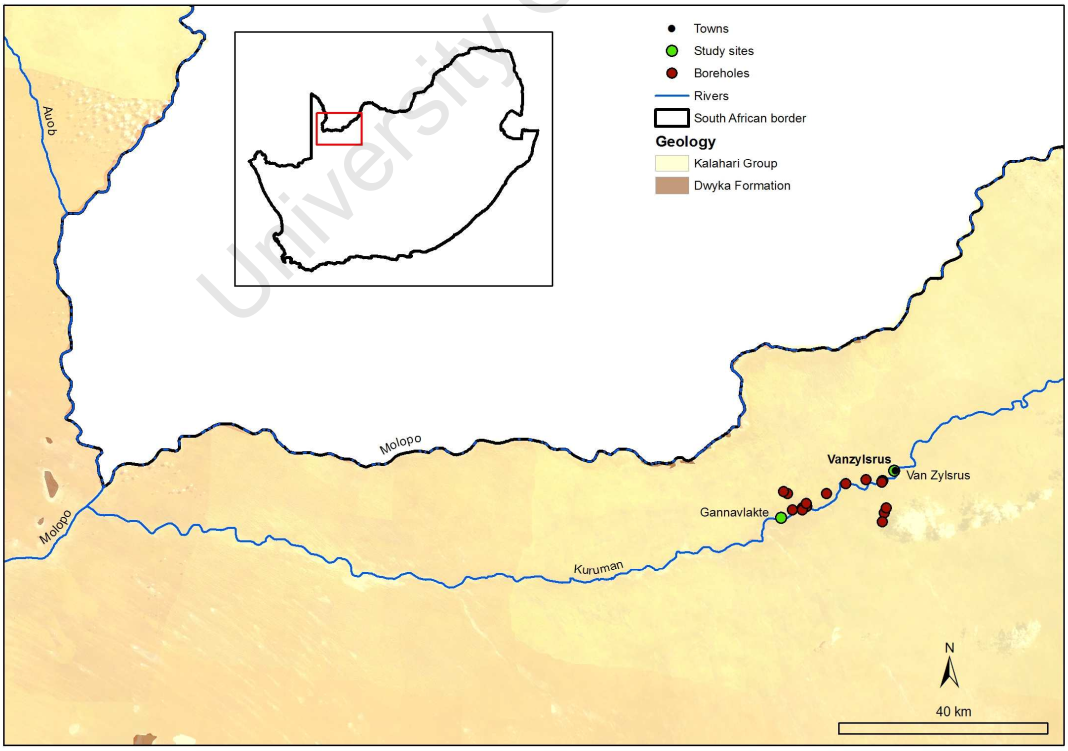


Figure 6.1: Map with the 32 closest boreholes in the vicinity of Gannavlakte and van Zylsrus

Table 6.1: Average, minimum and maximum borehole depth (m) and number of measurements for the closest boreholes between the study site and van Zylsrus

Borehole	# of times measured	Avg water level (m)	Max water level	Min water level
1	1	57.3	57.3	57.3
2	1	59.13	59.13	59.13
3	1	32	32	32
4	1	56.08	56.08	56.08
5	1	42.67	42.67	42.67
6	1	82.29	82.29	82.29
7	1	54.86	54.86	54.86
8	1	60.96	60.96	60.96
9	1	51.81	51.81	51.81
10	1	71.32	71.32	71.32
11	1	82.29	82.29	82.29
12	1	53.94	53.94	53.94
13	1	47.24	47.24	47.24
14	2	43.695	45.7	41.69
15	1	57.9	57.9	57.9
16	1	30	30	30
17	1	42.18	42.18	42.18
18	1	50	50	50
19	1	45.29	45.29	45.29
20	1	35.2	35.2	35.2
21	1	57.91	57.91	57.91
22	3	44.28	51.82	29.22
23	3	49.97	55.17	41.54
24	1	60.96	60.96	60.96
25	1	54.86	54.86	54.86
26	1	87.78	87.78	87.78
27	1	57.3	57.3	57.3
28	2	105.45	106	104.9
29	1	72.1	72.1	72.1
30	2	41.655	49.13	34.18
31	1	57	57	57
32	2	59.915	59.96	59.87
		56.11375	***106***	***29.22***

At all three sites water table depth was determined with the help of piezometers (Diver: Eijkelkamp/van Essen, Netherlands). Piezometers are submerged to a known water depth inside a borehole to determine groundwater variation over time. The internal dataloggers of each piezometer were set to record the sum pressure of air and water exerted on the equipment every hour. Upon retrieval, an associated software programme (Logger Data Manager 3.0.4, van Essen) was used to download the data. The software was also used to calculate actual water depth by subtracting known air pressure (obtained either from a local weather station (Gobabeb and Swartbank) or a Barometer (Baro Diver: Eijkelkamp/van Essen at Gannavlakte) from the recorded sum pressure. The water level data was expressed as average monthly water depth.

Stable $\delta^{18}O$ and $\delta^{2}H$ isotopes

Stable oxygen isotopes were used to determine the source waters of *A. erioloba* at all three sites. Oxygen isotope ratios for tree xylem water are more closely related to source water isotope values than hydrogen (Ellsworth and Williams, 2007). Especially in halophytic and xerophytic plants the passage of water from the root endodermis to the root xylem causes fractionation, leading to a decrease in ^{2}H of root xylem water relative to that in the surrounding soil medium (Ellsworth and Williams, 2007). Hence only oxygen isotope results are discussed in this chapter. The stable δ^{18}O isotope method is described in detail in Chapter 3.

In the field suberised twigs (0.5 – 1 cm diameter and 6 – 7 cm long) were collected from six *A. erioloba* trees per site. Groundwater was collected monthly at one Gobabeb borehole and two Swartbank boreholes from June 2004 until March 2006. Gannavlakte groundwater was collected from three boreholes, located within a five-kilometre radius of the site from April 2004 until November 2005. Fog water samples were obtained monthly from fog collectors at both Gobabeb and Swartbank. Both collectors consisted of a 30 x 40 cm meshed shade netting screen on which water collected during fog events and drained through a hose into 25 litre containers. A one-centimetre layer of silicon oil inside the container prevented evaporation. One rainwater and six floodwater samples were collected in the Namib and 31 rainfall events were sampled at Gannavlakte.

Plant moisture stress

Stable δ^{13}C isotopes

In April 2007 twenty fully mature leaves were collected from each tree and prepared as described in Chapter 4.

Xylem Pressure Potential

Xylem pressure potentials (XPP's) have been described in detail in Chapters 4 and 5. Each fieldtrip, predawn and midday XPPs were determined for each of the six trees at each study site using a Scholander Pressure Chamber (PMS Instrument Company, Corvallis, Oregon, USA).

Xylem hydraulic characteristics

Vessel diameters

Xylem vessel diameter is governed by water availability (Schume *et al.*, 2004). Diameters decrease with reduced water availability and increased path length resistance (Koch *et al.*, 2004). Average vessel diameters were obtained for *A. erioloba* at all three study sites to determine whether they changed in relation to depth of the water table. In April 2005 one twig from each of the six trees per site were used to determine average xylem vessel diameter. The twigs were brought back to the laboratory and processed as described in Chapter 5.

Plant phenology

Specific Leaf Area

Specific leaf area (SLA) is the ratio of wet leaf area to dry leaf mass (Reich *et al.*, 1999). In June 2005 thirty mature and fully exposed leaves were randomly selected per tree at each site. The leaves were sealed in plastic, cooled and transported back to the laboratory where all leaflets were separated from the rachis and pinnae, spread out next to a ruler on a white background and photographed within 48 hours. Average leaf area per specimen was determined by analysing the photographs using Sigma Scan Pro 5. These leaves were then oven-dried at 70˚C for 48 hours, after which they were weighed to determine dry mass. SLA was then determined from the equation:

SLA = leaf area (cm^2) / dry weight (g)

Canopy dieback

Recent canopy dieback is an integrative measure of plant physiological condition (Horton *et al.*, 2001b) and was already used in Chapter 4. Canopy dieback was determined for *A. erioloba* at all three sites to see if there was a relationship between the dieback rate and depth to the water table. In April 2007 two observers scored canopy dieback on all trees at each site, where 0 % = no dieback and 100 % = dead. Every tree was carefully observed from all angles and each observer estimated a dieback score, using 10% increments. The score average from the two observers was recorded as the percentage canopy dieback for each tree.

Shoot growth

Shoot growth measurements are a non-destructive and a fast way of determining environmental favourability for growth, especially water availability (Willms *et al.*, 1998; Gebauer *et al.*, 2002). Fresh branch growth of *A. erioloba* is bright red and clearly distinguishable from older wood. In April 2005 the latest growth increments of ten randomly selected branchlets from around the canopy were recorded per tree at each site.

Stem diameter growth

Dendrometer bands provide an accurate measurement of plant stem diameter growth over time (Bormann and Kozlowski, 1962). As plant growth is closely regulated by available water such measures are useful in showing the different growth rates of *A. erioloba* in relation to water table depth. In March 2005 dendrometer bands (Agricultural Electronics Corporation, Tucson, AZ, USA) were fitted to three *A. erioloba* tree stems per site. Dendrometer bands are thin metal bands (3 mm x 75 µm) that are fitted around the main trunk of a tree and held in place with a spring-loaded vernier gauge (February *et al.*, 2007a,b). Readings were taken each month for one year with the assistance of staff at Gobabeb and Gannavlakte. Gannavlakte dendrobands could not be read for December 2005 and January 2006 due to a lack of staff at the farm.

Data Analysis

Differences for δ^{13}C isotopes, vessel diameter, SLA, shoot length, stem growth and canopy dieback were assessed for statistical significance using One-way ANOVA and Tukey post hoc tests, generated with Statistica 7.0. The data was log transformed when assumptions of heterogeneity of variance and normality were not met. When transformations were unsuccessful, a non-parametric Kruskall-Wallis test was used. Repeated measures ANOVA tests were used for xylem pressure potentials between sites. They were done in SPSS, version 15.0. Standard correlations were performed between depth to water table and all other measurements, using Statistica 7.0. All data is presented as means, unless otherwise noted. A $p < 0.05$ was required for significance in all tests.

RESULTS

Water sources

Borehole depth

The ground water levels at Gobabeb showed the greatest variation (1.5 to 6.0 metres) over time (Fig. 6.2). A three-metre-high flood in March 2006 temporarily pushed the water table to one metre below the surface. Between floods, the water table dropped by an average of 17 centimetres per month. Over the same period water levels at the Swartbank borehole fluctuated between 18.5 and 21.5 metres with a 2.1 metre increase in the water table after the March 2006 flood. Between floods the water table at Swartbank declined at an average of three centimetres per month. The water table on the Kuruman River near Gannavlakte fluctuated between 54.2 and 57.8 metres. From March 2005 to March 2006 the water table dropped on average 27 cm per month. As of January 2006 the water level rose an average 30 cm per month, with a notable increase of 1.5 metres in June 2006. Recharge could not have been local, as there were no floods prior to the groundwater level increase and the local average annual rainfall was merely 357.5 mm until April 2006. The raise in water level is thus a likely reflection of groundwater movement from the upper catchment. It is also possible that the groundwater level increase was linked to the cessation of abstraction from another borehole in the close vicinity, thus leading to a local recovery of the water level. Sadly none of the assumptions could be validated.

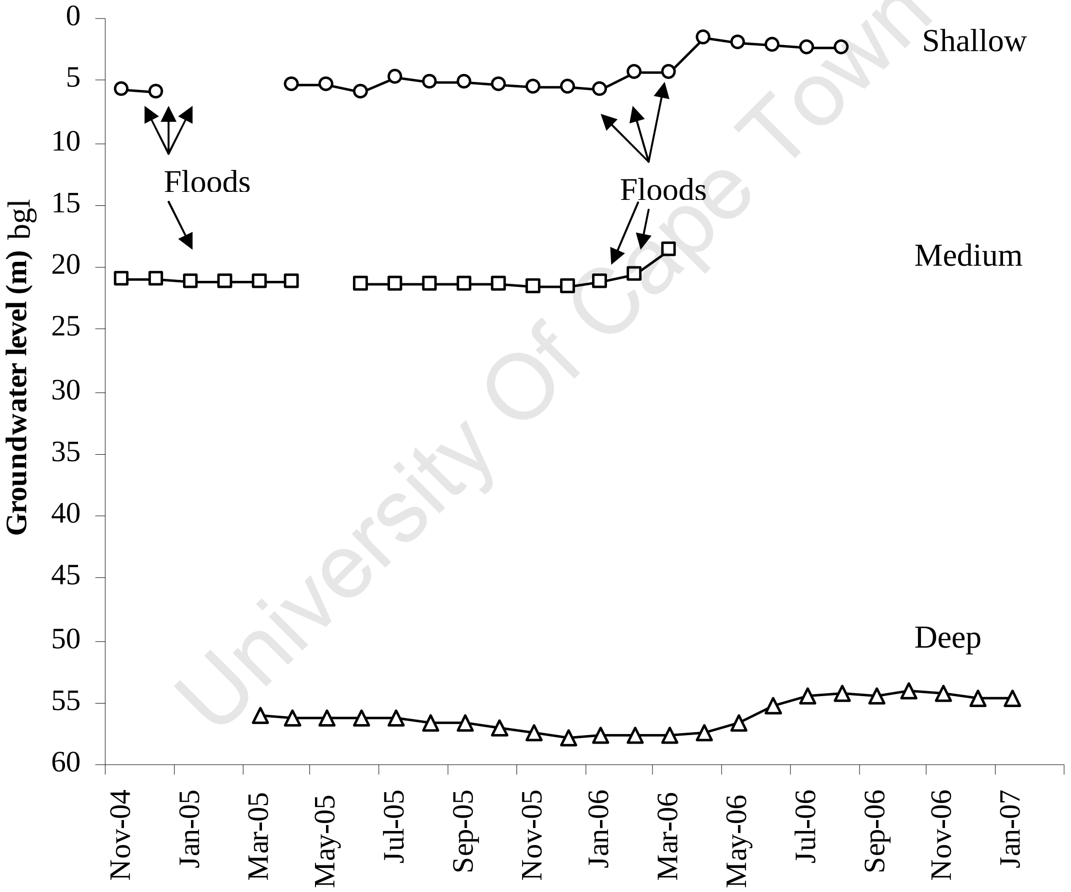


Figure 6.2: Groundwater levels from November 2004 to January 2007 for Gobabeb ○, Swartbank □ and Gannavlakte Δ. The graph highlights all months in which floods occurred at Gobabeb and Swartbank. It also illustrates the differences between the three sites in depth to the water table.

Stable δ^{18}O Isotopes

Gobabeb tree water isotope averages (-6.56 ‰) are significantly different from fog water (-1.45 ‰; Kruskall-Wallis nonparametric $p < 0.001$), but overlap with groundwater (-5.87 ‰) and flood water (-4.9 ‰). At Swartbank tree isotope values (-6.02 ‰) are similar to groundwater (-6.78 ‰). Fog isotope values (-0.8 ‰) are significantly different to tree water ($p < 0.001$). *A. erioloba* isotope values at Gannavlakte (-4.91 ‰) overlap with groundwater (-6 ‰).

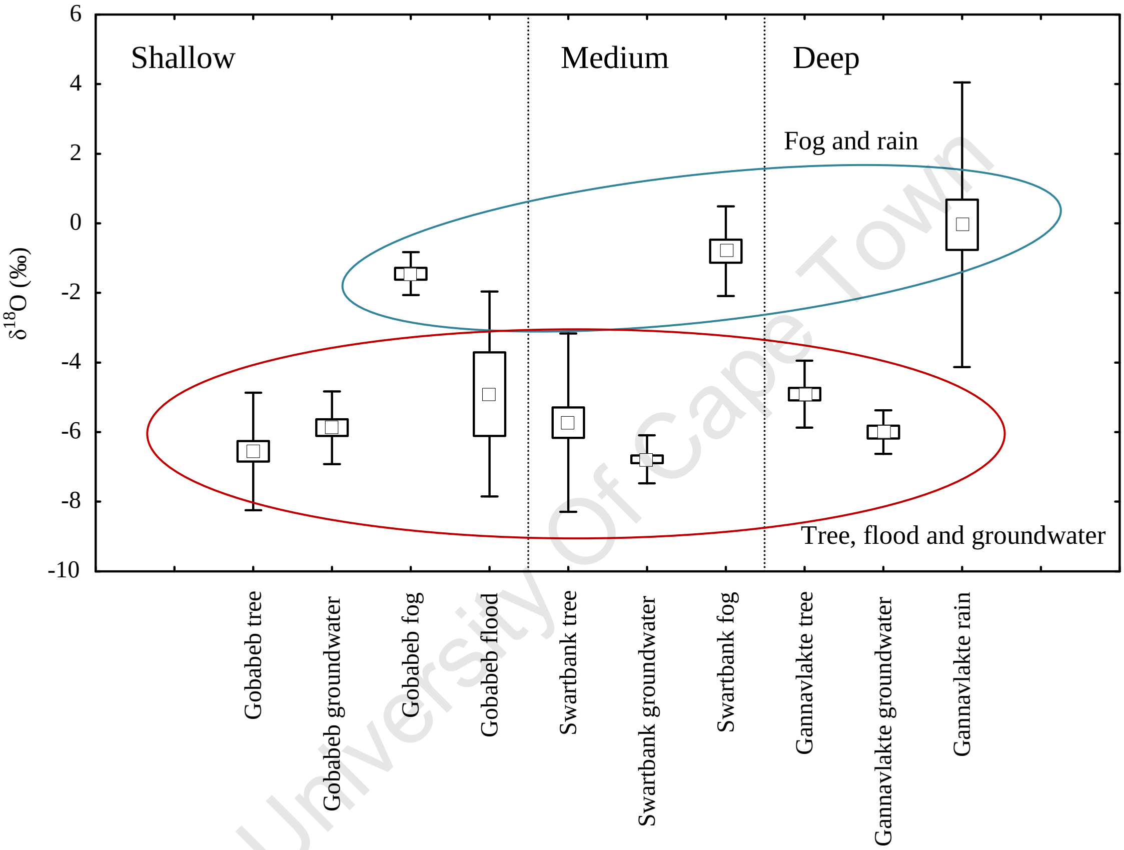


Figure 6.3: Overall average Gobabeb, Swartbank and Gannavlakte δ^{18}O values for *A. erioloba*, groundwater, rain, fog and floodwater. Standard error values are indicated by box values and standard deviations by whiskers.

Plant moisture stress

Carbon isotopes

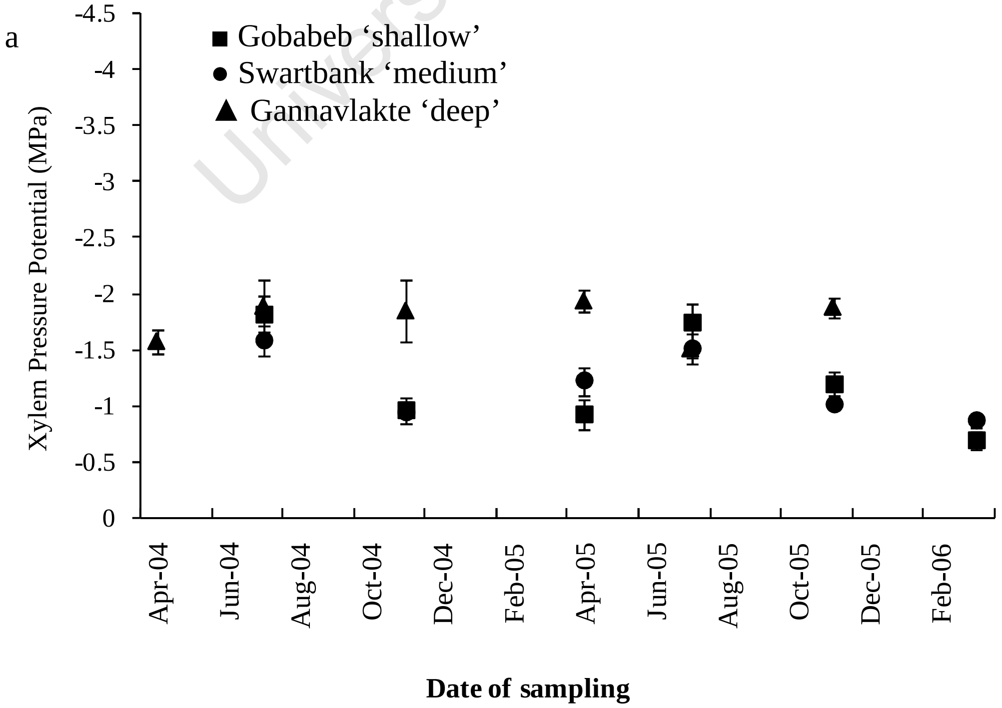
The samples for Gobabeb have the most depleted δ^{13}C values (-27.4 ‰, ± 0.78), while those for Swartbank and Gannavlakte are very similar (-25.7 ‰, ± 0.42; –26.09 ‰, ± 0.29 respectively). There are however no significant differences in leaf δ^{13}C values between the three sites (One-way ANOVA).

Xylem pressure potentials

There is a significant correlation between depth to water table and xylem pressure potentials between the three locations (predawn $y = - 1.155 x – 0.01$; $p < 0.02$ and midday $y = - 2.87 x – 0.01$; $p = 0.0001$; Fig 6.6A and 6.6B).

Overall average predawn (Repeated measures ANOVA; $F_2 = 12.23$, $p = 0.001$; Post-hoc details Table 7 Appendix) and midday ($F_2 = 22.2$, $p < 0.001$; Post-hoc details Table 8 Appendix) XPP's differ significantly between locations, with Gannavlakte being more stressed than both Gobabeb ($p \leq 0.004$) and Swartbank ($p = 0.001$).

Predawn XPP at Gobabeb and Swartbank were almost identical and followed the same pattern over time (Fig. 6.4a). Predawn XPP decreased in November 2004 and April 2004 around the flood season, peaking in the dry winter months of June 2004 and 2005. Gannavlakte XPP was almost stable over time, with slightly less negative XPP in April 2004 and July 2005. Gannavlakte XPP was significantly more negative in November 2004 (One-way ANOVA; $p = 0.004$), April 2005 ($p < 0.001$) and November 2005 ($p < 0.001$). Midday XPP's (Fig. 6.4b) for Gannavlakte were significantly lower than the Namib sites in July 2004 ($p < 0.001$), November 2004 ($p < 0.001$) and November 2005 ($p = 0.001$).



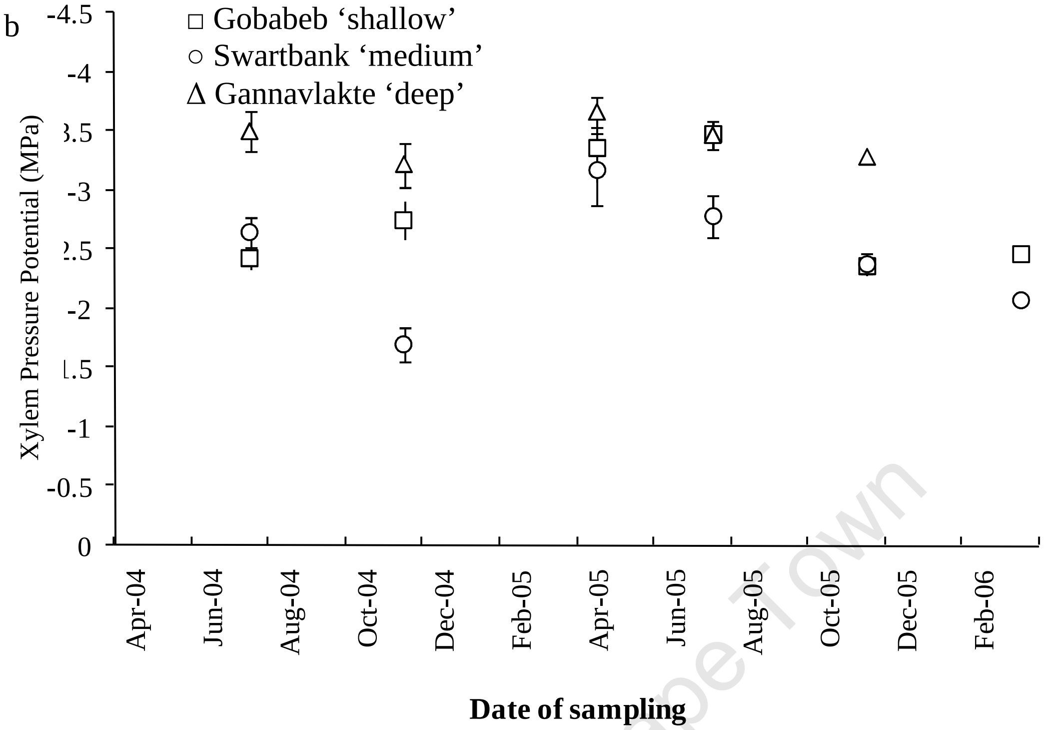


Figure 6.4: Average predawn (a) and midday (b) xylem pressure potential measurements in Mega Pascal (MPa; ± 1 SE) for all three sites from April 2004 to March 2006Xylem hydraulic characteristics

Vessel diameters

Groundwater level and vessel diameter are inversely and significantly correlated ($y = - 0.38 x + 48.6$, $r^2 = 0.72$, $p < 0.0001$; Fig 6.6C). The mean xylem vessel diameters at Gobabeb (46.05 µm, ± 1.73) and Swartbank (42.16µm, ± 2.28) are similar and both are significantly larger ($p = 0.001$; One-way ANOVA Table 9 Appendix) than at Gannavlakte (29 µm, ± 1.71).

Plant phenology

Specific Leaf Area

Specific leaf area is significantly correlated with groundwater levels ($y = 0.036 x + 13.8$, $r^2 = 0.27$, $p = 0.01$ Fig 6.6D). There are however no significant differences in SLA between the three sites (One-way ANOVA Table 10 Appendix) (Table 6.2).

Table 6.2: Specific leaf area (n = 18) (± 1 SE) and groundwater level at the three sites

Location	**Groundwater level (m)**		**SLA cm^2g^{-1}**
Gobabeb	Shallow	4	15.7 (0.94)
Swartbank	Medium	21	12.9 (0.55)
Gannavlakte	Deep	~ 56	12.2 (0.70)

Canopy dieback

Average percentage of dead material on trees increased with increasing groundwater depth between Gobabeb 21% (± 5.8 SE), Swartbank 29% (± 7.5 SE) and Gannavlakte 32% (± 4.6 SE), but the differences were not significant (One-way ANOVA; $F_{2,15} = 0.92$; $p = 0.42$). Depth to groundwater table and percentage canopy dieback were also not significantly correlated.

Shoot length

There is a highly significant inverse relationship between shoot length and groundwater level ($N = 180$, $y = -0.3x + 27.9$, $r^2 = 0.34$, $p > 0.001$; Fig 6.6E).

Average shoot length differed significantly ($F_{2,177} = 46.04$, $p = < 0.002$; One-way ANOVA Table 11 Appendix) between all three sites with 27.3 cm at Gobabeb (± 1.4 SE), 21.3 cm at Swartbank (± 1.3 SE) and 10.8 cm at Gannavlakte (± 0.9 SE). Shoot length differences were significant between Gobabeb and Swartbank ($p = 0.002$), and significantly different between Gobabeb and Swartbank ($p < 0.001$) as well as Swartbank and Gannavlakte ($p < 0.001$).

Stem diameter growth

Highest annual radial growth occurred at Gobabeb (14.55 mm, ± 4.6 SE), followed by Swartbank (6.66 mm, ± 2.7 SE). Lowest growth (2.45 mm, ± 1.5 SE) occurred at the deep groundwater site Gannavlakte (Fig. 6.5).

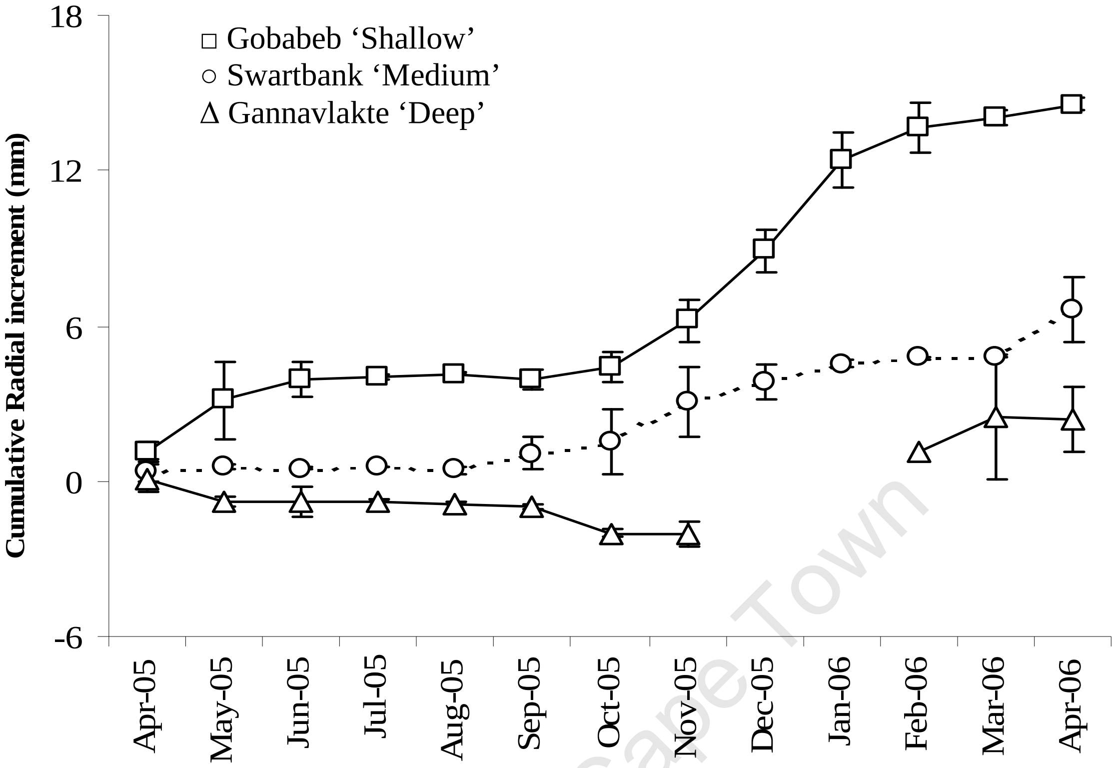


Figure 6.5: Cumulative radial growth increments (± 1 SE) at the three sites, April 2005 - April 2006

Gobabeb stem growth stabilises in the cold months, but the first onset of warmer temperatures results in rapid stem growth (2.70 mm, Dec 2005), independent of the floods that occurred from February to April 2006. Swartbank stem growth is equally stable over the cold months, with gradual growth occurring with the onset of warmer weather (0.68 mm, November 2005) and a definite sharp increase in growth from March to April 2006 (1.0 mm), with the onset of floods. Gannavlakte stems shrank markedly in the dry hot summer months (-2.02 mm, October 2005; -2.07 mm November 2005) and stem growth occurred during the wet summer season (2.44 mm, March 2006; 2.40 mm April 2006).

There is a significant, but low correlation between groundwater depth and stem growth (N = 64, y = -0.02x + 1.16, $r^2 = 0.06$, p = 0.05, Fig. 6.6F).

Correlations to groundwater gradient

The physiological responses of *A. erioloba* were correlated to the groundwater depth and plotted per location (Gobabeb, Swartbank and Gannavlakte) (Fig. 6.6 A-F). Out of the seven applied water-related measurements, five were significantly correlated with groundwater depth. These were predawn and midday xylem pressure potential ($p = 0.02$; $p = 0.0001$), xylem vessel diameter ($p < 0.0001$), specific leaf area ($p = 0.01$), branch growth ($p < 0.001$) and monthly stem growth ($p = 0.05$). δ^{13}C isotope values and canopy dieback showed no relationship to groundwater depth.

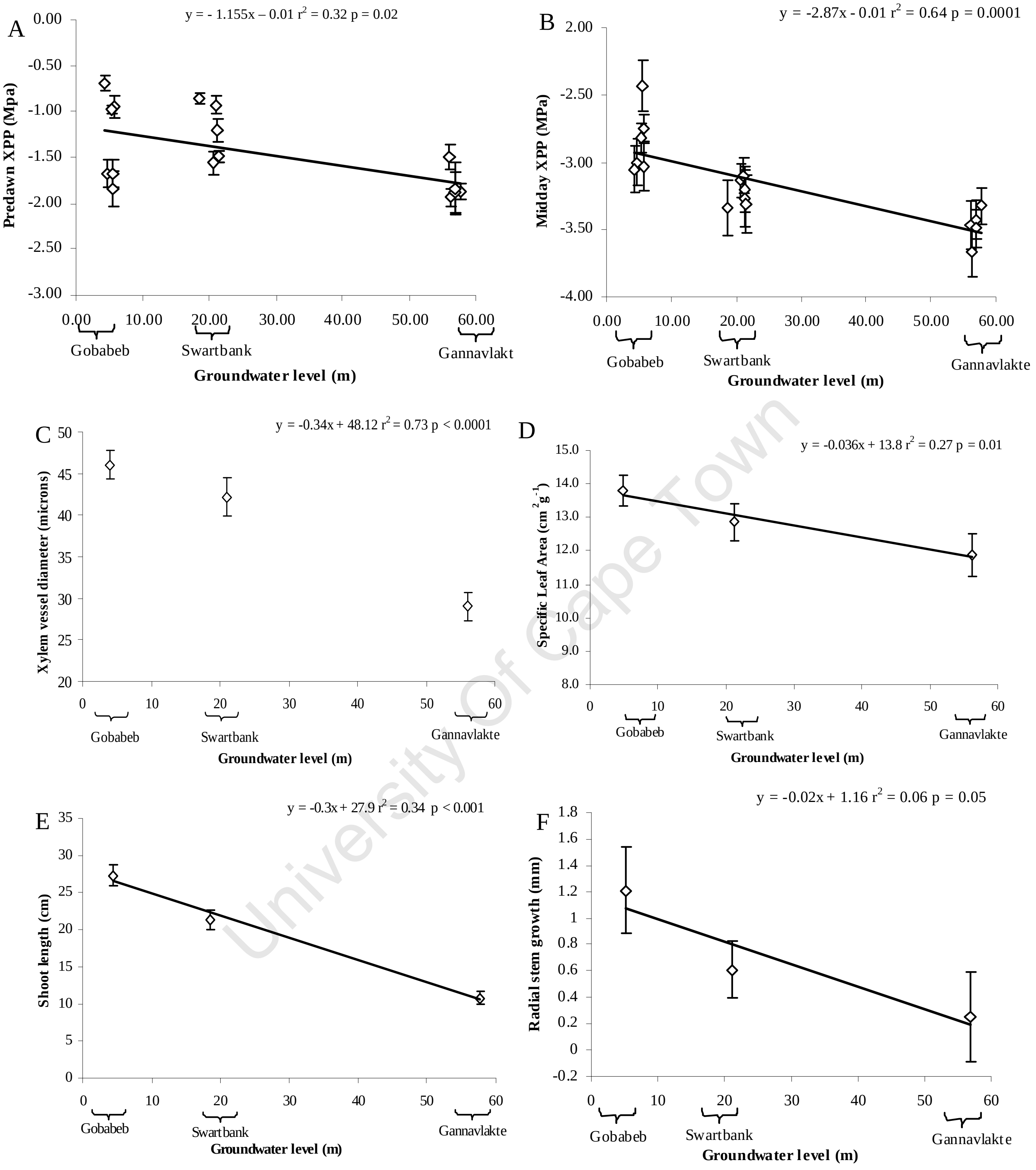


Figure 6.6 A – F: Correlations between groundwater level and *A. erioloba* A) Predawn XPP (Mpa) (n=83), B) Midday XPP (Mpa) (n=83), C) Xylem vessel diameter (µm) (n=18), D) Specific Leaf Area (cm^2g-1) (n=18), E) Shoot length (cm) (n=180), F) Monthly radial stem growth (mm) (n=64). Correlation trends and equations with r^2 values and level of significance (p) are displayed in each individual graph.

DISCUSSION

The results confirm the hypothesis that *A. erioloba* tree physiology responds proportionally to groundwater depth. Correlations show that there is a significant relationship between depth to water table and XPP's (predawn $p < 0.0001$; midday $p = 0.004$), SLA ($p = 0.01$), stem diameter growth ($p = 0.05$) and shoot length ($p < 0.001$). However there are no significant correlations between water table depth and $\delta^{13}C$ values, or average percentage of dead material on trees. The most deeply rooted trees at Gannavlakte show significant differences to both Namib sites in XPP's (predawn $p = 0.001$; midday $p < 0.001$) and vessel diameters ($p = 0.001$). Research in the USA showed that riparian *Prosopis velutina* experienced greater water stress, reduced leaflet size, and smaller canopy volumes when growing with a 15 to 18 metre deep groundwater table as opposed to trees growing with less than five metre deep groundwater (Stromberg *et al.* 1992). The results of this chapter agree with these results, but in the case of *A. erioloba* this is of particular interest, as it is considered one of the deepest rooting trees on earth (Canadell *et al.*, 1996).

Research on the world's tallest trees (*Sequoia sempervirens*) has suggested that maximum tree height (> 100 metres) is limited by a decreasing water supply through gravitational forces and friction in the xylem (Koch *et al.*, 2004; Burgess and Dawson, 2007). These results also show that the resistance of water flow due to a long hydraulic path leads to increased xylem pressure potentials, more enriched $\delta^{13}C$ values and reduced leaf area (Burgess and Dawson, 2007). As one of the deepest-rooting trees on earth (70 metres), *A. erioloba* may be similarly limited in water uptake due to the increased path length created by a deep root system. This speculation however goes beyond the scope of this chapter and may be of further research interest at a later stage.

This chapter provides an overarching insight into the relationship between groundwater depth and tree physiology. An aspect, not covered by this research is that of groundwater fluctuation. Research in the USA has shown that tree root distribution is linked to groundwater history. If a tree is adapted to high natural fluctuations in groundwater, it is more resistant to the ranges in these fluctuations(Shafroth *et al.*, 2000). It is therefore not possible to infer the vulnerability of trees to declining groundwater tables from my results, as they do not cover fluctuation in groundwater through time. Previous studies in the Kuiseb and Khan rivers (Theron *et al.* 1985, Rössing 2003, unpublished report) found that induced rapid declines in groundwater levels initially resulted in reduced leaf density, reduced flowers and pods of *A. erioloba*. When the groundwater decline continued it resulted in the die-off of branches. Similar observations were made with riparian vegetation in the USA (Stromberg *et al.* 1992, Horton *et al.* 2001, Rood *et al.* 2003). Rössing (2003, unpublished report) found trees to struggle when water tables were lowered faster than ten centimetres per month. At Swartbank on the Kuiseb River, a gradual groundwater drop of eight metres has occurred over the last 22 years (Moser 2006), without apparent detriment to tree stands (*pers. obs*.). At Gobabeb and Gannavlakte natural water table declines were seventeen and twenty-seven centimetres per month, without apparent detrimental effect to trees. I conclude that *A. erioloba*'s capacity to adapt to changes in groundwater levels is thus location specific, depending on the history of groundwater depth and fluctuation, as well as other aspects such as soil composition and tree age.

I conclude that *A. erioloba* has the capacity to source water from very deep groundwater, but that this occurs at a cost of increased water stress and reduced vitality. Trees depending on deep groundwater are closer to a water-induced survival threshold than those growing with access to shallower groundwater. However, added variables such the history of water table fluctuation will also affect tree adaptation irrespective of initial groundwater depth. There is a widespread concern to conserve the species (Bate and Walker, 1993; Milton and Dean, 1995; Barnes *et al.*, 1997; Dean *et al.*, 1999; Anderson and Anderson, 2001; Barnes, 2001a; Barnes, 2001b; Dean *et al.*, 2002; Powell, 2005; Eccard *et al.*, 2006; Moser, 2006; Seymour, 2007). Catchment managers should thus carefully consider the complexity of groundwater dependence of this ecological keystone species while accommodating new water intensive developments in the Namib and Kalahari Deserts.

CHAPTER 7: SUMMARY AND SYNTHESIS

INTRODUCTION

To gain a better understanding of the interrelations between floods, groundwater and riparian tree water use, this work took an ecophysiological perspective and investigated the water sources, drought tolerance levels and species interactions of four common riparian tree species in Southern Africa. Stable Hydrogen and Oxygen isotopes were used to determine the water sources for all selected tree species and age groups. Xylem structure, water potential and phenological measurements were done to compare levels of drought tolerance between species, to investigate resource competition among indigenous and invasive species and to compare the health and structure of one species with access to different groundwater depths. The well-documented surroundings of the Kuiseb River in Namibia and the patterns of alien tree felling in the South African Kuruman River have made these locations ideal study sites.

THE RELATIONSHIP BETWEEN WATER SOURCES AND TREE GROWTH

At Gobabeb, the stable Hydrogen and Oxygen isotope work has clarified that riparian trees are not fog water dependent and that they all rely on a seasonally fluctuating mix of groundwater, deep and shallow soil water. The isotope, as well as previous studies (Dahan *et al.*, 2008) show that bigger flood events provide groundwater recharge as well as soil wetting. Previous studies established that recharge was optimised during large flood events of long duration (Dahan *et al.*, 2008) and that seedling establishment depended on the wetting of soil and the deposition of seeds far up on floodbanks during large flood events (Moser, 2006). All previous and current findings highlight the intricate relationship between floods, groundwater and trees along ephemeral rivers. Particularly large floods of long duration are important for recharge, seed deposition, soil wetting and optimal tree functioning. Any alterations to large floods are likely to have the most detrimental ecological effects.

WATER STRESS OF INDIGENOUS SPECIES IN THE PRESENCE OF INVASIVES

In the USA much research has been done on the competitive advantages of invasive riparian trees of the genus *Tamarix* over indigenous *Populus* and *Salix* species (Pockmann and Sperry, 2000; Horton *et al.*, 2001ab; 2003). They found *Tamarix* species to be more flexible under reduced flood and lowered groundwater conditions than indigenous species. In Southern Africa the alien species *Prosopis* is known to transpire large amounts of water from its dense stands (le Maitre 1999), but the cause of *A. erioloba* mortality in the presence of *Prosopis* has hitherto not been clearly identified. An investigation was done into water stress of indigenous *A. erioloba* in the presence of *P. glandulosa* along the Kuruman River. Results show that *A. erioloba* and *P. glandulosa* use the same water resources when growing together in the riparian zone and that *A. erioloba* has significantly increased canopy dieback, XPP's and δ^{13}C in comparison to inland areas and riparian zones cleared of *P. glandulosa*. *A. erioloba* growing inland with *P. glandulosa*, shows no signs of increased water stress and the δ^{18}O and δ^{2}H isotope results suggest that the two species coexist through niche partitioning. *A. erioloba* is permanently groundwater dependent, while *P. glandulosa* switches from shallow surface water in the rainy season to groundwater in the dry season. The findings give the 'Working for Water' Programme, which eradicates alien invasives from riparian zones throughout South Africa, added impetus. In addition to its primary aim to reclaim water resources that would otherwise be transpired, it also plays a critical role in conserving *A. erioloba* in riparian corridors, where they are a key economic and ecological tree species in South Africa's arid areas.

XYLEM ANATOMY AND DROUGHT TOLERANCE

All four species investigated in this study are phreatophytic, in that they permanently depend on deep subsurface water resources and remain largely evergreen. Such plants are known to be relatively drought intolerant among arid land plants, as their deep root system allows constant water access (Hacke *et al.*, 2000; Horton *et al.*, 2003). Distinct drought tolerance differences have been proven between phreatophytes, annuals and deciduous desert vegetation in the USA (Hacke *et al.*, 2000). This study has shown however that drought tolerance among a group of phreatophytes is not that clearly distinguished. The species showed varied adaptations such as different levels of stomatal control or drought-deciduousness. *A. erioloba* xylem contained lignified cells around vessels and had the smallest vessel diameter, while *F. albida* had the largest vessel diameter. *F. albida* was consistently the most vulnerable of the investigated species, and *A. erioloba* the most drought tolerant. The mixed results for the other two species suggest that it is prudent to use more than one anatomical measurement to establish or explain drought tolerance for riparian vegetation. The necessity to combine several measurements when determining drought tolerance is crucial to consider in future EWR method development, when riparian water needs are included and require assessment.

PHYSIOLOGICAL ADAPTATIONS OCCUR WITH DEEPER WATER TABLES

Rooting depths and rooting patterns are typically unknown so that the ability of vegetation to reach the groundwater table is poorly understood (Obakeng, 2007). Obakeng (2007) succeeded in showing that *A. erioloba* is one of the deepest-rooting tree species on earth. The present study however, has also shown that deep water sourcing does affect its health and functioning, as tree structure and phenology, in particular xylem pressure potentials, xylem vessel diameters, shoot length and stem growth, responded proportionally to groundwater depth. A similar relationship between groundwater depth and plant traits was documented for *Prosopis velutina* in the Sonoran Desert in the USA (Stromberg *et al.*, 1992). *A. erioloba* is a protected and endemic species in Southern Africa (Coates-Palgrave, 1983) with a key ecological role in arid environments as well as high economic value (Dean *et al.,* 1999; Moser, 2006). Understanding its limits and water requirements is thus crucial. *A. erioloba* growing in areas with deep groundwater is already more strained than specimen growing in areas with shallower groundwater levels. Deep-rooting specimen are thus more vulnerable to reach water-induced survival thresholds sooner than those growing with access to shallower groundwater.

BIOINDICATOR IN TERMS OF WATER NEEDS

One of the overall study aims was to see whether the applied methods could help to define a particularly vulnerable species that could be used as a bioindicator for plant water needs. Previous observations in the 1980's droughts have showed that *F. albida* suffers highest mortalities among riparian species in the Kuiseb (Theron *et al.*, 1985). In Chapter 5 it was shown that *F. albida* is structurally the most vulnerable. These supporting results show that anatomical measurements can explain observed mortality patterns. The varied anatomical results in Chapter 5 among *T. usneoides*, *P. glandulosa* and *A. erioloba*, as well as the stable oxygen and hydrogen results in Chapters 3 and 4 show that it is advisable to use multiple methods to assess vulnerability, as riparian species may have different drought coping mechanisms while depending on the same water resources.

Away from plant water needs in arid areas, but nonetheless in line with plant indicators, an ongoing WRC research project in the Western Cape (South Africa) aims to find species that are characteristic of different wetland habitats. For this purpose, it tests whether wetland species can be grouped into functional groups (such as morphological form and resource acquisition). Other species are identified that act as indicators to discriminate between disturbed and undisturbed habitats (Corry, 2010, *pers. com.*). The ongoing project faces challenges, such as finding and defining levels of disturbance, defining of functional groups and dealing with the complexity of species, habitats and influencing environmental parameters. Projects such as these confirm that the concept of indicator plant species is complex, requiring a wide and carefully compiled dataset. Stromberg *et al.* (1996) selected wetland indicator plants from a complex dataset comprising herbaceous and woody species cover and composition, soils across gradients, geomorphology, groundwater level and site hydrology. Future efforts in defining bioindicator species for plant water needs in arid areas will benefit from testing more species. Ideally indicator species should be more vulnerable and less common than the economically and ecologically important *F. albida*, identified in Chapter 5. In that way an early warning species alerts to a water deficiency before large numbers of a key species are affected. Botha (2001) documented the death of *Ficus* species during a drought along the South African Luvhuvhu River, while *F. albida* survived. It would be useful to consider other riparian species in the Namib, including *Ficus sycomoris*, *Ficus cordata*, *Salvadora persica and Euclea pseudebenus*. In the Kalahari other riverine species should receive attention, including *Ziziphus mucronata*, *Acacia mellifera*, *Acacia hebeclada* and *Boscia albitrunca*.

THIS STUDY IN CONTEXT – ITS TRANSLATION AND APPLICATION IN CATCHMENT MANAGEMENT AND EWR METHOD DEVELOPMENT

The ecophysiological approaches and the species-specific information gained in Chapters 3 to 6 need to be translated into a format useful for management of ephemeral catchments and riparian corridors, as well as EWR's. One important aspect to consider includes the duration of plant responses that are measured by the different methods (summarised in Table 7.1). Ideally the selected methods should measure and reflect a wide range of plant response durations (hours to years) in order to gain a holistic picture of plant water status. Cost, time and human capital constraints are more aspects that need to be considered carefully among developing countries of Southern Africa. Hence it is essential to have a realistic impression of what the different methods involve (Table 7.1). The 'simplest', quickest and cheapest methods are: Shoot growth, canopy dieback and wood density. ^{13}C isotopes, xylem vessel diameter, stem diameter growth, xylem pressure potentials and specific leaf area are all 'intermediate' in terms of cost, time and training requirements. The most involved methods are vulnerability curves and ^{2}H and ^{18}O stable isotopes.

Apart from cost, labour, fieldwork time required and processing time considerations, there are other shortcomings with methods that need to be weighed up. Vulnerability curves, for example are laboratory-based and their interpretation would benefit from ground-truthing with field-based measurements such as xylem pressure potential measurements. Wood density measurements are a fast and rough indicator of xylem structure, as it is influenced by vessel area as well as percentage fibre wall (Jacobsen *et al.,* 2007). In order to obtain a more detailed insight into xylem anatomy, it would be beneficial to include vessel diameter measurements, which are far more involved than wood density in terms of skill and labout time. $\delta^{13}C$ measurements provided some useful (Chapter 4) and some less conclusive (Chapter 6) results, suggesting that it would be prudent to choose an additional method to see how a tree is performing.

The combination of xylem anatomy methods used in Chapter 5 helped to identify *F. albida* as the most vulnerable species, and prove that A. erioloba was the most vulnerable of the species. It also helped to identify *P. glandulosa* drought-deciduousness as an advantage over the other species. A depth of understanding was gained by the combination of methods, which would not have been possible if only one or two had been used. Hence more than one method should be chosen in an EWR setting, in order to get a broader understanding and cross-checks for a species' water use and drought tolerance levels. I support that at least three to four of the 'simple' and 'intermediate' methods should be completed simultaneously in a EWR process, in order to be able to cross-compare and to cover the different durations of plant responses to water availability. Stable Oxygen and Hydrogen isotopes are valuable to understand the dependence of key species on various water sources, making it possible to prioritise the protection or abstraction of a particular source, such as groundwater versus flood water. Its inclusion should be considered despite its cost and level of involvement. Vulnerability curves on the other hand did not provide sufficiently satisfying results in this study and may not be worthwhile, given the cost and time effort.

Table 7.1: A synthesis of applied methods and their potential application in EWR determinations

	Duration of plant response measured	**Cost**	**Time required**	**Ease of use**	**Applicable for what EWR level of detail**
Predawn and midday xylem pressure potentials	Measures plant response of last minutes to hours if once off or only 1 of 2 is done. If both done repeatedly, then seasonal or annual responses can be determined	Equipment purchase once off expensive (~ R 30 000), then cylinder fills (~ R 100/cylinder per trip)	Rapid (minutes to hours), but requires being on site for half a day (minimum) to include predawn and midday; requires repeats (monthly or seasonal)	Simple, but some training and repetititive practice required	Due to required repetition and prolonged field period: intermediate to comprehensive EWR's; baseline and operational monitoring
^{13}C isotopes	Measures plant response of last weeks (sample leaf) to years (sample branch or stem)	R 260+ per sample	Medium (days to weeks), once off, some lab time	Some training required for sampling, specialised staff required for lab work	Any EWR involving fieldwork
^{2}H and ^{18}O isotopes	Measures plant response of last hours to days, if repeated then determination of seasonal water use possible	R 150 - R 550 per sample	Very slow (weeks to months), preparation and lab work intensive	Some training required for sampling, lab analyses require specialised staff training	Any involving fieldwork, but preferably intermediate to comprehensive so as to capture seasonal changes
Canopy dieback	Seasons	No cost	Rapid (minutes to hours), once off in field	Simple, requires minimal training	Any involving fieldwork, but careful to ascertain that dieback is not frost, or flood damage related. Requires comparison
Stem diameter growth	Weeks to seasons	U$ 35 per vernier gauge plus import costs	Rapid once installed in field, requires repeated monitoring	Some training for installation, regular reading simple	Comprehensive, pre - and post determination due to required repetition
Specific leaf area	Weeks to seasons, even years (especially in evergreens)	Requires camera and software such as Sigma Scan	Medium (days to weeks), once off but preparation and lab work intensive	Some training required	Any involving fieldwork
Shoot growth	Seasons	No cost	Rapid (minutes to hours), once off in field	Simple, requires minimal training	Any, as long as it is known when the onset of the growing season is and preferable to be measured once growing season is over
Wood density	Seasons to years	No cost	Fast (hours to days), once off, some lab time	Simple, requires some training	Any EWR involving fieldwork
Xylem vessel diameter	Seasons to years	Requires microtome, camera and software such as Sigma Scan	Medium (days to weeks), once off but preparation and lab work intensive	Some training required	Any EWR involving fieldwork
Vulnerability curves	Seasons to years	Expensive, requires entire lab setup and sensitive scales	Medium (days), once off but preparation and lab work intensive	Extensive training required	Comprehensive, may require re-sampling

The table summarises the study experiences, but the format is inspired by similar tables completed in Rood *et al.* (2003) and Colvin *et al.* (2007).

CONCLUSION

This work has added to our understanding of the water sourcing and drought adaptations, interspecies effects on water availability and tree health in relation to groundwater depth for four key riparian species occurring in the Namib and the Kalahari Deserts. Much previous work in Southern Africa was based on observations of mortality, community structure analyses and recruitment studies (Theron *et al.*, 1985; Rőssing, 2003 *unpublished report*; Moser, 2006) and some reports have started to look at including riparian vegetation in EWR's (Birkhead *et al.*, 1997; Botha, 2001) and to determine groundwater dependence (Colvin *et al.*, 2002; 2007). One study in Botswana has employed ecophysiological approaches to establish evapotranspiration from deep rooting vegetation (Obakeng, 2007). This study applied ecophysiological methods and provided insight into the interaction between larger flood pulses, consequent groundwater recharge and soil wetting and soil/groundwater dependence of indigenous riparian tree species. It has shown that within the riparian zone, indigenous *A. erioloba* are significantly water stressed when *P. glandulosa* is established, while niche partitioning for water resources occurs further inland between the two species. It has also led to some drought vulnerability comparisons with *A. erioloba* being most tolerant and *F. albida* most vulnerable among the investigated species. Finally, Chapter 6 findings suggest that tree health and functioning correspond proportionally to groundwater depth. The perspectives, species information and applied methods in this study provide added perspective for when future EWR methods attempt to integrate riparian vegetation and groundwater.

FUTURE RESEARCH

Despite their frequent occurrence, ephemeral river systems are barely understood. So even in the progressive situation of South Africa where legislative frameworks protect the water needs of ephemeral river riparian vegetation, the existing knowledge gaps currently make the determination of sustainable water abstraction rates and the development of sustainable management strategies near-impossible. This shortcoming is now addressed in South Africa, where research is underway to formulate 'Environmental Water Requirement' methods for ephemeral rivers (Rossouw 2005). This process is challenging because ephemeral systems are strongly defined by pulse floods, groundwater and terrestrial riparian vegetation. All these aspects are notoriously difficult to assess, and their full scope of application has been limited because EWR methods have been developed by aquatic ecologists with a definite focus on surface water and aquatic lifeforms. An inclusion of non-aquatic disciplines is required to reformulate and develop EWR methods that appropriately address the subsurface and terrestrial faunal and floral aspects non-perennial rivers.

The new EWR method currently in development for South African non-perennial rivers highlights the high riparian habitat variability between rivers, from pool to dry riverbed habitat and from up-to downstream (Seaman *et al.*, 2009). Its vegetation perspective is still being formulated and to date it focuses on the structure, composition and variability of riparian vegetation zones (aquatic, marginal, lower and upper) and in how far they are influenced by drivers such as riparian soil water, height of water table, onset of flood, flood height and duration and periodicity of large flood events (Kemp, 2010, *pers. com.*). The arid areas in Southern Africa have several commonly occurring riparian tree species, some of which are *Acacia erioloba*, *Acacia karroo*, *Searsia lancea*, *Syzygium guineense, Faidherbia albida, Tamarix usneoides, Combretum imberbe*, *Combretum erythrophyllum, Colophospermum mopane* and *Ficus* species (Coates-Palgrave, 1983). A focus on such key species may be a possible route to consider, in order to understand their seedling establishment, water sourcing, rooting depth and growth and their health in relation to drivers such as flood onset, height and duration, groundwater depth and fluctuation and riparian soil moisture. Ultimately this information could lead to bioindicator species or the ability to categorise several species into functional groups. An ecophysiological understanding of common riparian species, gained by the methods applied in this thesis, will be highly valuable to consolidate the assumptions that the assigned vegetation specialists will have to make during EWR procedures. In the USA Stromberg *et al.* (1996) and Merritt *et al.* (2009) suggest that future research may consider the identification of key species that represent whole categories of species assemblies. These indicator species may be used to inform the riparian vegetation water needs at a community level. The applicability of this concept in arid parts of Southern Africa still requires investigation and the contribution of ecophysiologists to the EWR process needs to be translated so that it can be meaningfully applied in the EWR process.

REFERENCES

Abrams, M.M., Jacobson, P.M., Jacobson, K.M. and Seely, M.K. 1997. Survey of soil chemical properties across a landscape in the Namib Desert. *Journal of Arid Environments.* 35: 29-38.

ACITS. 1997. *Repeated measured ANOVA using SPSS Manova*. University of Texas at Austin. http://www.utexas.edu/cc/docs/stat38.html (12 March 2007)

Adar, E.M., Gev, I., Berliner, P. and Issar, A.S. 1995. The effect of forestation on a shallow groundwater reservoir in an arid sand dune terrain. *Journal of Arid Land Studies.* 58: 259-262.

Alder, N.N., Pockman, W.T., Sperry, J.S. and Nuismer, S. 1997. Use of centrifugal force in the study of xylem cavitation. *Journal of Experimental Botany.* 48: 665-674.

Amlin, N.M. and Rood, S.B. 2003. Drought stress and recovery of riparian cottonwoods due to water table alteration along Willow Creek, Alberta. *Trees.* 17: 351-358.

Anderson, M.D. and Anderson, T.A. 2001. Too much too quickly? Doubts about the sustainability of the camelthorn wood harvest. *African Wildlife.* 55: 21 – 23.

Aston, T. 2007. Geohydrological characteristics of Table Mountain Group aquifer-fed seeps and the plant ecophysiological consequences. Unpublished Master’s Thesis, Botany Department, University of Cape Town, Cape Town, South Africa.

Baas, P. 1976. Some functional and adaptive aspects of vessel member morphology. In Baas, P., Bolton, A. J. and Catling, D. M. ed. Wood structure in biological and technological research, Leiden Botanical Series No. 3, Leiden University Press, 157-181.

Bailey, I.W. 1916. The structure of the bordered pits of conifers and its bearing upon the tension hypothesis of the ascent of sap in plants. *Botanical Gazette*. 62:133-145.

Bao H., Thiemens, M.H. and Heine, K. 2001. Oxygen-17 excesses of the Central Namib gypcretes: spatial distribution. *Earth and Planetary Science Letters.* 192: 125-135.

Barnes, M.E. 2001 (a). Seed predation, germination and seedling establishment of *Acacia erioloba* in northern Botswana. *Journal of Arid Environments*. 49: 541-554.

Barnes, M.E. 2001 (b). Effects of large herbivores and fire on the regeneration of *Acacia erioloba* woodlands in Chobe National Park, Botswana. *African Journal of Ecology*. 39: 340-350.

Barnes, R.D., Fagg, C.W. and Milton S.J. 1997. *Acacia erioloba* Monograph and annotated Bibliography. *Tropical Forestry Papers No. 35*. Oxford Forestry Institute, Department of Plant Sciences, University of Oxford.

Basson, W. 2009. Freshwater ecosystems protected for a water-safe future. *ScienceScope*. 4 (2): 8-9.

Bate, G.C. and Walker, B.H. 1980. Water use by the vegetation in the lower Kuiseb River, South West Africa, and the possible effects on this vegetation of water extraction. Unpublished report, University of the Witwatersrand, Johannesburg, South Africa.

Bate, G.C. and Walker, B.H. 1993. Water relations of the vegetation along the Kuiseb River, Namibia. *Madoqua*. 18: 85-91.

Bethune, S. 1996. Sustainable water use. Namibia Environment 1, 185-190.

Birkhead, A.L., Olbrich, B.W., James, C.S. and Rogers, K.H. 1997. *Developing and integrated approach to predicting the water use of riparian vegetation.* Water Research Commission Report: 474/1/97.

Bormann, F.H. and Kozlowski, T.T. 1962. Measurements of tree growth with dial gauge dendrometers and vernier tree ring bands. *Ecology*. 43: 289-294.

Botha, M. 2001. *Dynamics of two South African floodplain forests*. Water Research Commission Report: KV 131/01.

Boulton, A.J., Sheldon, F., Thoms, M.C. and Stanley, E.H. 2000. Problems and constraints in managing rivers with variable flow regimes. In Boon, P.J., Davies, B.R. and Petts, G.E. ed. *Global perspectives on river conservation: Science, Policy and Practice*. Wiley, Chichester: John Wiley and Sons: 411-426.

Brock, M.A., Capon, S.J. and Porter, J.L. 2006. Disturbance of plant communities dependent on desert rivers. In Kingsford, R.T. *Ecology of desert rivers*. New York: Cambridge University Press, 100-132.

Brodribb, T.J. and Holbrook, N.M. 2005. Water stress deforms tracheids peripheral to the leaf vein of a tropical conifer. *Plant Physiology*. 137: 1139-1146.

Brown, C.J., Macdonald. I.A.W. and Brown, S.E. 1985. *Invasive alien organisms in South West Africa/Namibia.* Pretoria: Foundation for Research Development.

Brown C.J. and Gubb, A.A. 1986. Invasive alien organisms in the Namib Desert, Upper Karoo and semi-arid savannas of western southern Africa. In Macdonald, I.A.W., Kruger, F.J. and Ferrar., A.A. ed. *The ecology and management of biological invasions in Southern Africa.* Cape Town: Oxford University Press: 93-108.

Brown, C. and King, J. 2002. Environmental flows, requirements and assessments. In Hirji, R., Johnson, P., Maro, P. Matiza-Chiuta, T. ed. *Defining and mainstreaming environmental sustainability in Water Resources Management in Southern Africa.* Maseru/Harare/Washington DC: SADC, IUCN, SARDC, World Bank.

Brown, C.J., McDonald, I.A.W. and Brown, S.E. 1985. *Invasive alien organisms in South West Africa/Namibia.* South African National Scientific Programmes Report No 119, Foundation for Research Development, Pretoria.

Brown, C.J. and Gubb, A.A. 1986. Invasive alien organisms in the Namib Desert, Upper Karoo and the arid and semi-arid savannas of western southern Africa. In Macdonald, I.A.W., Kruger, F.J. and Ferrar, A.A. *The Ecology and Management of Biological Invasions in Southern Africa.* Cape Town, Oxford University Press, 93-108.

Brown, C.J. 1990. Potential impacts of prospecting and mining in desert environments. In *Environmental implications of the prospecting and mining in the Namib.* The Geological Society of Namibia and the Desert Ecological Research Unit of Namibia, Windhoek: 12.

Burgess, S.S.O. and Dawson, T.E. 2007. Predicting the limits to tree height using statistical regressions of leaf traits. *New Phytologist.* 174: 626-636.

Busch, D.E., Ingraham, N.L. and Smith, S.D. 1992. Water uptake in woody riparian phreatophytes of the Southwestern United States: a stable isotope study. *Ecological Applications.* 2 (4): 450-459.

Canadell, J., Jackson, R.B., Ehleringer, J.R., Mooney, H.A., Sala, O.E. and Schulze, E.D. 1996. Maximum rooting depth of vegetation types at the global scale. *Oecologia.* 108: 583-595.

Carlquist, S. 1977. Ecological factors in wood evolution: a floristic approach. *American Journal of Botany.* 64 (7): 887-896.

Cavelier, J. and Goldstein, G. 1989. Mist and fog interception in elfin cloud forest in Colombia and Venezuela. *Journal of Tropical Ecology*. 5: 309-322.

Cavelier, J., Solis, D. and Jaramillo, M.A. 1996. Fog interception in montane forests across the Central Cordillera of Panamá. *Journal of Tropical Ecology*. 12: 357–369.

Centre Technique Forestier Tropical. 1989. *Faidherbia albida a Monograph.* Nogent sur Marne, France: CIRAD.

Christelis, G. and Struckmeier, W. 2001. *Groundwater in Namibia*. Namibia: Ministry of Agriculture, Water and Rural Development.

Coates-Palgrave, K.C. 1983. *Trees of Southern Africa.* South Africa: Struik Publishers.

Cochard, H. and Tyree, M.T. 1990. Xylem disfunction in Quercus: vessel size, tyloses, cavitation and seasonal changes in embolism. *Tree Physiology.* 6: 393-407.

Cohn, J.P. 2005. Tiff over the Tamarisk: can a nuisance be nice, too? *BioScience.* 55 (8): 648-654.

Coleman, M.L., Shepherd, T.J., Durham, J.J., Rouse, J.E. and Moore, G.R. 1982. Reduction of Water with Zinc for Hydrogen isotope analysis. *Analytical Chemistry.* 54: 993-995.

Colvin, C., le Maitre, D., Hughes, S. 2002. *Assessing terrestrial groundwater dependent ecosystems in South Africa.* Water Research Commission Report: 1090-2/2/03.

Colvin, C., le Maitre, D., Saayman, I. and Hughes, S. 2007. *Aquifer dependent ecosystems in key hydrogeological typesettings in South Africa*. Water Research Commission Report: TT 301/07.

Cooper, D.J., D'Amico, D.R. and Scott, M.L. 2003. Physiological and morphological response patterns of *Populus deltoids* to alluvial groundwater pumping. *Environmental Management.* 31 (2): 215-226.

Cooper, D.J., Sanderson, J.S., Stannard, D.I. and Groenewald, D.P. 2006. Effects of long-term water table drawdown on evapotranspiration and vegetation in an arid region phreatophyte community. *Journal of Hydrology.* 325: 21 – 34.

Craig, H. 1957. Isotope standards for carbon and oxygen and correction factors for mass spectrometric analysis of carbon dioxide. *Geochimica et Cosmochimica Acta.* 12: 133-149.

Craig, H. 1961. Isotopic variations in meteoric waters. *Science.* 133: 1702-1703.

Cramer, V.A., Thorburn, P.J. and Fraser, G.W. 1999. Transpiration and groundwater uptake from farm forest plots of *Casuarina glauca* and *Eucalyptus camaldulensis* in saline areas of southeast Queensland, Australia. *Agricultural Water Management.* 39: 187-204.

Craven, P. and Marais, C. 1986. *Namib Flora.* Windhoek: Gamsberg Macmillan.

Crombie, D.S. 1992. Root depth, leaf area and daytime water relations of Jarrah (*Eucalyptus marginata*) Forest overstorey and understorey during summer drought. *Australian Journal of Botany.* 40: 113-122.

Cunningham, A. 2008. The geology and mineralogy of uranium deposits in Namibia: A brief overview. *Roan News, Special Edition on Uranium Mining and Mining in Parks.* March 2008, 5-6.

Curtis, B.A. and Mannheimer, C.A. 2005. *Tree Atlas of Namibia.* Windhoek, Namibia: National Botanical Research Institute, Ministry of Agriculture, Water and Rural Development.

Dahan, O. 2007. Monitoring floodwater infiltration and recharge in ephemeral rivers. Paper presented at the International workshop on Groundwater recharge in ephemeral rivers of Southern Africa: Implications for water management, 27 November 2007, Cape Town, South Africa.

Dahan, O., Tatarsky, B., Enzel, Y., Kuells, C., Seely, M.K. and Benito, G. 2008. Dynamics of flood-water infiltration and groundwater recharge in hyperarid Desert. *Groundwater.* 46 (3): 450-461.

Dangasuk, O.G., Gudu, S. and Okalebo, J.R. 2001. Early growth performance of sixteen populations of *Faidherbia albida* in semi-arid Baringo District in Kenya. In Scott, D.E., Mohtar, R.H. and Steinhardt, G.C. ed. *Sustaining the Global Farm*. Selected papers from the 10th International Soil Conservation Organization Meeting held May 24 – 29, 1999 at Purdue University and the USDA-ARS National Soil Erosion Research Laboratory: 412-418.

Darwall, W.R.T., Smith, K.G., Tweddle, D. and Skelton, P. 2009. *The status and distribution of freshwater biodiversity in Southern Africa.* Switzerland: IUCN.

Davies, B.R., O'Keeffe J.H. and Snaddon, C.D. 1993. *A synthesis of the ecological functioning, conservation and management of South African river systems*. Pretoria: Water Research Commission Report: TT62/93.

Dawson, T.E. and Ehleringer, J.R. 1991. Streamside trees that do not use stream water. *Nature.* 350: 335-337.

Dawson, T.E. and Pate, J.S. 1996. Seasonal water uptake and movement in root systems of Australian phreatophytic plants of dimorphic root morphology: a stable isotope investigation. *Oecologia.* 107: 13-20.

Dawson, T.E. 1998. Fog in the California redwood forest: ecosystem inputs and use by plants. *Oecologia.* 117: 476-485.

Dawson, T.E., Mambelli, S., Plamboeck, A.H., Templer, P.H. and Tu, K.P. 2002. Stable isotopes in plant ecology. *Annual Review of Ecology and Systematics*. 33: 507-559.

Dean, W.R.J., Milton, S.J. and Jeltsch, F. 1999. Large trees, fertile islands, and birds in arid savanna. *Journal of Arid Environments.* 41: 61-78.

Dean, W.R.J., Anderson, M.D., Milton, S.J. and Anderson, T.A. 2002. Avian assemblages in native Acacia and alien Prosopis drainage line woodland in the Kalahari, South Africa. *Journal of Arid Environments.* 51: 1-19.

Department of Water Affairs and Forestry. 1997. *The working for water programme, 1996/97 Annual Report.*South Africa.

De Wit, M. and Stankiewicz, J. 2006. Changes in surface water supply across Africa with predicted climate change. *Science.* 311: 1917-1921.

Dupuy, N.C and Dreyfus, B. 1992. Bradrhyzobium populations occur in deep soil under the leguminous tree *Acacia albida. Applied and Environmental Microbiology.* 58 (8): 2415-2419.

Eccard, J.A., Dean, W.R.J., Wichmann, M.C., Huttunen, S.M., Eskelinen, E., Moloney, K.A. and Jeltsch, F. 2006. Use of large *Acacia* trees by the cavity dwelling Black-tailed tree rat in the southern Kalahari. *Journal of Arid Environments.* 64: 604-615.

Ehleringer, J.R. 1984. Intraspecific competitive effects on water relations, growth and reproduction in *Encelia farinose. Oecologia.* 63: 153-158.

Ehleringer, J.R. and Cooper, T.A. 1988. Correlations between carbon isotope ratio and microhabitat in desert plants. *Oecologia*. 76: 562-566.

Ehleringer, J.R. and Dawson, T.E. 1992. Water uptake by plants: perspectives from stable isotope composition. *Plant, Cell and Environment.* 15: 1073-1082.

Ehleringer, J.R. 1993 (a). Carbon and water relations in desert plants: an isotopic overview. In Ehleringer, J.R., Hall, A.E., Farquhar, G.D. *Stable Isotopes and Plant-Carbon – Water relations*, San Diego, CA, USA: Academic Press: 155-171.

Ehleringer, J.R. 1993 (b). Variation in leaf carbon isotope discrimination in *Encelia farinose*: implications for growth, competition, and drought survival. *Oecologia.* 95: 340-346.

Ellsworth, P.Z. and Williams, D.G. 2007. Hydrogen isotope fractionation during water uptake by woody xerophytes. *Plant Soil.* 291: 93-107.

Evans, R.D. and Ehleringer, J.R. 1994. Water and nitrogen dynamics in an arid woodland. *Oecologia.* 99: 233-242.

Farquhar, G.D., Hubick, K.T., Condon, A.G. and Richards, R.A. 1989. Carbon isotope fractionation and plant water-use efficiency. In Rundell, P.W., Eherlinger, J.R. and Nagy, K.A. ed. *Stable isotopes in ecological research.* New York, USA: Springer: 21-40.

February, E.C. 1994. Rainfall reconstruction using wood charcoal from two archaeological sites in South Africa. *Quaternary Research.* 42: 100-107.

February, E.C., Stock, W.D., Bond, W.J. and le Roux, D.J. 1995. Relationship between water availability and selected vessel characteristics in *Eucalyptus grandis* and two hybrids. *IAWA Journal*. 16: 269-276.

February, E.C. and Manders, P. 1999. Effects of water supply and soil type on growth, vessel diameter and vessel frequency in seedlings of three fynbos shrubs and two forest trees. *South African Journal of Botany*. 65 (5-6): 382-387.

February, E.C., Higgins, S.I., Newton, R. and West, A.G. 2007 (a). Tree distribution on a steep environmental gradient in an arid savanna. *Journal of Biogeography*. 34: 270-278.

February, E.C., West, A.G. and Newton, R. 2007 (b). The relationship between rainfall, water source and growth for an endangered tree. Austral Ecology. 32 (4): 397-402.

Franklin, J.F., Shugart, H.H. and Harmon, M.E. 1987. Tree death as an ecological process. *Bioscience*. 27: 259-288.

Gabriel, G. and Jauze, L. 2008. Fog water interception by *Sophora denudata* trees in a Reunion upper-montane forest, Indian Ocean. *Atmospheric Research*. 87: 338–351.

Gat, J.R. 1996. Oxygen and hydrogen isotopes in the hydrologic cycle. *Annual Review of Earth and Planetary Science*. 24: 225-262.

Gebauer, R.L.E., Schwinning, S. and Ehleringer, J.R. 2002. Interspecific competition and resource pulse utilization in a cold desert community. *Ecology*. 83 (9): 2602-2616.

Gillespie, R.D., Sym, S.D. and Rogers, K.H. 1998. A preliminary investigation of the potential to determine the age of individual trees of *Breonadia salicina* (Rubiaceae) by relating xylem vessel diameter and area to rainfall and temperature data. *South African Journal of Botany*. 64 (6): 316-321.

Glen, E.P. and Nagler, P. L. 2005. Comparative ecophysiology of *Tamarix ramosissima* and native trees in western U.S. riparian zones. *Journal of Arid Environments*. 61: 419-446.

Glenn, E., Tanner, R., Mendez, S., Kehret, T., Moore, D., Garcia, J. And Valdes, C. 1998. Growth rates, salt tolerance and water use characteristics of native and invasive riparian plants from the delta of the Colorado River, Mexico. *Journal of Arid Environments*. 40: 281-294.

González Rodríguez, H., Cantu Silva, I., Gómez Meza, M.V. and Jordan, W.R. 2000. Seasonal plant water relationships in *Acacia berlandieri*. *Arid soil Research and Rehabilitation*. 14: 343-357.

Hacke, U.G., Sperry, J.S. and Pittermann, J. 2000. Drought experience and cavitation resistance in six shrubs from the Great Basin, Utah. *Basic Applied Ecology.* 1: 31-41.

Hacke, U.G., Sperry, J.S., Pockman, W.T., Davis, S.D. and McCulloh, K.A. 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia.* 126: 457-461.

Harding, G.B. 1987. Review- The status of *Prosopis* as a weed. *Applied Plant Science.* 1 (1): 43-48.

Hattle, A. 1985. Surface water hydrology of the Kuiseb. In Huntley, B.J. ed. 1985. *The Kuiseb environment: the development of a monitoring baseline.* South Africa. South African National Scientific Programmes Report: no. 106: 27-32.

Hedman, E.R. and Osterkamp, W.R. 1982. Streamflow characteristics related to channel geometry of streams in Western United States. *U.S. Geological Survey Water Supply Paper*. 2193: 1-17.

Henschel J.R. and Seely M.K. 2008. Ecophysiology of atmospheric moisture in the Namib Desert. *Atmospheric Research*. 87: 362-368.

Heyns, P., Montgomery, S., Pallett, J. and Seely M.K. ed. 1998. *Namibia's water, a decision makers guide.* Windhoek, Namibia: Ministry of Agriculture, Water and Rural Development/ Desert Research Foundation of Namibia.

Horton, J.L. and Clark, J. 2001. Water table decline alters growth and survival of *Salix gooddingii* and *Tamarix chinensis* seedlings. *Forest Ecology and Management.* 140: 239-247.

Horton, J.L, Kolb, T.E. and Hart, S.C. 2001 (a). Responses of riparian trees to interannual variation in groundwater depth in a semi-arid river basin. *Plant, Cell and Environment.* 24: 293-304.

Horton, J.L, Kolb, T.E. and Hart, S.C. 2001 (b). Physiological response to groundwater depth varies among species and with river flow regulation. *Ecological Applications.* 11 (4): 1046-1059.

Horton, J.L, Hart, S.C. and Kolb, T.E. 2003. Physiological condition and water source use of Sonoran Desert riparian trees at the Bill Williams River, Arizona, USA. *Isotopes Environment and Health Studies.* 39 (1): 69-82.

Hou, P., Beeton, R.J.S., Carter, R.W., Dong, X.G. and Li, X. 2007. Response to environmental flows in the lower Tarim River, Xinjiang, China: Ground water. *Journal of Environmental Management*. 83: 371-382.

Hultine, K.R., Koepke, D.F., Pockman, W.T., Fravolini, A., Sperry, J.S. and Williams, D.G. 2005. Influence of soil texture on hydraulic properties and water relations of a dominant warm-desert phreatophyte. *Tree Physiology.* 26: 313-323.

Huntley, B.J. ed. 1985. *The Kuiseb environment: the development of a monitoring baseline.* South Africa. South African National Scientific Programmes Report: no. 106: 7-20.

Impson, F.A.C., Moran, V.C. and Hoffman, J.H. 1999. A review of the effectiveness of seed-feeding bruchid beetles in the biological control of Mesquite, Prosopis species (Fabaceae), in South Africa. *African Entomology. Biological control of weeds in South Africa (1990 – 1998).* Memoir 1: 81-88.

Iponga, D.M., Milton, S.J. and Richardson, D.M. 2008. Superiority in competition for light: A crucial attribute defining the impact of the invasive alien tree *Schinus molle* (Anacardiaceae) in South African savanna. *Journal of Arid Environments.* 72: 612-623.

Jacobsen, A.L., Agenbag, L., Esler, K.J., Pratt, R.B., Ewers, F.W. and Davis, S.D. 2007. Xylem density, biomechanics and anatomical traits correlate with water stress in 17 evergreen shrub species of the Mediterranean-type climate region of South Africa. *Journal of Ecology.* 95: 171-183.

Jacobson, P., Jacobson, K. and Seely, M.K. 1995. *Ephemeral rivers and their catchments, sustaining people and development in western Namibia.* Windhoek, Namibia: Desert Research Foundation of Namibia.

Jacobson, P. 1997. An ephemeral perspective of fluvial ecosystems: viewing ephemeral rivers in the context of current lotic ecology. PhD Thesis. Virginia Polytechnic Institute and State University, USA.

Jarbeau, J.A., Ewers, F.W. and Davis, S.D. 1995. The mechanism of water stress-induced embolism in two species of Chaparral shrubs. *Plant, Cell and Environment.* 18: 1-8.

Junk, W.J., Bayley, P.B. and Sparks, R.E. 1989. The flood pulse concept in river floodplain systems. In Dodge, D.P. ed. Proceedings of the International Large River Symposium. *Canadian Special Publication of Fisheries and Aquatic Sciences*. 6: 110-127.

Kemper, N. and Boucher, C. 2000. Vegetation. In King, J.M., Tharme, R.E. and de Villiers, M.S. ed. *Environmental Flow Assessments for rivers: manual for the Building Block Methodology.* Water Research Commission Report: TT 131/00.

Kemper, N.P. 2001. *(RVI) Riparian Vegetation Index.* Water Research Commission Report: 850/3/01.

King, J.M., Tharme, R.E., de Villiers, M.S. ed. 2000. *Environmental Flow Assessments for rivers: Manual for the Building Block Methodology*. Water Research Commission Report: TT131/00.

King, J.M. 2004. Environmental Water Requirements, Proceedings of a one-day open conference. Water Research Commission Report: K5/1414.

King, J.M and Brown, C. 2006. Environmental flows: striking the balance between development and resource protection. Ecology and Society. 11(2): 26. (online) URL: http://www.ecologyandsociety.org/vol11/

Kingsford, R.T. 2000. Protecting rivers in arid regions or pumping them dry? *Hydrobiologica*. 427: 1 – 11.

Kleynhans, C.J., Mackenzie, J. and Louw, M.D. 2007. River ecoclassification: manual for ecostatus determination (Version 2) Module F: Riparian vegetation response assessment index (VEGRAI) Water Research Commission Report: TT 329/08.

Kleynhans, C.J. and Louw, M.D. 2008. River ecoclassification: manual for ecostatus determination (Version 2) Module A: ecoclassification and ecostatus determination. Water Research Commission Report: TT 329/08.

Koch, G.W., Sillett, S.C., Jennings, G.M. and Davis, S.D. 2004. The limits to tree height. *Nature*. 428: 851-854.

Komor, S.C. and Emerson, D.G. 1994. Movements of water, solutes, and stable isotopes in the unsaturated zones of two sand plains in the upper Midwest. *Water Resources Research*. 30(2): 253-267.

Kozlowski, T.T. and Winget, C.H. 1964. Diurnal and seasonal variation in radii of tree stems. *Ecology*. 45: 149-155.

Kuells, C., Haring, M., Klaus, J., Wachter, A. and Eichinger, L. 2007. Reconnaissance field methods for the fast identification and estimation of flood recharge. Paper presented at the International workshop on Groundwater recharge in ephemeral rivers of Southern Africa: Implications for water management, 27 November 2007, Cape Town, South Africa.

Lancaster, J., Lancaster, N. and Seely, M.K. 1984. Climate and the central Namib Desert. *Madoqua*. 14: 5-61.

Le Maitre, D.C. 1999. *Prosopis and groundwater: a literature review and bibliography*. South Africa: Report for the Department of Water Affairs and Forestry.

Lerner, D.N. 2003. Surface water – groundwater interaction in the context of groundwater resources. In: Xu, Y. and Beekman, H.E. 2003. *Groundwater recharge estimation in Southern Africa*. Paris, France: UNESCO: 91-107.

Le Roux, D., Stock, W.D., Bond, W.J. and Maphanga, D. 1996. Dry mass allocation, water use efficiency and δ^{13}C in clones of *Eucalyptus grandis, E. grandis* X *camaldulensis* and *E. grandis* X *nitens* grown under two irrigation regimes. *Tree Physiology*. 16: 497-502.

Li, Y., Sperry, J.S. and Shao, M. 2009. Hydraulic conductance and vulnerability to cavitation in corn (*Zea mays* L.) hybrids of differing drought resistance. *Environmental and Experimental Botany*. 66: 341-346.

Logan, R.F. 1960. *The Central Namib Desert.* National Academy of Sciences- National Research Council. Publication 758.

Lo Gullo, M.A. and Salleo, S. 1991. Three different methods for measuring xylem cavitation and embolism: a comparison. *Annals of Botany*. 67: 417-424.

Lo Gullo, M.A., Salleo, S., Piaceri, E.C. and Rosso, R. 1995. Relations between vulnerability to xylem embolism and xylem conduit dimensions in young trees of Quercus cerris. *Plant, Cell and Environment*. 18: 661-669.

Lopez, O.R., Kursar, T.A., Cochard, H. and Tyree, M.T. 2005. Interspecific variation in xylem vulnerability to cavitation among tropical tree and shrub species. *Tree Physiology*. 25: 1553-1562.

Louw, G.N. and Seely M.K. 1980. Exploitation of fog water by perennial Namib dune grass *Stipagrostis sabulicola*. *South African Journal of Science*. 76: 38-39.

Lubczynski, M.W. 2009. The hydrogeological role of trees in water-limited environments. *Hydrogeological Journal*. 17: 247-259.

Mace, A.C. 1971. Osmotic water stress: Mesophyll saturation deficit and transpiration rates of Tamarisk. *The Southwestern Naturalist*. 16 (1): 117-120.

MacKay, H. and Moloi, B. 2002. The importance of instream flow requirements for decision-making in the Okavango River basin. In Turton, A., Ashton, P. and Cloete, E. ed. *Transboundary Rivers, sovereignity and development: Hydropolitical drivers in the Okavango River basin.* Pretoria, South Africa: AWIRU and Green Cross International.

Mahoney, J.M. and Rood, S.B. 1998. Streamflow requirements for cottonwood seedling recruitment – an integrative model. *Wetlands*. 18(4): 634-645.

Marker, M.E. 1977. Aspects of the geomorphology of the Kuiseb River, South West Africa. *Madoqua.* 10 (3): 199-206.

Martinez-Vilalta, J.M., Prat, E., Oliveras, I. and Pinol, J. 2002. Xylem hydraulic properties of roots and stems of nine Mediterranean woody species. *Oecologia.* 133: 19-29.

McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D.G. and Yepez, E.A. 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist.* Transley Review: 1-15.

McMahon, T. A. 1979. Hydrological characteristics of arid zones. In The Hydrology of Areas of Low Precipitation. Canberra: IAHS–AISH.

Mencuccini, M. and Comstock, J. 1997. Vulnerability to cavitation in populations of two desert species, *Hymenoclea salsola* and *Ambrosia dumosa*, from different climatic regions. *Journal of Experimental Botany.* 48: 1323-1334.

Merritt, D.M., Scott, M.L., Poff, N.L., Auble, G.T. and Lytle, D.A. 2009. Theory, methods and tools for determining environmental flows for riparian vegetation: riparian vegetation-flow response guilds. *Freshwater Biology*. 55: 206-225.

Meyer, R., Duvenhage, A.W.A., de Beer, J.H. and Huyssen, R.M.J. 1985. A geophysical-geohydrological study along the Kuruman River in the Kuruman and Gordonia districts. *Transactions Geological Sociely of South Africa.* 88: 501-515.

Middleton, N.J. and Thomas, D.S.G. 1997. *World Atlas of Desertification.* 2nd ed. London: UNEP.

Milton, S.J. 1991. Plant spinescence in arid southern Africa: does moisture mediate selection by animals? *Oecologia.* 87: 279-287.

Milton, S.J. and Dean, W.R.J. 1995. How useful is the keystone species concept, and can it be applied to *Acacia erioloba* in the Kalahari Desert? *Zeitschrift für Őkologie und Naturschutz.* 4: 147-156.

Mizuno K. 2010. Environmental change and vegetation succession along an ephemeral river: The Kuiseb in the Namib Desert. *African Study Monographs*. 40: 3-18.

Moser, P. and Henschel, J. 2004. !Nara use by people. In Henschel, J., Dausab, R., Moser, P. and Pallet, J. eds. *!Nara. Fruit for development of the !Khuiseb Topnaar.* Windhoek, Namibia: Namibia Scientific Society: 49-53.

Moser, P.M. 2006. Regeneration and utilization of *Faidherbia albida* and *Acacia erioloba* along ephemeral rivers of Namibia. *Ecology and Development Series. No 42*. Göttingen, Germany: Cuvillier Verlag.

Moustakas, A., Guenther, M., Wiegand, K., Mueller, K.H., Ward, D., Meyer, K., Jeltsch, F. 2006. Long-term mortality patterns of the deep-rooted Acacia erioloba: The middle class shall die! *Journal of Vegetation Science*. 17 (4): 473-480.

Mucina, L. and Rutherford, M.C. 2006. *The vegetation of South Africa, Lesotho and Swaziland*. Strelizia 19. Pretoria: Sanbi.

Naiman, R.J. and Décamps, H. ed. 1990. *The ecology and management of aquatic-terrestrial ecotones*. Carnforth, UK: UNESCO, Paris and Parthenon Publishing Group.

Naiman, R.J., Décamps, H. and Pollock, M. 1993. The role of riparian corridors in maintaining regional biodiversity. *Ecological Applications.* 3: 209-212.

Namibia Water Resources Management Review. 2000. *Socio-economics and financial issues.* Theme Report. Windhoek. Ministry of Agriculture, Water and Rural Development.

Namibia. Water Resources Management Act of 2004.

Nilsen, E.T., Rundell, P.W., Sharifi, M.R. 1981. Summer water relations of the desert phreatophytes *P. glandulosa* in the Sonoran Desert of Southern California. *Oecologia*. 50 (2): 271-276.

Nilsen, E.T., Sharifi, M.R., Rundell, P.W., Jarrell, W.M. and Virginia, R.A. 1983. Diurnal and seasonal water relations of the desert phreatophyte *P. glandulosa* (honey mesquite) in the Sonoran Desert of California. *Ecology.* 64: 1381-1393.

Nilsen, E.T., Sharifi, M.R. and Rundell, P.W. 1984. Comparative water relations of phreatophytes in the Sonoran desert of California. *Ecology.* 65 (3): 767-778.

Nilsson, C. and Berggren, K. 2000. Alterations of riparian ecosystems caused by river regulation. *BioScience.* 50 (9): 783-792.

Noy-Meir, I. 1973. Desert ecosystems, environment and producers. *Annual Review of Ecology and Systematics.* 4: 25-41.

Obakeng, O.T. 2007. Soil moisture dynamics and evapotranspiration at the fringe of the Botswana Kalahari, with emphasis on deep rooting vegetation, unpublished PhD Thesis, Dissertation No. 141, ITC, Netherlands.

O'Connor, T.G. 2001. Effect of small catchment dams on downstream vegetation of a seasonal river in semi-arid African savanna. *Journal of Applied Ecology.* 38: 1314-1325.

O'Grady, A.P., Eamus, D., Cook, P.G. and Lamontagne, S. 2005. Comparative water use by the riparian trees *Melaleuca argentea* and *Corymbia bella* in the wet-dry tropics of northern Australia. *Tree Physiology*. 26: 219-228.

O'Keefe, J. 2000. Environmental flow assessments: background and assumptions. In King, J.M., Tharme, R.E. and de Villiers, M.S. ed. *Environmental Flow Assessments for rivers: manual for the Building Block Methodology*. Water Research Commission Report: TT 131/00.

Pallett, J. 2008. Cumulative environmental risks of uranium mining. *Roan News, Special Edition on Uranium Mining and Mining in Parks,* March 2008, 13-14.

Pammenter, N.W. and van der Willigen, C. 1998. A mathematical and statistical analysis of the curves illustrating vulnerability of xylem to cavitation. *Tree Physiology.* 18: 589-593.

Phillips, D.L. and Gregg, J.W. 2003. Source partitioning using stable isotopes: coping with too many sources. *Oecologia.* 136: 261-269.

Phillips, D.L., Newsome, S.D. and Gregg, J.W. 2005. Combining sources in stable isotope mixing models: alternative methods. *Oecologia.* 144: 520- 527.

Pockman, W.T. and Sperry, J.S. 2000. Vulnerability to xylem cavitation and the distribution of Sonoran Desert vegetation. *American Journal of Botany.* 87 (9): 1287-1299.

Poff, N.L. and Ward, J.V. 1990. Physical habitat template of lotic systems: recovery in the context of historical pattern of spatiotemporal heterogeneity. *Environmental Management.* 14 (5): 629-645.

Powell, E. 2005. What is happening to the camel thorns of Kathu? *Veld & Focus,* March 2005, 34-35.

Quereteja, J.I., Estrada-Medina, H., Allen, M., Jiménez-Osornio, J.J. 2007. Water source partitioning among trees growing on shallow karst soils in a seasonally dry tropical climate. *Oecologia.* 152: 26-36.

Ractliffe, S.G. and King, J.M. 1997. Bulk water estimate of the instream flow requirements for the Malibamatso River technical memorandum. Cape Town: Southern Waters, No. 1-13/D10A/00.

Reich, P.B., Ellsworth, D.S., Walters, M.B., Vose, J.M., Gresham, C., Volin, J.C. and Bowman, W.D. 1999. Generality of leaf trait relationships: a test across six biomes. *Ecology*. 80(6): 1955-1969.

Reinecke, M.K., Pigot, A.L. and King, J.M. 2008. Spontaneous succession of riparian fynbos: is unassisted recovery a viable restoration strategy? *South African Journal of Botany*. 74: 412-420.

Reinecke, K. 2009. *Linking hydrology and lateral riparian vegetation zones*. WRC proposal # 1002956. Pretoria: Water Research Commission.

Ritchie, G.A. and Hinckley, T.M. 1975. The pressure chamber as an instrument for ecological research. *Advances in Ecological Research.* 9: 165-254.

Robertson, I., and Woodborne, S. 2002. Carbon isotopes confirm the competitive advantages of *Prosopis* over *Acacia erioloba*. *Study of Environmental Change using Isotope Techniques.* Vienna: International Atomic Energy Agency, IAEA-CSP-13/P.

Rood, S.B., Braatne, J.H. and Hughes, F.M.R. 2003. Ecophysiology of riparian cottonwoods: stream flow dependency, water relations and restoration. *Tree Physiology.* 23: 1113-1124.

Rössing Uranium. 2003. *Results of the Khan River vegetation survey at Rössing Uranium Mine.* Unpublished report to the Ministry of Agriculture, Water and Rural Development, Namibia.

Rossouw, L., Avenant, M.F., Seaman, M.T., King, J.M., Barker, C.H., du Preez, P.J., Pelser, A.J., Roos, J.C., van Staden, J.J., van Tonder, G.J. and Watson, M. 2005. Environmental Water requirements in non-perennial systems. Pretoria: Water Research Commission Report, No 1414/1/05.

Roupsard, O., Ferhi, A., Granier, A., Pallo, F., Depommier, D., Mallet, B., Joly, H.I. and Dreyer, E. 1999. Reverse phenology and dry-season water uptake by *Faidherbia albida* (Del.) A. Chev. in an agroforestry parkland of Sudanese west Africa. *Functional Ecology.* 13: 460-472.

Rundell, P.W. and Sharifi, M.R. 1993. Carbon isotope discrimination and resource availability in the desert shrub *Larrea tridentata. Journal of Experimental Botany.* 44: 481-487.

Sala, O.E., Golluscio, R.A., Lauenroth, W.K., Soriano, A. 1989. Resource partitioning between shrubs and grasses in a Patagonian steppe. *Oecologia.* 81: 501-505.

Sala, A., Smith, S.D. and Devitt, D.A. 1996. Water use by *Tamarix ramosissima* and associated pheatophytes in the Mojave desert floodplain. *Ecological Applications.* 6: 888-898.

Scholander, P.F., Hemmingsen, E. and Garey, W. 1961. *Science.* 134 (3493): 1835-1838.

Scholander, P.F., Hammel, H.T., Bradstreet, E.D. and Hemmingsen, E.A. 1965. Sap pressure in vascular plants. *Science.* 148: 339-346.

Schulze, E.D., Turner, N.C., Nicole, D. and Schumacher, J. 2006. Leaf and wood carbon isotope ratios, specific leaf areas and wood growth of Eucalyptus species across a rainfall gradient in Australia. *Tree Physiology.* 26 (4): 479-492.

Schume, H., Grabner, M. and Eckműllner, O. 2004. The influence of an altered groundwater regime on vessel properties of hybrid poplar. *Trees.* 18: 184-194.

Schwinning, S. and Ehleringer, J.R. 2001. Water use trade-offs and optimal adaptations to pulse-driven arid ecosystems. *Journal of Ecology.* 89: 464-480.

Scott, M.L., Shafroth, P.B., Auble, G.T. 1999. Responses of riparian cottonwoods to alluvial water table declines. *Environmental Management.* 23: 347-358.

Seaman, M.T., Avenant, M.F., Watson, M., King, J., Armour, J., Barker, C.H., Dollar, E., du Preez, P.J., Hughes, D., Rossouw, L. and van Tonder, G. 2009. *Developing a method for determining the environmental water requirements for non-perennial systems*. Draft Final Water Research Commission Report of Project: K5/1587.

Seely M.K. 1979. Irregular fog as a water source for desert dune beetles. *Oecologia*. 42: 213-227.

Seely, M.K. 1987. *Die Namib.* Windhoek, Namibia: Shell Oil Namibia.

Seely, M.K., Henderson, J., Heyns, P., Jacobson, P., Nakale, T., Nantanga, K. and Schachtschneider, K. 2003. Ephemeral and Endorheic river systems: their relevance and management challenges. In Turton, A., Ashton, P. and Cloete, E. ed. *Transboundary Rivers, sovereignity and development: Hydropolitical drivers in the Okavango River basin.* Pretoria, South Africa: AWIRU and Green Cross International: 187-212.

Selaolo, E.T. 1998. Tracer studies and groundwater recharge assessment in the eastern fringe of the Botswana Kalahari. PhD Thesis, Vrije University, Amsterdam.

Seymour, C.L. 2007. Grass, rainfall and herbivores as determinants of *Acacia erioloba* (Meyer) recruitment in an African savanna. *Plant Ecology.* 197: 131-138.

Seymour, C.L. and Huyser, O. 2008. Fire and the demography of camelthorn (*Acacia erioloba* Meyer) in the southern Kalahari – evidence for a bonfire effect? *African Journal of Ecology*. 46: 594-601.

Shafroth, P.B., Stromberg, J.C. and Patten, D.T. 2000. Woody riparian vegetation response to different alluvial water table regimes. *Western North American Naturalist*. 60(1): 66-76.

Shafroth, P.B., Cleverly, J.R., Dudley, T.L., Taylor, J.P., van Riper, C., Weeks, E.P. and Stuart, J.N. 2005. Control of *Tamarix* in the Western United States: Implications for water salvage, wildlife use and riparian restoration. *Environmental Management*. 35(3): 231-246.

Shanyengana E.S., Henschel J.R., Seely M.K. and Sanderson R.D. 2002. Exploring fog as a supplementary water source in Namibia. *Journal of Atmospheric Research*. 64: 251-259.

Shiferaw, H., Teketay, D., Nemomissa, S. and Assefa F. 2004. Some biological characteristics that foster the invasion of *Prosopis juliflora* (Sw.) DC. at Middle Awash Rift Valley Area, north-eastern Ethiopia. *Journal of Arid Environments.* 58: 135-154.

Shipley, B., Keddy, P.A., Moore, D.R.J. and Lemky, K. 1989. Regeneration and establishment strategies of emergent macrophytes. *Journal of Ecology*. 77: 1093-1110.

Shrestha, M.K., Stock, W.D., Ward, D. and Golan-Goldhirsch, A. 2003. Water status of isolated Negev Desert populations of Acacia raddiana with different mortality levels. *Plant Ecology.* 168 (2): 297-307.

Simonin, K.A., Santiago, L.S. and Dawson, T.E. 2009. Fog interception by *Sequoia sempervirens* (D. Don) crowns decouples physiology from soil water deficit. *Plant, Cell and Environment.* 32: 882-892.

Smith, S.D., Devitt, D.A., Sala, A., Cleverly, J.R. and Busch, D.E. 1998. Water relations of riparian plants from desert regions. *Wetlands*. 18: 687-696.

Snyder, K.A., Williams, D.G. and Gempko, V.L. 1998. Water source determination in cottonwood/willow and mesquite forests on the San Pedro river in Arizona. In Wood, E.F., Chebouni, A.G., Goodrich, D.C., Seo, D.J. and Zimmerman, J.R. ed. *Proceedings of Special Symposium Hydrology.* Boston, MA: American Meteorological Society: 185-188.

Snyder, K.A. and Williams, D.G. 2000. Water sources used by riparian trees varies among stream types on the Sam Pedro River, Arizona. *Agricultural and Forest Meteorology*. 105 (1-3): 227-240.

Snyder, K.A. and Williams, D.G. 2003. Defoliation alters water uptake by deep and shallow roots of *Prosopis velutina* (Velvet Mesquite). *Functional Ecology*. 17: 363-374.

Snyder, K.A., Donovan, L.A., James, J.J., Tiller, R.L. and Richards, J.H. 2004. Extensive summer water pulses do not necessarily lead to canopy growth of Great Basin and northern Mojave Desert shrubs. *Oecologia.* 141: 325-334.

Snyder, K.A. and Williams, D.G. 2007. Root allocation and water uptake patterns in riparian tree saplings: responses to irrigation and defoliation. *Forest Ecology and Management.* 246: 222-231.

Socki, R.A., Karlsson, H.R. and Gibson, E.K. 1992. Extraction technique for the determination of Oxygen – 18 in water using preevacuated glass vials. *Analytical Chemistry*. 64: 829-831.

South Africa. Water Act no. 36 of 1998.

Sperry J.S., Donnelly J.R. and Tyree M.T. 1988. A method for measuring hydraulic conductivity and embolism in xylem. *Plant, Cell and Environment.* 11: 35-40.

Sperry, J.S. and Hacke, U.G. 2002. Desert shrub water relations with respect to soil characteristics and plant functional type. *Functional Ecology*. 16: 367-378.

Sperry, J.S., Hacke, U.G., Oren, R. and Comstock, J.P. 2002. Water deficits and hydraulic limits to leaf water supply. *Plant, Cell and Environment.* 25: 251-263.

Sperry, J.S. and Tyree, M.T. 1990. Water-stress-induced xylem embolism in three species of conifers. *Plant, Cell and Environment*. 13 (5): 427-436.

Sperry J.S., Hacke, U.G. and Pittermann, J. 2006. Size and function in conifer tracheids and angiosperm vessels. Physiology and Biochemistry. *American Journal of Botany*. 93: 1490-1500.

Steenkamp, C.J., Vogel, J.C., Fuls, A., van Rooyen, N and van Rooyen, M.W. 2008. Age determination of *Acacia erioloba* trees in the Kalahari. *Journal of Arid Environments*. 72: 302-313.

Stengel, H.W. 1964. The rivers of the Namib and their discharge into the Atlantic, Part 1. Namibia: *Scientific Papers of the Namib Desert Research Station*, No. 22.

Stromberg, J.C. and Patten, D.T. 1990. Riparian vegetation instream flow requirements: a case study from a diverted stream in the Eastern Sierra Nevada, California, USA. *Environmental Management*. 14 (2): 185-194.

Stromberg, J.C., Tress J.A., Wilkins S.D. and Clark, S. 1992. Response of velvet mesquite to groundwater decline. *Journal of Arid Environments.* 23: 45-58.

Stromberg, J.C. and Patten, D.T. 1996. Instream flow and cottonwood growth in the eastern Sierra Nevada of California, USA. *Regulated Rivers.* 12: 1-12.

Stromberg, J.C., Tiller, R. and Richter, B. 1996. Effects of groundwater decline on riparian vegetation of semi-arid regions: the San Pedro, Arizona. *Ecological Applications.* 6: 113-131.

Stromberg, J.C. 2001. Restoration of riparian vegetation in the south-western United States: importance of flow regimes and fluvial dynamism. *Journal of Arid Environments.* 49: 17-34.

Stromberg, J.C., Beauchamp, V.B., Dixon, M.D., Lite, S.J. and Paradzick, C. 2007. Importance of low-flow and high-flow characteristics to restoration of riparian vegetation along rivers in arid south-western United States. *Freshwater Biology*. 52: 651-679.

Swiegers, W. 2008. Uranium in Namibia: Perspectives from the chamber of mines. *Roan News, Special Edition on Uranium Mining and Mining in Parks*, March 2008: 9-10.

Swift, C.C., Jacobs, S.M. and Esler, K.J. 2008. Drought induced xylem embolism in four riparian trees from the Western Cape Province: Insights and implications for planning and evaluation of restoration. *South African Journal of Botany.* 74: 508-516.

Tabacchi, E., Lambs, L., Guilloy, H., Planti-Tabacchi, A., Muller, E. and Décamps, H. 2000. Impacts of riparian vegetation on hydrologic processes. *Hydrological Processes*. 14: 2959-2976.

Tardieu, F. and Simonneau, T. 1998. Variability among species of stomatal control under fluctuating soil water status and evaporative demand: modelling isohydric and anisohydric behaviours. *Journal of Experimental Botany*. 49: 419-432.

Tharme R.E. 2003. A global perspective on environmental flow assessment: emerging trends in the development and application of environmental flow methodologies for rivers. *River Research and Applications.* 19: 397-441.

Theron, G.K., van Rooyen, N. and van Rooyen M.W. 1980. Vegetation of the lower Kuiseb River. *Madoqua.* 11 (4): 327-345.

Theron, G.K., van Rooyen, N., van Rooyen M.W. and Jankowitz, W.J. 1985. Vegetation structure and vitality in the lower Kuiseb. In Huntley, B.J. ed. *The Kuiseb environment: the development of a monitoring baseline.* South Africa: South African National Scientific Programmes Report, No. 106: 81-91.

Todd, S. and Hoffman, T. 2007. Riparian vegetation pattern and processes in the Buffels River, Namaqualand. Paper presented at the International workshop on Groundwater recharge in ephemeral rivers of Southern Africa: Implications for water management, 27 November 2007, Cape Town, South Africa.

Tyree, M.T. and Dixon, M.A. 1986. Water stress induced cavitation and embolism in some woody plants. *Physiologia Plantarum.* 66: 398-405.

Tyree, M.T. and Sperry, J.S. 1989. Vulnerability of xylem to cavitation and embolism. *Annual Review of Plant Physiology and Plant Molecular Biology*. 40: 19-38.

Tyree, M.T. and Ewers, F.W. 1991. The hydraulic architecture of trees and other woody plants, Transley Review, No. 34. *New Phytologist.* 119: 345-360.

Tyree, M.T., Kolb, K.J., Rood, S.B. and Patino, S. 1994. Vulnerability to drought-induced cavitation of riparian cottonwoods in Alberta: a possible factor in the decline of the ecosystem? *Tree Physiology*. 14: 455-466.

Tyree, M.T. and Zimmermann, M.H. 2001. *Xylem structure and the ascent of sap*. 2nd ed. Springer Verlag.

Tyson, P.D. and Crimp, S.J. 1999. The climate of the Kalahari transect. *Transactions of the Royal Society of South Africa*. 53 (2): 93-112.

Van der Walt, P. and le Riche, E. 1999. *The Kalahari and its plants*. South Africa, published by authors.

Vander Willigen, C. 1996. The relationship between xylem hydraulic characteristics, growth rates and water availability in Eucalyptus clones. Unpublished Masters Thesis, Department of Biology, University of Natal, Durban.

Van Rooyen, N., Bezuidenhout, H. and de Kock, E. 2001. *Flowering plants of the Kalahari Dunes*. South Africa: Ekotrust.

Van Rooyen, N. and van Rooyen, M.W. 1985. Vegetation of the lower Kuiseb River. In Huntley, B.J. ed. *The Kuiseb environment: the development of a monitoring baseline.* South Africa: South African National Scientific Programmes Report, No. 106: 73-80.

Van Rooyen, N. and van Rooyen, M.W. 1998. Vegetation of he South-western Kalahari: an overview. *Transactions of the Royal Society of South Africa*. 53: 113-140.

Van Wyk, A.J., Opperman D.P.J. and Kok, O.B. 1985. Availability, quality and utilization of the riverine vegetation of the lower Kuiseb and canyon area. In Huntley, B.J. ed. *The Kuiseb environment: the development of a monitoring baseline.* South Africa, South African National Scientific Programmes Report, No. 106: 107-112.

Van Wyk, B. and van Wyk, P. 1997. *Field guide to trees of Southern Africa*. Cape Town, South Africa: Struik Publishers.

Verhagen, B.Th. 1983. Environmental isotope study of a groundwater supply project in the Kalahari of Gordonia. International Symposium on isotope hydrology in water resource development, 1984. Vienna, Austria: International Atomic Energy Agency. 250 (50): 415-432.

Verhagen, B. Th. 1985. Isotope hydrology of groundwaters of the Kalahari, Gordonia. *Transactions of the Geological Society of South Africa.* 88: 517-522.

Vile, D., Garnier, E., Shipley, B., Laurent, G., Navas, M., Roumet, C., Lavorel, S., Diaz, S., Hodgson, J., Lloret, F., Midgley, G., Poorter, H., Rutherford, M., Wilson, P. and

Wright, I. 2005. Specific leaf area and dry matter content estimate thickness in laminar leaves. *Annals of Botany*. 96: 1129-1136.

Waisel, Y. 1960. Ecological studies on *Tamarix aphilla* (L.) Karst. II. The water economy. *ΦΊΤΟΝ*. 15 (1): 19-28.

Waisel, Y. 1972. *Biology of halophytes*. New York, USA: Academic Press.

Walker, K.F., Sheldon, F. and Puckridge, J.T. 1995. A perspective on dryland river ecosystems. *Regulated Rivers: Research and Management*. 11: 85-104.

Ward, J.D. and Breen, C.M. 1983. Drought stress and the demise of *Acacia albida* along lower Kuiseb River, Central Namib Desert: Preliminary findings. *South African Journal of Science*. 79: 444-447.

Ward, J.D. and von Brunn, V. 1985. Sand dynamics along the lower Kuiseb River. In Huntley, B.J. ed. *The Kuiseb environment: the development of a monitoring baseline.* South Africa: South African National Scientific Programmes Report, No. 106: 21-26.

West, A.G., Hultine, K.R., Burtch, K.G. and Ehleringer, J.R. 2007. Seasonal variations in moisture use in a piñon-juniper woodland. *Oecologia*. 153: 787-798.

White, J.W.C, Cook, E.R., Lawrence, J.R. and Broecker, W.S. 1985. The D/H ratios of sap in trees: implications for water sources and tree ring D/H ratios. *Geochimica Cosmochimica Acta*. 49: 237-246.

Willms, J., Rood, S.B., Willms, W. and Tyree, M. 1998. Branch growth of riparian cottonwoods: a hydrologically sensitive dendrochronological tool. *Trees*. 12: 215-223.

Wilson, P., Thompson, K. and Hodgson, J. 1999. Specific leaf area and dry leaf matter content as alternative predictors of plant strategies. *New Phytologist*. 143: 155-162.

Woodborne, S. And Robertson, I. 2000. Isotopic evidence for inter-species water competition: The impact of exotic *Prosopis* trees on Kalahari ecosystems. Paper presented at Drylands Conference, 2000, Upington, South Africa.

Woodborne, S. 2004. A water stress history of an *Acacia erioloba* (Kameeldoring) tree from the Koichab. Pretoria: CSIR Environmentek, Unpublished report.

Xu, H., Li, Y., Xu, G. and Zou, T. 2007. Ecophysiological response and morphological adjustments of two Central Asian desert shrubs towards variation in summer precipitation. *Plant, Cell and Environment*. 30: 399-409.

Yamanaka, T. and Yonetani, T. 1999. Dynamics of the evaporation zone in dry sandy soils. *Journal of Hydrology*. 217: 135-148.

Zencich, S.J., Froend, R.H., Turner, J.V. and Gailitis, V. 2002. Influence of groundwater depth on the seasonal sources of water accessed by *Banksia* tree species on a shallow, sandy coastal aquifer. *Oecologia.* 131: 8-19.

Zimmermann, M.H. 1983. *Xylem structure and the ascent of sap*. New York: Springer Verlag.

APPENDIX

Table 1: Chapter 4 carbon isotope (‰) ANOVA and Tukey HSD Post hoc test results

	***A. erioloba* cl river**	***A. erioloba* cl inland**	***A. erioloba* inv river**	***A. erioloba* inv inland**	***P. glandulosa* inv riv**	***P. glandulosa* inv inl**
ANOVA	$F_{5,28} = 12.43$; p = 0.00002					
***A. erioloba* cl river**		0.99	0.03*	1	0.0002*	0.03*
***A. erioloba* cl inland**	0.99		0.01*	0.99	0.0001*	0.01*
***A. erioloba* inv river**	0.03*	0.01*		0.03*	0.18	0.999
***A. erioloba* inv inland**	1	0.99	0.03*		0.0002*	0.03*
***P. glandulosa* inv riv**	0.0002*	0.0001*	0.18	0.0002*		0.47*
***P. glandulosa* inv inl**	0.03*	0.01*	0.999	0.03*	0.47*	

* Statistically significant

Table 2: Chapter 4 predawn XPP (MPa) Repeated Measures ANOVA (a) and Tukey Post Hoc Test (b)

(a) Tests of Between-Subjects Effects Gannavlakte predawn					
Source	**Type III Sum of Squares**	**df**	**Mean Square**	**F**	**Sig.**
Grouping	22.238	5	4.448	10.081	0.0001

(b) Tukey HSD		
(I) grouping	(J) grouping	Sig.
Ae clinl	Ae clriv	0.988
	Ae invin	0.977
	Ae invri	0.002*
	P invinl	0.973
	P invriv	0.006*
Ae clriv	Ae clinl	0.988
	Ae invin	1
	Ae invri	0
	P invinl	0.736
	P invriv	0.001*
Ae invin	Ae clinl	0.977
	Ae clriv	1
	Ae invri	0
	P invinl	0.678
	P invriv	0.001
Ae invri	Ae clinl	0.002*
	Ae clriv	0
	Ae invin	0
	P invinl	0.017*
	P invriv	0.999
P invinl	Ae clinl	0.973
	Ae clriv	0.736
	Ae invin	0.678
	Ae invri	0.017*
	P invriv	0.042*
P invriv	Ae clinl	0.006*
	Ae clriv	0.001*
	Ae invin	0.001*
	Ae invri	0.999
	P invinl	0.042*
Based on observed means.		
The error term is Mean Square(Error) = .074.		
*. The mean difference is significant at the .05 level.		

Table 3: Chapter 4 midday XPP (MPa) Repeated Measures ANOVA (a) and Tukey Post Hoc Test (b)

(a) Tests of Between-Subjects Effects Gannavlakte midday					
Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Grouping	6.405	5	1.281	3.144	0.023

(b) Tukey HSD		
grouping	**grouping**	**Sig.**
Ae clinl	Ae clriv	0.978
	Ae invin	0.992
	Ae invri	0.122
	P invinl	0.136
	P invriv	0.08
Ae clriv	Ae clinl	0.978
	Ae invin	1
	Ae invri	0.393
	P invinl	0.425
	P invriv	0.305
Ae invin	Ae clinl	0.992
	Ae clriv	1
	Ae invri	0.384
	P invinl	0.414
	P invriv	0.302
Ae invri	Ae clinl	0.122
	Ae clriv	0.393
	Ae invin	0.384
	P invinl	1
	P invriv	1
P invinl	Ae clinl	0.136
	Ae clriv	0.425
	Ae invin	0.414
	Ae invri	1
	P invriv	1
P invriv	Ae clinl	0.08
	Ae clriv	0.305
	Ae invin	0.302
	Ae invri	1
	P invinl	1
Based on observed means.		
The error term is Mean Square (Error) = .081.		

Table 4: Chapter 5 predawn (a), midday (b) and diurnal depression (c) XPP (Mpa) ANOVA, nonparametric tests and Post Hoc results

(a)	Kruskal-Wallis test: H (4, N= 160) =96.15 p =0.0001				
	T. usneoides	***F. albida***	***P. glandulosa***	***A. erioloba Ganna***	***A. erioloba* Gobabeb**
T. usneoides		0.065*	0.000003*	0.000007*	1
F. albida	0.065*		<0.00001*	<0.00001*	0.797
P. glandulosa	0.000003*	<0.00001*		1	<0.00001*
***A. erioloba* Ganna**	0.000007*	<0.00001*	1		<0.00001*
***A. erioloba* Gobabeb**	1	0.797	<0.00001*	<0.00001*	

* Statistically significant

(b) Tukey HSD test					
	T. usneoides	***F. albida***	***P. glandulosa***	***A. erioloba* Ganna**	***A. erioloba* Gobabeb**
T. usneoides		0.00002*	0.00002*	0.00002*	0.0007*
F. albida	0.00002*		0.00002*	0.00002*	0.0002*
P. glandulosa	0.00002*	0.00002*		0.75	0.00002*
***A. erioloba* Ganna**	0.00002*	0.00002*	0.75		0.00002*
***A. erioloba* Gobabeb**	0.0007*	0.0002*	0.00002*	0.00002*	

* Statistically significant

(c)	Kruskal-Wallis test: H (4, N= 165) =23.72 p =.0001				
	T. usneoides	***F. albida***	***P. glandulosa***	***A. erioloba* Ganna**	***A. erioloba* Gobabeb**
T. usneoides		0.002*	0.0004*	0.024937	1
F. albida	0.002*		1	1	0.27
P. glandulosa	0.0004*	1		1	0.08
***A. erioloba* Ganna**	0.03*	1	1		1
***A. erioloba* Gobabeb**	1	0.27	0.08	1	

* Statistically significant

Table 5: Chapter 5 vessel diameter (μm) ANOVA and Tukey HSD Post hoc test results

	F. albida	***A. erioloba* Gobabeb**	***T. usneoides***	***P. glandulosa***	***A. erioloba* Gannavlakte**
ANOVA	$F_{4,25} = 24.4$; $p < 0.0001$				
F. albida		0.0005*	0.24	0.05*	0.0001*
***A. erioloba* Gobabeb**	0.0005*		0.0001*	0.31	0.62
T. usneoides	0.24	0.0001*		0.0004*	0.0001*
P. glandulosa	0.05*	0.31	0.0004*		0.02*
***A. erioloba* Gannavlakte**	0.0001*	0.62	0.0001*	0.02*	

* Statistically significant

Table 6: Chapter 5 xylem density (g/cm^3) ANOVA and Tukey HSD Post hoc test results

	F. albida	***A. erioloba* Gobabeb**	***T. usneoides***	***P. glandulosa***	***A. erioloba* Gannavlakte**
ANOVA	$F_{4,30}$ = 8.04; p = 0.0002				
F. albida		0.001	0.18	0.03	0.0003*
***A. erioloba* Gobabeb**	0.001		0.23	0.74	0.95
T. usneoides	0.18	0.23		0.89	0.06
P. glandulosa	0.03	0.74	0.89		0.32
***A. erioloba* Gannavlakte**	0.0003	0.95	0.06	0.32	

* Statistically significant

Table 7: Chapter 6 predawn XPP (MPa) Repeated Measures ANOVA between subjects effect (a) and Tukey Post Hoc Test (b)

(a) Tests of Between-Subjects Effects					
Source	**Type III Sum of Squares**	**df**	**Mean Square**	**F**	**Sig.**
Location	5.67	2	2.835	12.231	0.001

(b) Tukey HSD		
Location	**Location**	**Sig.**
Gobabeb	Swartbank	0.813
	Kalahari	0.004*
Swartbank	Gobabeb	0.813
	Kalahari	0.001*
Kalahari	Gobabeb	0.004*
	Swartbank	0.001*
Based on observed means.		
The error term is Mean Square (Error) = .046.		
*. The mean difference is significant at the .05 level.		

Table 8: Chapter 6 midday XPP (MPa) Repeated Measures ANOVA (a) and Tukey Post Hoc Test (b)

(a) Tests of Between-Subjects Effects					
Source	**Type III Sum of Squares**	**df**	**Mean Square**	**F**	**Sig.**
Location	9.992	2	4.996	22.236	0.0001

(b) Tukey HSD		
Location	**Location**	**Sig.**
Gobabeb	Swartbank	0.04*
	Kalahari	0.003*
Swartbank	Gobabeb	0.04*
	Kalahari	0*
Kalahari	Gobabeb	0.003*
	Swartbank	0*
The error term is Mean Square(Error) = .045.		
*. The mean difference is significant at the .05 level.		

Table 9: Chapter 6 vessel diameter (µm) ANOVA and Tukey HSD Post hoc test results

	Gobabeb	**Swartbank**	**Gannavlakte**
ANOVA	$F_{2,15} = 21.50$; $p < 0.0001$		
Gobabeb		0.35	0.0002*
Swartbank	0.35		0.0007*
Gannavlakte	0.0002*	0.0007*	

* Statistically significant

Table 10: Chapter 6 SLA (g/cm^2) ANOVA and Tukey HSD Post hoc test results

	Gobabeb	**Swartbank**	**Gannavlakte**
ANOVA	$F_{2,15} = 2.98$; $p < 0.08$		
Gobabeb		0.47	0.067
Swartbank	0.47		0.45
Gannavlakte	0.067	0.45	

* Statistically significant

Table 11: Chapter 6 shoot length (cm) ANOVA and Tukey HSD Post hoc test results

	Gobabeb	**Swartbank**	**Gannavlakte**
ANOVA	$F_{2,177} = 46.04$; $p < 0.0001$		
Gobabeb		0.0019*	0.00002*
Swartbank	0.0019*		0.00002*
Gannavlakte	0.00002*	0.00002*	

* Statistically significant