Top-down or bottom-up?

Impacts of giraffe browse and water abstraction on two keystone tree species of the Kgalagadi Transfrontier Park

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Photograph: Giraffe eating *Acacia haematoxylon* in the Auob River: J Weeber

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Photograph: The dry riverbed of the Auob, looking towards the Kamqua borehole: E Shadwell

ABSTRACT

In this thesis I determine how an emphasis on tourism may have both a top-down and bottom-up affect on the two most dominant tree species in the southern Kalahari Desert of central southern Africa. Both tree species are considered as keystone species especially along ephemeral rivers. My focus is on the impact of the introduction of an extralimital megaherbivore, *Giraffa camelopardalis,* (top-down) and anthropogenic water abstraction (bottom-up) on the reproductive output and vegetation structure of *Acacia erioloba* and *Acacia haematoxylon* in the Kgalagadi Transfrontier Park.

I determine the impact of giraffe on canopy structure and reproductive potential of the two tree species by comparing three zones of giraffe density (high, medium and low) along the Auob River. I do this through a series of transects through the river to determine both giraffe and tree density and also photographed several trees to determine change in canopy width, percentage canopy death and change in the number of flowers and pods between the three zones and between species. My results show a significant negative impact of giraffe browse on canopy structure, specifically for *A. haematoxylon*. I did not however find any significant differences in recruitment between the different giraffe density zones. However, a noticeable decrease in numbers of flowers and pods in the giraffe browse height of trees (2 – 5 m) between zones suggest that giraffe will have a negative effect on the *A. haematoxylon* population but not the *A. erioloba* population in the future.

I use stable hydrogen and oxygen isotope ratios to determine the water source for the two tree species. I do this relative to the stable isotope ratio of the water extracted from nearby boreholes. I also determine how close to physiological stress the trees are (using specific leaf area, leaf δ^{13}C values, canopy death and midday xylem pressure potentials) both upstream and downstream of active boreholes used for two tourist camps. One camp, Nossob, in the Nossob River is abstracting at a high rate while the other camp, Urikaruus, in the Auob River is abstracting at a lower rate. My results for water isotope ratios show that both *A. erioloba* and *A. haematoxylon* are using deep groundwater. My results also show that in the dry season, *A. erioloba* in the Nossob are losing contact with groundwater and have to rely on some as yet unmeasured water source in the soil profile. This ‘stress’ is not reflected in canopy dieback as yet. The trees continue to transpire in the dry season suggesting that they are physiologically able to adapt to fluctuations in the water table of between 4.5 – 5.2 m between the wet and dry season by closing their stomata but are prone to drought-induced carbon starvation, specifically for trees in the Nossob.

Overall, my results show that the impact of giraffe on vegetation structure is already evident for *A. haematoxylon,* indicative of future negative effects on reproduction. My research also shows that although current levels of water abstraction are as yet not affecting vegetation structure below the abstraction points, the trees are edging closer to thresholds of water stress that would be exacerbated with drought. These findings are discussed within the context of ecosystem health and management implications for the giraffe population and water use within the Park.

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INTRODUCTION

By combining South Africa's Kalahari Gemsbok National Park (KGNP) and Botswana's Gemsbok National Park (KGP), the Kgalagadi Transfrontier Park was formally opened in early 2000, becoming the first and largest Transfrontier Park in Africa (SANParks 2008). The 38 000 km^2 Park is situated in the south-western Kalahari between 24°15′ S to 26°30′ S, and 20°00′ E to 20°45′ E (SANParks 2008) and the former two separate parks are now managed as a single ecological unit. The World Bank has estimated that the majority of African countries are focusing on tourism as a source of economic growth, with one in every twenty jobs related to tourism and the travel industry (Christie *et al.* 2013). Southern Africa receives 40 % of all tourism receipts in Sub-Saharan Africa, with South Africa being the leading destination where tourism-related sales earn more foreign exchange than do exports of gold (Christie *et al.* 2013; Biggs *et al.* 2014). This is reflected in the South African National Park's (SANParks) contribution of R6.7 billion annually to the South African economy (SANParks 2014). Tourist numbers for the Kgalagadi Transfrontier Park (the Park) have increased continuously from 24 600 visitors per year in 2004 to 33 000 in 2014 (SANParks 2004, 2014). This Park currently has the highest annual accommodation unit occupancy of all South African National Parks at 88% (SANParks 2014). This increase in tourism and its contribution to the economy has driven the need for further development in the Park with several new units planned for 2015 (SANParks 2016).

The main tourist camps in the Park are situated in the Nossob and Auob riverbeds. The Auob and the Nossob are tributaries in the Molopo network, draining into the Molopo and eventually into the Atlantic Ocean (Thomas and Shaw 1991). These rivers rise on bedrock which contributes to their unusual hydrological regimes but still have a close link between surface and sub-surface flows (Thomas and Shaw 1991). The Nossob and the Auob (with its tributaries the Oanob, Skaap, Olifants and Seeis) are known to be very active rivers in their upstream reaches in Namibia (Strobach 2008) but carry little or no water in the shallow downstream river valleys in the Park. The Nossob River last flowed at the surface in 1934 and 1963 (Steenkamp *et al.* 2008) while the Auob, which is said to flow every 11 years, last flowed in 1973, 1974 and 2000 (SANParks 2010). In the Park, both the Auob and Nossob riverbeds are made up of higher clay content with harder calcrete outcrops than surrounding sandy areas (van Rooyen 1984). They are comprised of three main layers with Kalahari sand on the top, sedimentary Kalahari Beds in the middle and Karoo basalt at the bottom (Malherbe 1984; van Rooyen 1984; Rutherford *et al.* 2006). Groundwater has been encountered almost everywhere in the Karoo and older Precambrian rocks beneath the Kalahari Beds, but the well-draining aeolian Kalahari sand itself does not form extensive aquifers (Thomas and Shaw 1991). Under areas with large pans, small localised water bodies are found in the Kalahari Beds, usually resulting from episodic flooding and rapid infiltration through fractured duricrust deposits (de Vries *et al.* 2000). It is the deeper water in the underlying Karoo basalt that is tapped into via boreholes in the Park (Thomas and Shaw 1991; de Vries *et al.* 2000; Altchenko and Villholth, 2013). Plant and animal species found in this ecosystem need to be adapted to this environment which has no water on the surface.

Development and resource allocation issues within countries around the world are based on maximising economic benefits that can and will impact on the environment (Turpie and Joubert 2001; Grant *et al.* 2011). Savannas occupy about 20 % of the Earth's land surface (Lehmann *et al.* 2011) and when considered as an ecozone, are home to most of southern Africa's wildlife, livestock and human population (Eriksen and Watson 2009a,b). Understanding ecosystems from the perspective of humans as beneficiaries has tremendous potential for protecting these ecosystems and the services they provide (Brauman *et al.* 2007), but over time has proved complex to determine and slow to affect actual land management and economic and policy decisions (Mace *et al.* 2012; Logsdon and Chaubey 2013).

Arid savanna such as at my study site in the Park occur across the world, from the Caatinga east of the Cerrado in northeast Brazil, through to the thorn forests in the Gibson Desert of south-western Australia (Rutherford *et al.* 2006). Savanna may be defined as a system with a continuous layer of grasses interspersed by scattered trees (Baudena and Rietkerk 2012). Dry arid savanna systems are considered 'stable' systems with water as the main constraint on woody cover (Sankaran *et al.* 2005). In these arid systems woody species such as *Acacia erioloba*, *Boscia albitrunca* and *Acacia haematoxylon* are dependent on deep underground water reserves (>60 m in depth) to survive (Steenkamp *et al.* 2008; Schachtschneider and February 2010, 2013).

In lower biodiversity areas such as arid savannas, keystone species are more noticeable than in higher diverse ecosystems such as fynbos or tropical jungles. Keystone species are critical to ecosystem function (Mills *et al.* 1993; Davic 2003). In an expansive grassy and bare ground matrix typical of arid savanna, large trees can act as keystone species, representing islands with higher levels of species diversity due to altered microclimates and increased habitat diversity (Milton and Dean 1995; Dean *et al.*1999; Seymour 2008). *Acacia erioloba* and *Acacia haematoxylon* are two such keystone tree species in the Park (Milton and Dean 1995; Schachtschneider and February 2013). Any accumulative negative impact on, or loss of these species through anthropogenic activities would dramatically affect both the vegetation structure and biodiversity of the ecosystem (Milton and Dean 1995; Seymour 2008; Shackleton *et al.* 2015). In National Parks, human activities are minimised but still present. My project focuses on both top-down and bottom-up anthropogenic effects on vegetation structure in the Park. Both the introduction of large charismatic herbivores and groundwater abstraction could potentially irreversibly change this arid savanna ecosystem. These two activities are closely linked to tourism in the Park.

The combination of many species of predatory cats, ungulates and birds in the Park (Bothma 1971; SANParks 2010) that occur in few other places in South Africa, and the special dune landscape are the great attractions for tourists to the Park (SANParks 2014). Surveys and questionnaires on tourist preferences around South African Parks show that large mammals, especially megaherbivores have a disproportionate draw for visitors (Bond and Loffell 2001; Buckley 2011; Di Minin *et al.* 2013; Maciejewski and Kerley 2014). In view of conservation and visitor concerns SANParks normally only re-introduce species into National Parks in which they occurred naturally (Penzhorn 1971; Bond and Loffell 2001). Through motivation to boost tourism and on the basis that other nearby arid regions have populations of giraffe (*Giraffa camelopardalis* Linnaeus, 1758; family Giraffidae), such as the central Kalahari and southern Namibia (Kruger 1994; Knight 1995; Bezuidenhout *et al.* 2010), giraffe were introduced into the Park in 1990 (Hall-Martin and De Graaf 1978; Bezuidenhout *et al.* 2010). There are however, no historic records for the red sand dunes of the southwest Kalahari having supported megaherbivores, such as giraffe or elephant (Hall-Martin and De Graaf 1978; Kruger 1994; Bezuidenhout *et al.* 2010), and concern has been raised over the browse impact by this extralimital megaherbivore on keystone large trees in the Park.

Giraffe browse at heights from between 2-5 m, and are able to modify canopy structure (du Toit 1990; Staver and Bond 2014) by eating the shoot tips, flowers and pods (Pellew 1983; Pellew 1984b; Woolnough and du Toit 2001; Moncrieff *et al.* 2011). If the trees cannot compensate with rapid re-growth to replace those parts lost, the trees will be kept to a certain height (Staver and Bond 2014) and typically lose most of their reproductive potential. This reflects at a broader scale in changing plant communities through decline of certain favoured palatable species within savannas (Bond and Loffell 2001; Birkett and Stevens-Wood 2005). In a savanna with only two main tree species, both of which occur sparsely and are the main fodder for giraffe, the gradual loss of these species with no recruitment would result in a collapse of the ecosystem.

Heavy browsing of the flowers and seeds impedes the natural regeneration and recruitment of trees (Malagnoux *et al.* 2007), creating an 'old population'. Without regeneration and together with large mature trees progressively losing their resilience to climatic stress, a single drought could destroy a whole population, such as happened in the Senegal River Valley in the early 1970s, when most of the *Acacia nilotica* forests died after a severe drought (Malagnoux *et al.* 2007).

Climate variability, strongly correlated with aridity, is a major factor influencing the ecological, economic and social sustainability of ephemeral rivers such as those found in the Kalahari (Botes *et al.* 2003). Water for human consumption in these arid areas primarily comes from aquifers in the river beds, accessed via boreholes. These aquifers also support the major tree species growing in these river beds (Moleele and Mainah 2003; Chen *et al.* 2014). The progressive 1998 National Water Act of South Africa makes allowance for an ecological reserve (Act 36; RSA 1998; Turpie and Joubert 2001; Schachtschneider and February 2013). Effectively, this means that the quantity and quality of water required by natural ecosystem processes have to be considered in the management of water reserves (Act 36; RSA 1998; Turpie and Joubert 2001). Keeping the requirements of an exponentially growing tourism industry in balance with the needs of natural ecosystems is difficult. Despite this, achieving tourist satisfaction and increasing the economic return from tourism (Maciejewski and Kerley 2014) seems to be of greater importance in environmental decision-making than monitoring and sustainable use of the natural ecosystems (Grant *et al.* 2011).

This drive for increasing tourist revenue and subsequent expansion of infrastructure to accommodate higher numbers of tourists means a concomitant increase in water abstraction.

The effect that this may have on vegetation structure is not clear. It has been shown that *Acacia erioloba* trees can grow their roots as deep as 60 m (Canadell *et* al.1996; de Vries 2000; Obakeng 2007). Schachtschneider and February (2013) demonstrated that the deep-rooted trees growing in the riverbed of the ephemeral Kuruman River, are heavily reliant on deep water (56 m) in this arid savanna despite it being available on the surface for part of the year. Even in ecosystems that are not arid savanna, but have limited surface water, changes in the water table from groundwater abstraction can have significant effects on vegetation. In southwest Australia, Groom *et al.* (2000) found that a 2.2 m drawdown in the water table from abstraction for Perth's water supply combined with hotter and drier than normal climate conditions caused significant negative effects on *Banksia* trees growing near the abstraction point.

In this thesis I determine how an emphasis on tourism may have both a top-down (extralimital giraffe) and bottom-up (water abstraction) effect on the population dynamics and vegetation structure in the Kgalagadi Transfrontier Park. I do this firstly in Chapter 2 using a series of transects across the Auob River for which I collected demographic information about *A. erioloba* and *A. haematoxylon* and validated estimated giraffe occurrence in three giraffe density areas along the River. Using photography and field estimates of canopy dimensions, flower and pod numbers, dead/alive canopy percentage within and without giraffe browse range, I compared trees in the different giraffe density areas to see how giraffe browse may be affecting canopy structure and recruitment (flower numbers and seed pod numbers) for both species.

Following this, in Chapter 3, I determined the water source for the two acacia species *A. erioloba* and *A. haematoxylon* in the Auob and Nossob Rivers and whether this is the same source used by camps for human consumption in each of the rivers using oxygen and hydrogen isotope ratios. I monitored seasonal groundwater fluctuation in unused boreholes upstream and downstream of an actively pumped borehole in each river. Over three seasons, I sampled trees of both *Acacia* species for specific leaf area, carbon isotope ratios, midday xylem pressure potentials and estimated percentage canopy death upstream and downstream of both active boreholes to determine whether they were showing signs of water stress.

My study concludes with a summary of my findings in Chapter 4, reflection on the anthropogenic effect on the environment in the Kgalagadi Transfrontier Park with climate change predictions, and suggestions of some management considerations.

CHAPTER 2:

Effects of an extralimital megaherbivore (*Giraffa camelopardalis)* on two keystone tree species in the Kgalagadi Transfrontier Park

Introduction

Ecosystems include various trophic levels of mainly primary producers, primary consumers and secondary consumers (e.g. grass, gemsbok and lion respectively). These trophic levels are influenced either positively or negatively by top-down and bottom-up processes (Power 1992). Bottom-up processes are usually governed by abiotic factors such as available water and nutrients (e.g. affecting plant growth), while top-down processes involve interactions between biotic influences such as predation (e.g. herbivory, carnivory) and abiotic influences such as fire (Power 1992; Riginos *et al.* 2008). Top-down controls by megaherbivores such as giraffe (*Giraffa camelopardalis*) can exert substantial control over the different demographic stages of trees altering vegetation structure and function (Bond and Loffell 2002; Sankaran *et al.* 2013). Also in savanna systems bottom-up controls, such as water availability, regulate both vegetation structure and community composition (February *et al.* 2007a; Hempson *et al.* 2007).

Large trees in arid savannas create micro-habitats by providing a variety of food resources, shade, nesting sites, and increases in nutrients and soil water for many other species of animals and plants and are considered keystone species because of the services they provide (Milton and Dean 1995; Dean *et al.* 1999). Two such keystone species are *Acacia erioloba* (E. Mey.) and *Acacia haematoxylon* (Willd.) (family Leguminosae) both biogeographically endemic to the Kalahari, with the only tree form of *A. haematoxylon* found in the Auob River (Ross 1979; van Rooyen *et al.* 2008). As these trees are keystone species, any detrimental environmental effects on the species, such as drought or high browse pressure, will have a knock-on effect on the entire ecosystem, for example, loss of food and shelter, resulting in a decrease in herbivore numbers which will in turn impact on carnivores. If densities are high enough, megaherbivores such as giraffe can significantly affect keystone tree species through their heavy browse, leading to loss of microhabitats and species diversity (Jones *et al.* 1994).

Giraffe have a distinct browse range, typically between 2 - 5 m, which is higher than all other browsing species (e.g. eland, kudu) at my study site in the Kgalagadi Transfrontier Park (the Park; Pellew 1984a; du Toit 1990; Birkett 2002). Giraffe browsing impact in general has been shown to vary throughout the year, being highest in the dry season when production rates are lower (Pellew 1984b). Primarily selecting new shoots and leaves, giraffe are entirely dependent on the presence of palatable tree species as their source of energy, nutrients and at certain times water (Pellew 1984 a,b). Heavy giraffe browse has been shown to structurally shape trees in savanna (Bond and Loffell 2002). In water-scarce systems, such as that found in the Park, trees are slow-growing with episodic recruitment usually dependent on above-average rainfall (Seymour and Milton 2003; Seymour 2008; Smithers 1971 in Hall-Martin and de Graaf 1979; Bezuidenhout *et al.* 2010). Pellew (1984b) found that giraffe can exert a major impact on *Acacia* regeneration, sometimes removing up to 85% of new shoot production and lessening recruitment. Thus if browsing pressure is high, giraffe browse effects in arid environments are amplified as trees are unable to recover.

Increased browsing pressure is one of the most likely effects to occur when megaherbivores are introduced into an area (Bond and Loffell 2002) such as my study site, the Auob River in the Park. As giraffe are extremely charismatic megaherbivores, these animals have been introduced into several National Parks in South Africa to attract tourists (Kruger 1994; Bond and Loffell 2002; Parker 2004). There are no historic records for resident populations of giraffe in the Auob River and surrounding red sand dunes where they are considered to be extralimital (Hall-Martin and de Graaf 1978; Bezuidenhout *et al.* 2010). Giraffe were introduced into an enclosure near the Craig Lockhart borehole in the Auob River in early 1990. Five years later the small population (~35 giraffe) was released into the Park, and was estimated to be around 50 individuals in 2010 (Bezuidenhout *et al.* 2010) with between 1 – 55 giraffe sightings per month in 2013 (SANParks 2014 *unpub. data*). With 41 artificial waterholes in the Auob, this extralimital species does not have to rely fully on fodder to meet their water requirements but are still found primarily in the dry riverbed system due to the high density of trees. Perceptions are that heavy browse on the trees in the riverbed are affecting the vegetation structure (Bezuidenhout *et al.* 2010).

In this chapter I address this perception by determining the effects of giraffe browse on *Acacia erioloba* and *Acacia haematoxylon,* two keystone tree species in the Auob River. I hypothesise that the impact of giraffe on the structure of these two tree species is not only through heavy browse on the leaves and twigs but also by reducing the reproductive potential of trees by removing flowers and therefore reducing seed pod production. I examine this hypothesis with respect to three different levels of giraffe population density (low, medium and high). I want to determine the relationship between the amount of flowers and the amount of pods. It is not possible to look at seed directly as the pods drop to the ground without opening and the seed is only dispersed after the pods are eaten by animals. I expect to find lower *A. erioloba* and *A. haematoxylon* recruitment where population density of giraffe is high. I also expect altered canopy structure, more canopy dieback, and fewer flowers and pods in the giraffe browsing range of 2 – 5 m on larger trees in the high giraffe density area (Pellew 1984a; du Toit 1990; Birkett 2002).

Methods

Description of the study area

The Kgalagadi Transfrontier Park is situated in the south-western Kalahari and can be characterized as an arid savanna with a sandy subsurface, deep groundwater tables and annual rainfall ranging from 120 – 400 mm, increasing as one moves northwest from the top of the Northern Cape Province of South Africa (de Vries *et al.* 2000; Rutherford *et al.* 2006). The summer and autumn rainfall (late November to early April) occur as erratic and highly localised thunderstorms usually peaking in February (Fig. 1; van Rooyen and van Rooyen 1998). Mean monthly maximum and minimum temperatures are extreme, ranging from 41.5°C for December to - 4.0°C for July (Fig. 1; Rutherford *et al.* 2006).

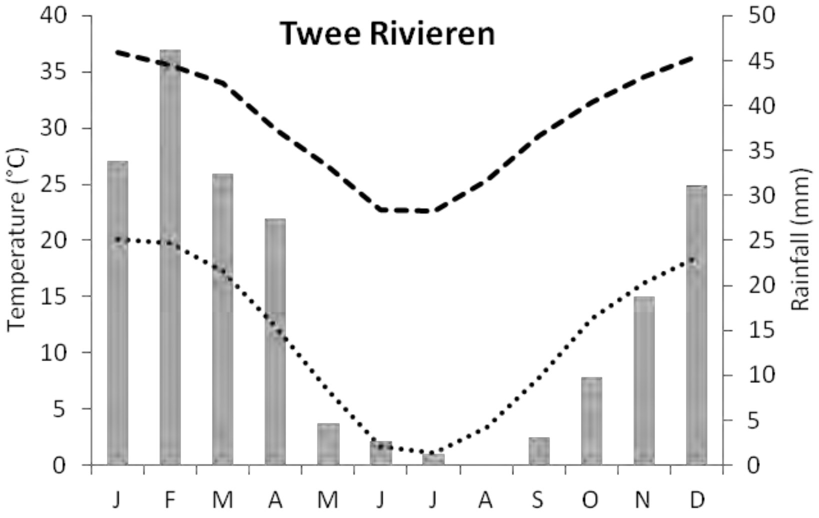

Figure 1: *Average monthly rainfall (bars) and average maximum (--) and minimum (…) temperatures from 1984 to 2014 for Twee Rivieren in the Kgalagadi Transfrontier Park (Station No. 0461208 4; SAWS 2015).*

In the Park the Auob riverbed has a narrow channel 100 – 500 m wide with yellow sands and high clay content of the Goeboe Goeboe Formation set in 30 – 50 m high banks of calcrete of the Mokalanen Formation (Malherbe 1984; Mills and Retief 1984; van Rooyen and van Rooyen 1998). The Auob River last flowed in 1973, 1974 and 2000 (SANParks 2010) and lies above an aquifer between 38 – 59 m deep (see Chapter 3) which has been tapped into at semi-regular intervals via boreholes to supply 15 permanent artificial waterholes for animals (Mills and Retief 1984; van Wyk and le Riche 1984; SANParks 2008).

Within this river system, *A. erioloba* and *A. haematoxylon* dominate the open shrubland as the only large tree species, along with scattered smaller trees (e.g. *Boscia albitrunca*) and bushes (e.g. *Acacia mellifera*), dwarf shrubs such as *Rhigozum trichotomum,* and grasses (e.g. the annual *Schmidtia kalahariensis* and the perennial *Stipagrostis obtusa*) occurring in sparse clumps (Leistner 1959; Rutherford *et al.* 2006; van Rooyen *et al.* 2008).

Presence of giraffe

Giraffe were originally introduced into the Auob in 1977 in a camp at the Craig Lockhart borehole (waterhole) (-25.8655°, 20.1031°). The results for monthly surveys show that the highest densities of giraffe are still in this area, decreasing in number down to the confluence with the Nossob River where giraffe have rarely been seen.

Table 1: *The beginning and end of each giraffe density zone within the Auob river valley starting from Mata Mata down to the confluence of the Auob and Nossob rivers, showing the percentage of monthly road surveys with giraffe present within each zone (% Surveys giraffe) as well as the average (±SE) number of giraffe present in each survey (n = 24 months; data taken from SANParks 2014* unpub. data*).*

Giraffe Density	Position	Lat	Long	% Surveys giraffe	Avg (±SE) giraffe
High	Start	-25.7944°	20.0354°	65.5	5.1 ± 0.34
	End	-25.9636°	20.2446°		
Medium	Start	-26.9989°	20.3468°	34.5	4.4 ± 0.41
	End	-26.1760°	20.5432°		
Low	Start	-26.1926°	20.5488°	0	0
	End	-26.4216°	20.6234°		

Based on the monthly game surveys conducted by SANParks between 2012 and 2014, I divided the Auob River downstream of the Mata Mata Rest Camp (-25.7680°, 20.0005°) into three consecutive zones, ~30 km in length (Fig. 2; Table 1; SANParks 2014 *unpub. data*). These zones start as high giraffe density from just below Mata Mata near the Sitzas borehole (-25.8208°, 20.0478°), through medium giraffe density to low giraffe density finishing near the confluence of the Auob and Nossob Rivers (Table. 1; Fig. 2).

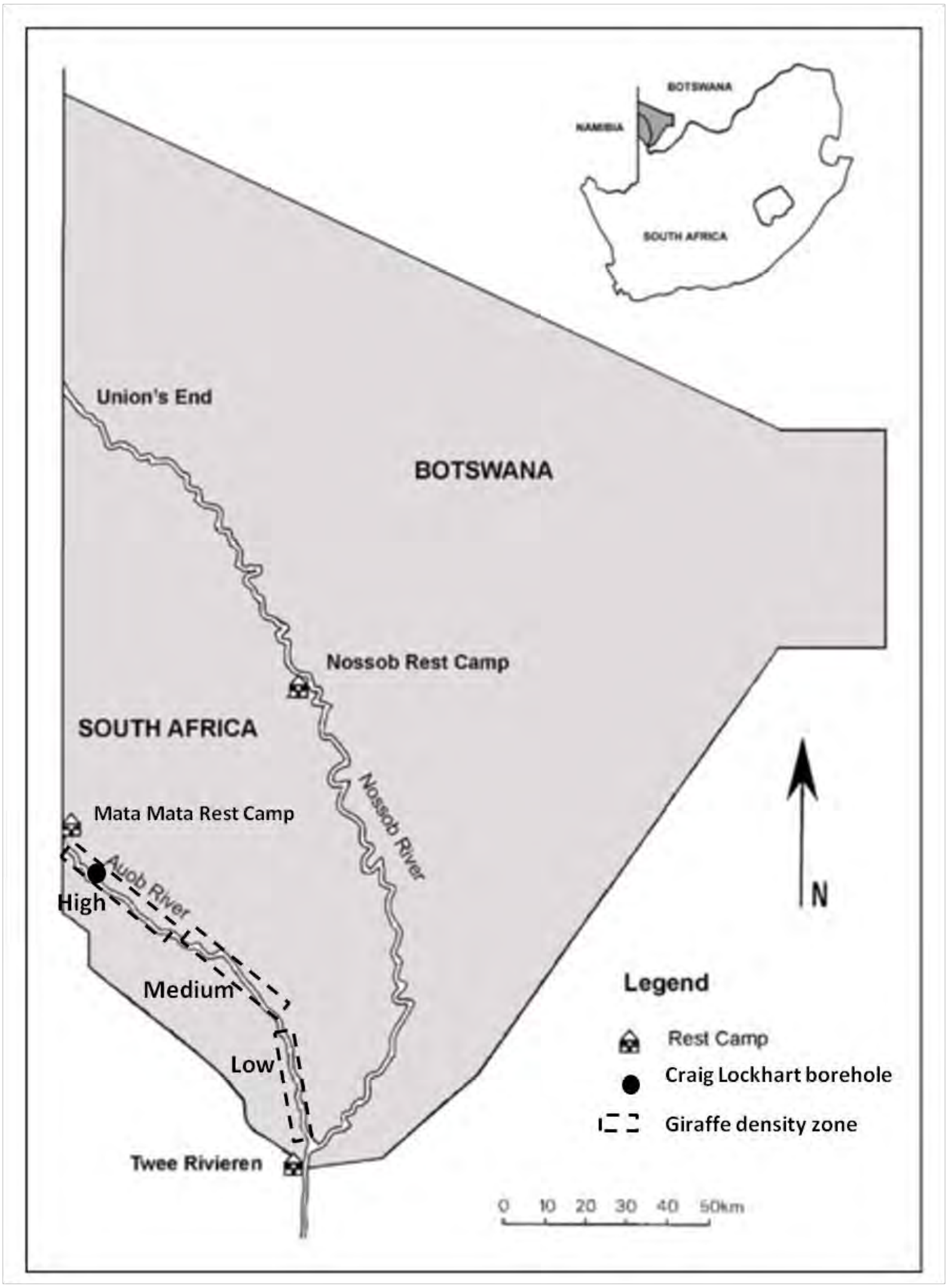

Figure 2: *Location of the Kgalagadi Transfrontier Park (shaded area) within Southern Africa, with the three giraffe density zones along the Auob River depicted (Map adjusted from van Rooyen* et al. *2008).*

My assessment of giraffe density in each zone based on the monthly surveys was confirmed by walking 50 transects in each zone perpendicular to the riverbed from the mid-slope of one bank to the mid-slope of the opposite bank and counting every occurrence of spoor and dung within that transect. These transects were walked once at the beginning of the project in each zone (total of 150) as giraffe numbers do not vary significantly seasonally as they are confined to the Auob River. Each transect was done as a pair, with 150 m between each transect and 1 km between each pair of transects. If a borehole (waterhole) were to occur between a pair, a kilometer margin was given on either side to discount the increase in trampling and herbivory associated with the waterhole. Giraffe density for each transect was determined by two people 5 m apart, each person scanning for spoor and dung 2.5 m on either side of the individual transect for a total width of 10 m on each transect.

Each observer also noted the occurrence of any *A. erioloba* and *A. haematoxylon* trees in each transect in three specific height classes: 0 - 0.3 m, 0.3 - 2 m, and above 2 m (juvenile, intermediate and large trees respectively).

Impact of Giraffe browse

I used repeat photography in the three zones to determine the impact of giraffe browse on canopy dieback and reproductive success (flowers and pods) for both *A. erioloba* and *A. haematoxylon* trees. Within each giraffe density zone, photographs at two angles (90° to each other) were taken in January 2013 of two trees of each species selected within three height classes to ensure a range in tree height: 2 – 4 m, 4.1 – 6 m and above 6 m. Browse impact was determined for each tree at every meter from 2 m above ground level to the top of the canopy. I did this because several studies have shown the highest intensity of giraffe browse to be between 2 m and 4.5 m (Pellew 1984a; du Toit 1990; Birkett 2002) despite some studies showing that male giraffe can reach up to 6 m (Pellew 1980; Young and Isbell 1991).

All the photographs were taken using a D60 Nikon camera (Nikon, Ayuthaya, Thailand) when the entire tree was just inside the field of view through a 18-200 mm f/3.5 - 6.3 HSM DC lens (Sigma, Fukushima, Japan) fitted with a PRO1 D UV (W) filter (Kenko, Tokyo, Japan). The aperture was fixed at 52 mm, F8. A retractable 5 m aluminium ranging rod (levelling staff; Leica Geosystems, St. Gallen, Switzerland) was held vertically at the edge of the canopy for calibration.

The photographs were taken in RAW format and adjusted into TIFF images when analysed in Adobe Photoshop CS5 v12.0 x 32© (Adobe Systems Software Ltd, Ireland). Each photograph was overlaid by a calibrated grid (50 cm boxes, subdivided by 10; Fig.3). To determine canopy structure I measured canopy width from edge to edge at every vertical meter starting from 2 m above ground. Canopy dieback was determined by marking all living (green leaves) and dead material (brown leaves or twigs < 5 cm thick) at each grid intercept (11 points) occurring within each of the 50 cm lengths starting from the outer edge of the canopy moving inwards along the meter-line. I did this for both photographs for each tree. Intercepts occurring in space or with main branches were disregarded. Canopy dieback at each meter-line was calculated as the number of intercepts denoting dead material over the total number of intercepts (living + dead material) and averaged over two photographs. Canopy dieback was also calculated for two sections of each tree, within browse height (2 - 5 m) and above browse height (> 5 m) by averaging the percentage of canopy dieback for each meter-line within each section.

To determine the effects of giraffe browse on reproduction, the numbers of visible flowers and pods were counted in a 50 cm square box 25 cm around each horizontal meter-line and 50 cm inwards from the outer edges of the canopy. The number of boxes depended on how many edges of the canopy there were at each meter. These values were averaged for all boxes over two photographs for each meter-line and then also averaged for the two sections of within and above browse height for each tree.

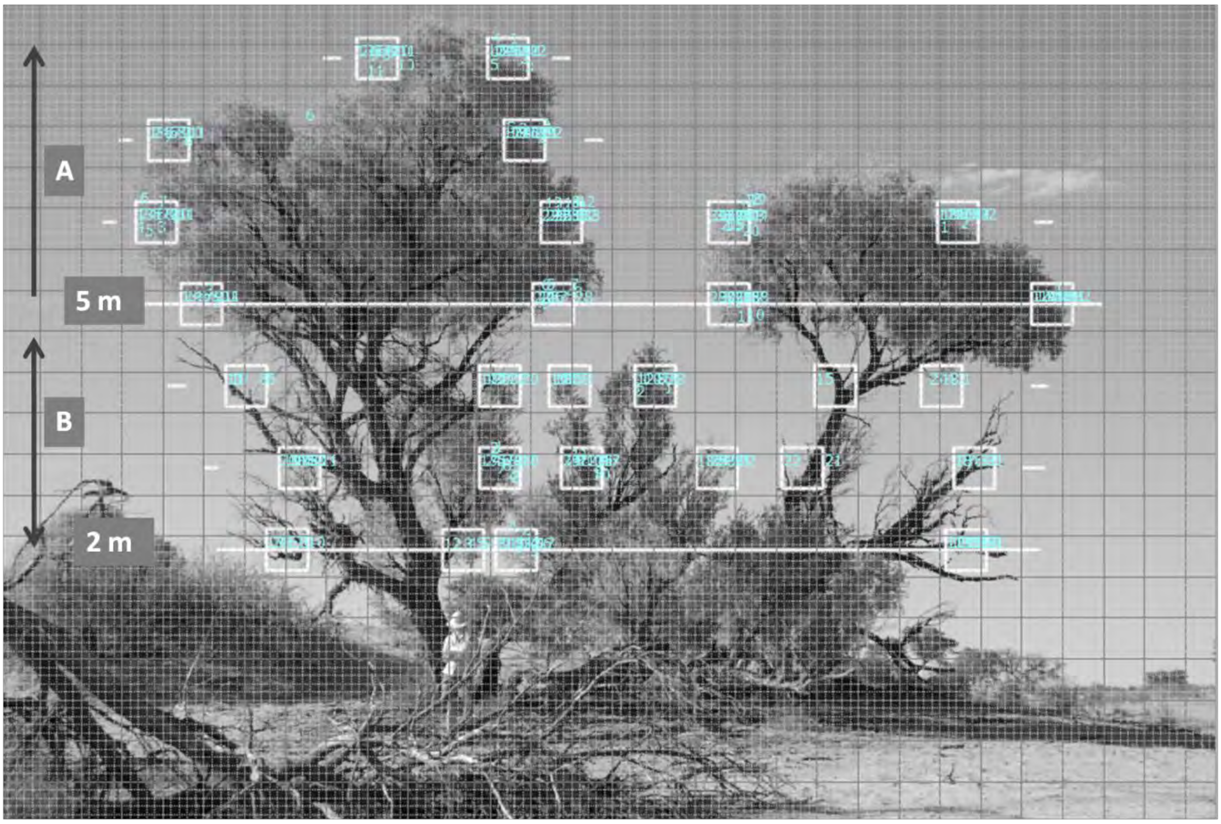

Figure 3: *Illustration of photograph grid overlay and intercept counting method used for determining amount of live/dead canopy material and recruitment (flowers and pods) within the browse (B = 2 - 5 m) and above browse (A = > 5m) sections.*

Statistics

The data were split into two sets: transect data and photograph data. Giraffe density between zones from spoor and dung counts within transects were each tested using a Chi-squared test followed by a post-hoc paired t-test. Differences in densities of large trees/ha between zone and tree species were tested with a Poisson generalised linear model using an offset of log (transect area) to account for any differences in area covered. In order to compare the densities of juveniles and intermediates relative to the presence of large trees across giraffe density zones, transformed (square root) densities of juveniles/large tree/ha and intermediates/large tree/ha of each species were both tested with a generalised linear model again using an offset of log (transect area) to account for any differences in area covered. Transects that had juveniles/intermediates but no large trees were removed from the analyses.

As giraffe browse at heights between 2 and 5 m, I compared every meter of canopy width measurement within the browse range (2, 3, and 4 m), and above the browse range (> 5 m), with the 5 m level. I compared these across different giraffe density zones using a linear mixed effects model after square-root transforming the data.

Average percentage canopy dieback for browse height (2 - 5 m) and above browse height (> 5 m) was transformed (arcsine-square root (data + 1)) and compared relative to each other, between zones and species using a generalised linear mixed effects model, fitted with multivariate normal random effects using Penalized Quasi-Likelihood. The same test was used to compare average number of flowers and pods between browse height and above browse height for *A. haematoxylon* (*A. erioloba* was not flowering) after transforming the data using (log (data +1)) due to the high numbers of zeroes. For every analysis, the variance between individual trees was accounted for by including tree number as a random effect. If the interactions between zone and species were not significant then the analyses were run separately on each species. All tests on the data were assessed in R© v3.1.2 (R Core Development Team 2014) and a value of $p < 0.05$ required for significance.

Results

Presence of Giraffe

Spoor and dung counts

My transect results for spoor and dung counts confirmed my assumptions based on the road survey data for giraffe density in the Auob River. There is a significant increase in both spoor ($\chi^2_{(2)} = 90.96$, $p < 0.00$) and dung ($\chi^2_{(2)} = 85.06$, $p < 0.00$) from the low giraffe density zone to the high density zone. Giraffe spoor and dung were present in 28 % and 8 % of transects in the low density zone, 56 % and 46 % of transects in the medium density zone and 94 % and 72 % of transects in the high density zone.

Tree densities

There is a significantly higher density of large (above 2 m in height) *A. erioloba* compared to large *A. haematoxylon* trees in the Auob River ($\text{Est.}_{(2.5\%, 97.5\%)} = -1.34_{(-2.02, -0.74)}$, $Z_{(294)} = -4.15$, p-value < 0.00, Table 2). For large *A. erioloba* trees there is a significant increase ($\text{Est.}_{(2.5\%, 97.5\%)} = 0.54_{(0.17, 0.93)}$, $Z_{(147)} = 2.80$, p-value < 0.01) in the average densities of large trees above 2 m in height from 4.35/ha at Mata Mata in the high giraffe density zone to 7.11/ha in the medium density zone, and a significant decrease to 1.15/ha at the confluence in the low density zone (Est. $_{(2.5\%, 97.5\%)}$ = -1.23 $_{(-1.94,-0.61)}$, Z $_{(147)}$ = -3.67, p-value < 0.00). These results are also reflected non-significantly in the relative proportion of juveniles (< 0.3 m in height) and intermediates (from 0.3 to 2 m in height) per large tree/ha. These ranged from 6.73, 7.57 to 3.79/large tree/ha for juveniles and from 5.61, 5.00 to 3.28/large tree/ha for intermediates in the high, medium and low giraffe density zones respectively.

For *A. haematoxylon*, there are significantly fewer large trees at Mata Mata (1.30/ha; Table 2) in the high giraffe density zone relative to the low (Est. $_{(2.5\%, 97.5\%)}$ = 1.05 $_{(0.39, 1.76)}$, Z $_{(147)}$ = 3.03, p-value < 0.00) and medium (Est. $_{(2.5\%, 97.5\%)}$ = 1.11 $_{(0.46, 1.82)}$, Z $_{(147)}$ = 3.23, p-value < 0.00) density zones respectively. There are however, no distinct patterns or significant differences for the very low number of juveniles (0.42, 0.28, 0.18/large tree/ha) and intermediates (3.50, 2.25, 4.31/large tree/ha) between high, medium and low giraffe density zones respectively.

Table 2: *Relative tree densities in three specific height classes: juvenile, intermediate and large trees (0 - 0.3 m, 0.3 - 2 m, and above 2 m respectively) in each of the three giraffe density zones, 'Low, medium or high'.*

Species	**Giraffe density zone**	**Juvenile (Ave juveniles/large tree/ha ±SE)**	**Intermediate (Ave intermediates /large tree/ha ±SE)**	**Large (Ave tree/ha ±SE)**
Acacia erioloba	Low	3.79 (±1.63)	3.28 (±2.28)	1.15 (±0.16)
Acacia haematoxylon	Low	0.18 (±0.18)	4.31 (±1.86)	3.03 (±0.43)
Acacia erioloba	Medium	7.57 (±1.86)	5.00 (±1.11)	7.11 (±1.01)
Acacia haematoxylon	Medium	0.28 (±0.29)	2.25 (±0.83)	3.23 (±0.46)
Acacia erioloba	High	6.73 (±3.13)	5.61 (±1.99)	4.35 (±0.62)
Acacia haematoxylon	High	0.42 (±0.42)	3.50 (±0.91)	1.30 (±0.18)

Impact of Giraffe Browse

Canopy Structure

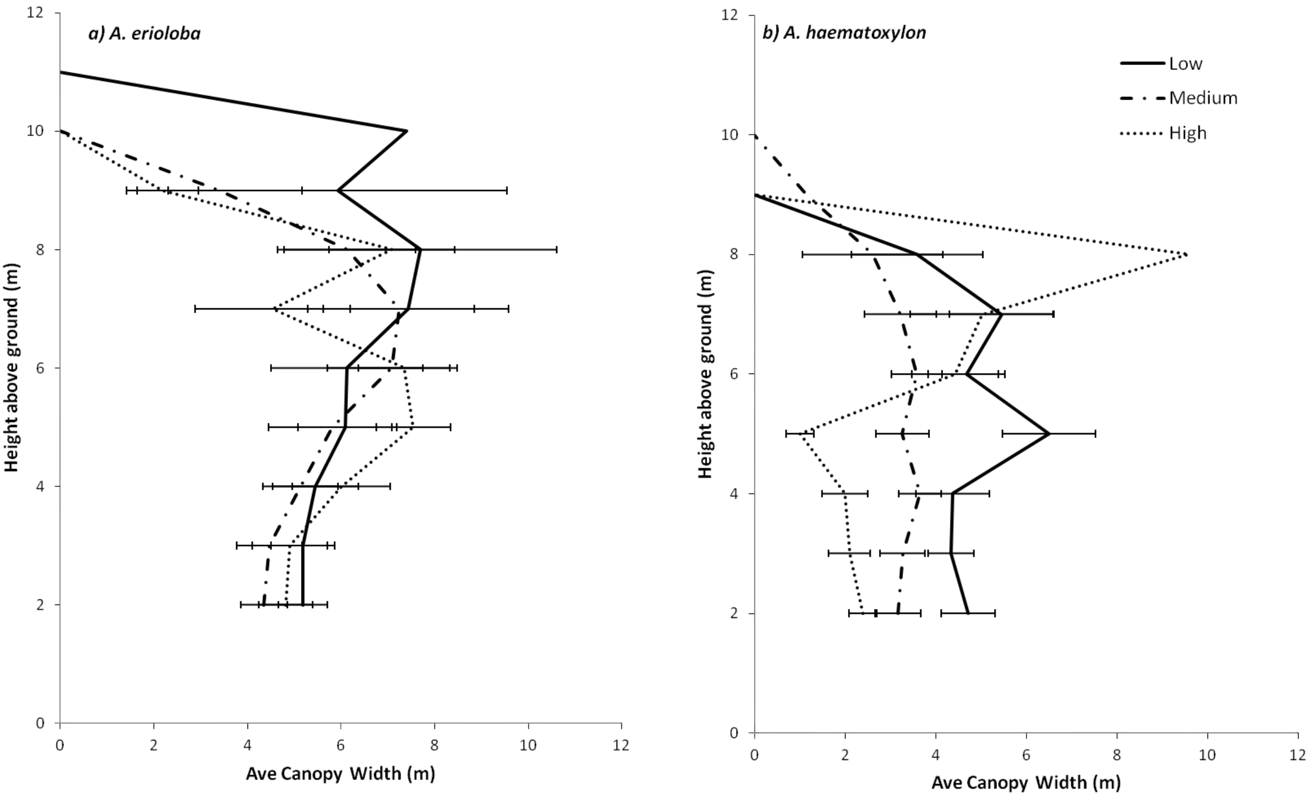

Figure 4: *Average canopy widths (±SE) for a)* Acacia erioloba *and b)* Acacia haematoxylon *in each of the giraffe density zones (low, medium and high).*

My results show a normal distribution of canopy width for *A. erioloba* with no significant effects of giraffe browse (Fig. 4*a*). My results for *A. haematoxylon* however show significantly narrower canopies below 5 m, and particularly at 2m (Est.$_{(2.5\%, 97.5\%)}$ = 0.28$_{(0.03, 0.52)}$, T$_{(143)}$ = 2.24, p-value = 0.03), with an increase in giraffe density (Fig. 4*b*). Canopy structure outside of the main browsing range at 6 and 7 m are significantly wider relative to that at 5 m (Table 3).

Table 3: *Summary of statistical results for a linear mixed-effects model comparing* Acacia haematoxylon *canopy width measurements. Significant differences at $p < 0.05$ indicated by **. 'Low, medium or high' refers to giraffe density zones.*

Factor	**Estimate (2.5%, 97.5% CI)**	**df**	**Test statistic**	**P-value**
Low: Medium	-0.35 (-0.67, -0.03)	49	-2.17	0.03 **
Low: High	-0.62 (-0.94, -0.30)	49	-3.86	0.00 **
Height level 5 m: 2 m	0.28 (0.03, 0.52)	143	2.24	0.03 **
Height level 5 m: 3 m	0.19 (-0.06, 0.44)	143	1.51	0.13
Height level 5 m: 4 m	0.16 (-0.10, 0.41)	143	1.23	0.22
Height level 5 m: 6 m	0.39 (0.09, 0.70)	143	2.53	0.01 **
Height level 5 m: 7 m	0.50 (0.16, 0.83)	143	2.92	0.00 **
Height level 5 m: 8 m	-0.00 (-0.47, 0.47)	143	-0.01	0.99
Height level 5 m: 9 m	-0.72 (-1.79, 0.34)	143	-1.34	0.18

Percentage Canopy Dieback

My results show significantly higher levels of canopy dieback in *A. haematoxylon* trees relative to *A. erioloba* in all giraffe density zones (Est. $_{(2.5\%, 97.5\%)}$ = 18.33$_{(9.50, 27.16)}$, T $_{(99)}$ = 3.96, p-value < 0.00). Average percentage canopy dieback for *A. haematoxylon* is twice that of *A. erioloba* (Fig.5).

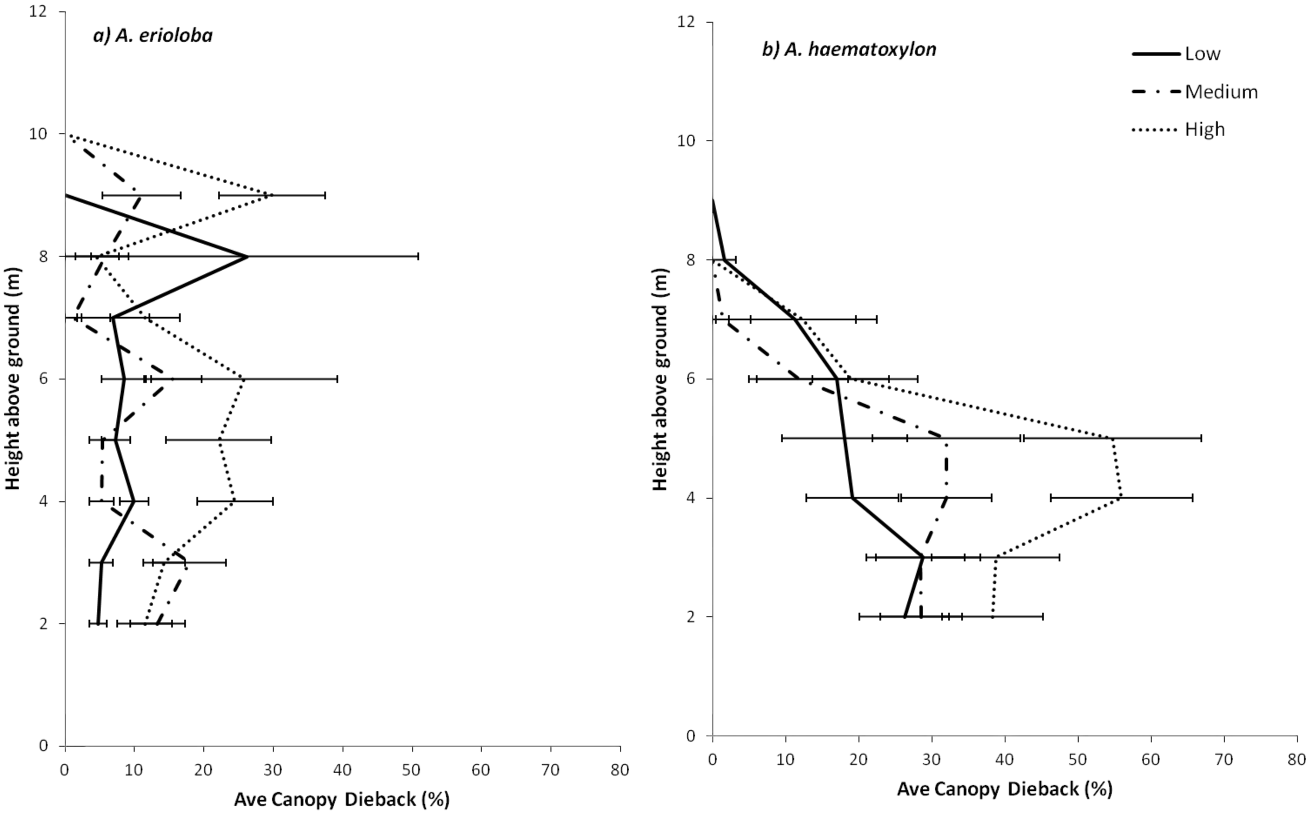

Figure 5: *Average canopy dieback (±SE) for a)* Acacia erioloba *and b)* Acacia haematoxylon *in each of the giraffe density zones (low, medium and high).*

There was a significant increase in canopy dieback for *A. erioloba* within the browse range (2 – 4 m) with an increase in giraffe density from low to high (Est. $_{(2.5\%, 97.5\%)}$ = 7.28 $_{(1.83, 12.72)}$, T $_{(50)}$ = 2.58, p-value = 0.01; Fig. 5*a*), and significantly more canopy dieback within the browse range compared to above the browse range in the medium giraffe density zone (Est. $_{(2.5\%, 97.5\%)}$ = 6.84 $_{(0.58, 13.11)}$, T $_{(24)}$ = 2.17, p-value = 0.04).

For *A. haematoxylon,* there was an increase in canopy dieback with an increase in giraffe density, with the greatest percentage dieback in the high giraffe density zone between 2 m and 4 m, significantly different to the browse range in the low giraffe density zone (Est. $_{(2.5\%, 97.5\%)}$ = -13.5 $_{(1.71, 25.20)}$, T $_{(49)}$ = -2.21, p-value = 0.03; Fig. 5*b*).

Reproductive Potential

Flowers

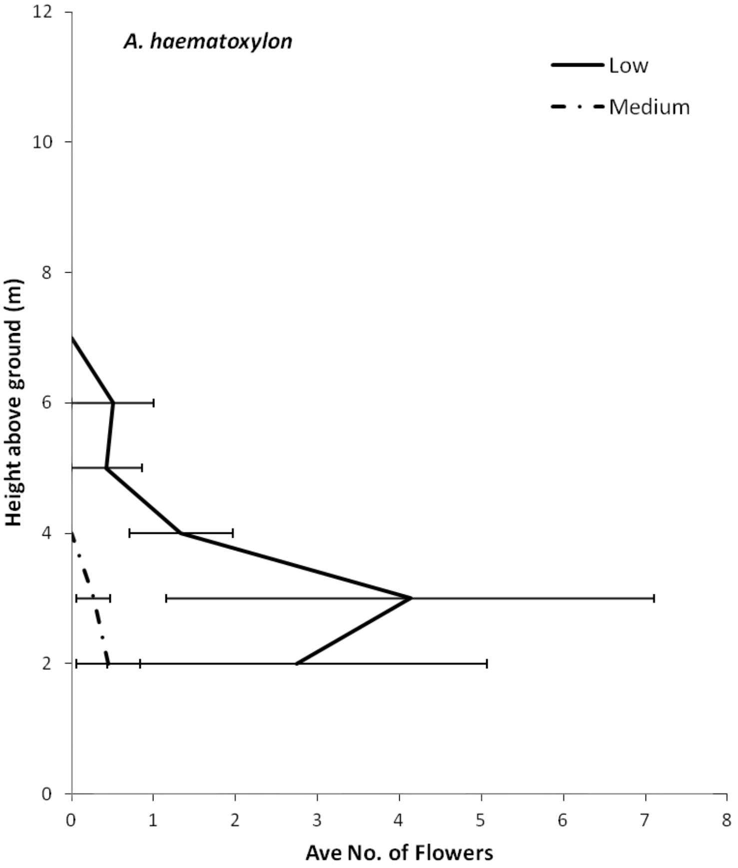

Figure 6: *Average number of flowers per height level (±SE) for* Acacia haematoxylon *in each of the giraffe density zones (low, medium and high).*

There were significantly more flowers in the low density zone than in the medium (Est. $_{(2.5\%, 97.5\%)}$ = 0.22 $_{(0.05, 0.40)}$, T $_{(49)}$ = 2.53, p-value = 0.02) and no flowers on *A. haematoxylon* trees in the high giraffe density zone (Fig. 6). There were no significant differences in number of flowers between browse range and above browse range for any of the giraffe density zones (Fig. 6).

Pods

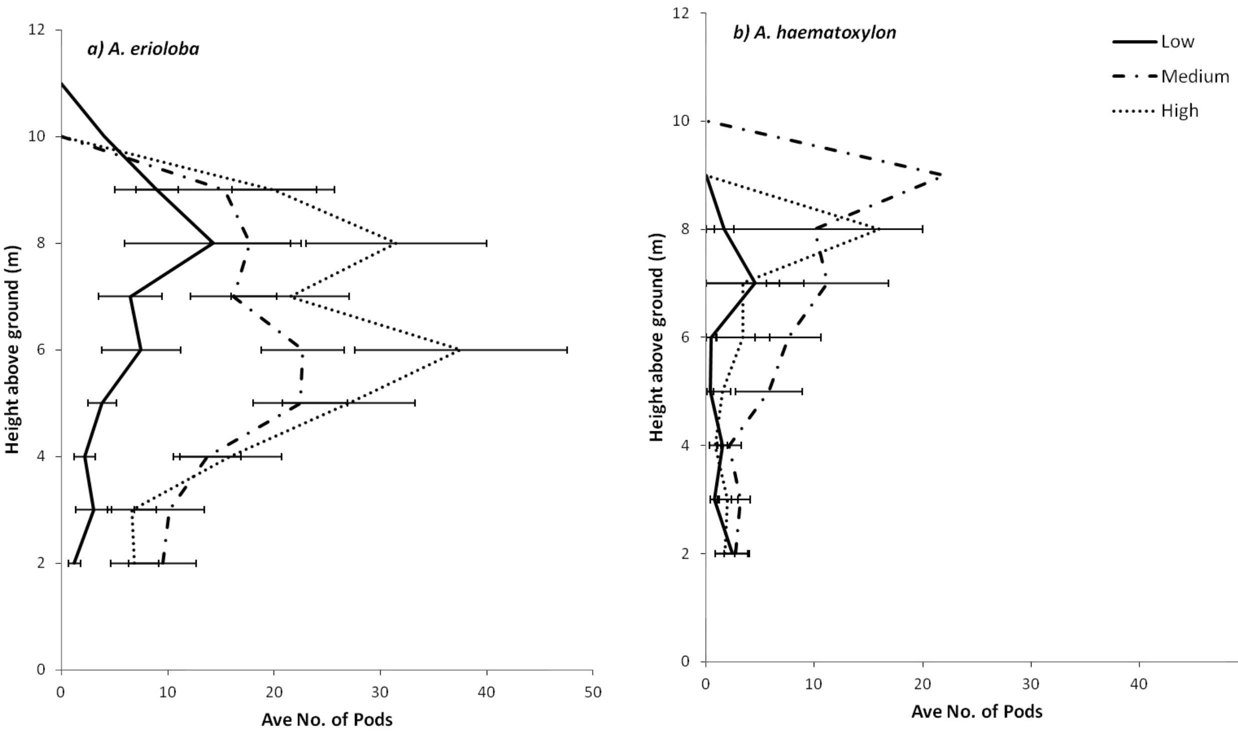

Figure 7: *Average number of pods (±SE) for a)* Acacia erioloba *and b)* Acacia haematoxylon *in each of the giraffe density zones (low, medium and high).*

There were twice as many pods on *A. erioloba* trees than there were on *A. haematoxylon* trees (Fig. 7). For *A. erioloba,* within the browse range of 2 m to 4 m, there were more numbers of pods in the high and significantly more pods in the medium (Est.$_{(2.5\%, 97.5\%)}$ = 0.52$_{(0.19, 0.84)}$, T$_{(50)}$ = 3.10, p-value = 0.00) compared to the low giraffe density zone. For *A. haematoxylon*, however, there were no significant differences in pod numbers between the high, medium and low giraffe density zones. There were however, very low average numbers of pods in the browse range in all giraffe density zones.

Discussion

Giraffe are considered extralimital to the Kgalagadi Transfrontier Park as concluded from historic records (Hall-Martin and De Graaf 1978; Kruger 1994; Bezuidenhout *et al.* 2010). Due to how attractive giraffe are to tourists, a small population of these megaherbivores was introduced into the Park in 1990, slowly increasing in numbers to more than 50 individuals in 2014 (SANParks 2013 *unpub. data*). My results for spoor and dung counts confirm that giraffe densities were highest in the zone closest to their original point of release at Craig Lockhart in the Auob River decreasing downriver towards the confluence with the Nossob. My transect surveys also demonstrate that the lowest density of large *A. erioloba* are in the low giraffe density zone, whereas the lowest density of large *A. haematoxylon* are in the high giraffe density zone. There are more juveniles and intermediates of *A. erioloba* compared to *A. haematoxylon*, with extremely low densities of *A. haematoxylon* juveniles all along the riverbed. These results suggest that the reason why the giraffe have not moved far away from the Craig Lockhart borehole is because there are much higher densities of large trees in the upper reaches of the Auob River.

This study shows that the highest impact of giraffe browse on large trees of both species is in the high giraffe density zone. Within the 2 to 5 m browse range in the highest giraffe density zone there was a significant increase in canopy dieback but little change in canopy structure for *A. erioloba* trees whereas *A. haematoxylon* trees have much narrower canopy widths and significantly more canopy dieback (twice that of *A. erioloba*).

Looking at the impact of giraffe browse on the reproductive potential of the trees, I found no flowers in the high giraffe density zone and significantly fewer flowers in the medium compared to the low density zone for *A. haematoxylon*. The results also show fewer pods at giraffe browse height for both species but significantly fewer pods for *A. haematoxylon* than *A. erioloba,* with more pods in the medium and high zones for *A. erioloba*. These results suggest that giraffe browse is not only affecting canopy structure of *A. haematoxylon* but also having a higher impact on the recruitment of *A. haematoxylon* compared to *A. erioloba*. These trends for flowers and pods are reflected in the decrease in the relative proportion to large trees of *A. haematoxylon* juveniles and intermediates from the low to the high giraffe browse zones while juveniles and intermediates of *A. erioloba* increase. The lack of flowers and very few pods on *A. haematoxylon* relative to *A. erioloba* across all giraffe density zones and relative to the total number of trees for each species suggests giraffe browse will have a greater effect on germination and establishment rates for *A. haematoxylon* than on *A. erioloba*.

In savanna systems, trees have a high resilience to stem mortality, often persisting as juveniles for many years (Higgins *et al.* 2007). Those trees top killed by fire or animal browse will resprout from the base using stored resources (Schutz *et al.* 2009). The juvenile trees in my surveys may therefore not be representative of a continuum of recruitment and establishment as many could be several decades old (Higgins *et al.* 2007). Rather, my results could suggest that already low numbers of juvenile *A. haematoxylon* will become even fewer as less seed becomes available for germination and establishment.

There are several species in the Park other than *A. haematoxylon* accessible as available browse to giraffe including *Acacia erioloba, A. hebeclada, Boscia albatrunca* and *Terminalia sericea* with only *A. erioloba* in sufficient quantity in the Auob for giraffe to browse constantly (Smithers 1971 in Hall-Martin and de Graaf 1978; Kruger 1994). My results suggest that the highest density of *A. erioloba* is below the Craig Lockhart borehole. However, it is clear that impacts of giraffe browse are significantly higher on *A. haematoxylon* than on *A. erioloba,* as evident in a change in canopy structure, higher canopy dieback and lower production of seeds. Recent research has demonstrated that the thorns of *A. erioloba* are long, thick and robust relative to those of *A. haematoxylon* (Viljoen 2013). This relative lack of structural defence makes it easier for giraffe to exploit *A. haematoxylon* which is reflected in 79 % of the giraffes' diet comprising of *A. haematoxylon* (Viljoen 2013).

Within the Keystone Species concept (Payton *et al.* 2002), if we consider the two *Acacia* species in the Park to be the keystones, we do not know what will actually replace them if they disappear. The Kalahari ecosystem has low species redundancy; therefore its ecosystem processes could be very sensitive to variations in biodiversity (Naeem 1994, 1998). These variations can be caused by changes in climate. However, current climate models for the drier northern parts of South Africa are unable to inform us as to what the ecosystem might resemble in the future except that there is a high likelihood of increased drought frequency and duration (Hulme *et al.* 2001; de Wit and Stankiewicz 2006; Kusangaya *et al.* 2014). With the potential to get drier, an increase in water abstraction by humans and reduction in germination and recruitment from giraffe browse, there might be a shift in the ecosystem to one that resembles a desert.

Conclusion

There are low numbers of juvenile trees in this ecosystem but I cannot demonstrate a decrease in number of juvenile trees is as a result of intense giraffe browse, as 25 years (time since the giraffe were introduced) is too short an amount of time for great impacts to be reflected in this system. However, there is high potential that there will be a cascading negative effect on the ecosystem from giraffe browse in the near future. Giraffe are significantly reducing the canopy structure, eating flowers and causing canopy dieback for both common tree species in the Auob River. These trends are far more evident for *A. haematoxylon* than *A. erioloba* (the preference is not clearly understood), and if not curtailed could mean the local extinction of *A. haematoxylon* as a large tree species in the Park in the future. With no obvious replacements of large trees, the removal of one of these two keystone species in the Auob River will have cascading negative effects on the many species that rely on the trees. This trophic structure will change and in this arid system may evolve into a different trophic structure over time, possibly similar to desert but unknown. Future research should determine the extent of the effect that giraffe may have on the only tree form of *A. haematoxylon,* to feed into a management plan for the Park to prevent giraffe population numbers from exceeding a defined threshold or carrying capacity, leading to irreparable changes to the ecosystem.

CHAPTER 3:

Effects of groundwater abstraction on two keystone tree species in the Kgalagadi Transfrontier Park

Introduction

Water availability is important for terrestrial plants, particularly those in arid regions. In photosynthesis, water is lost to the atmosphere when the stomata are open to allow for carbon dioxide uptake. This water is replaced in a continuous stream from the roots through the stems to the leaves (Simonin *et al.* 2009). Plants access water from the soil and many aspects of plant form and function are influenced by the availability of soil water (Simonin *et al.* 2009). For example in arid savanna many trees are deciduous during the dry season, shedding their leaves as available soil water decreases with lack of precipitation (Jolly and Running 2004). The ability to exploit a deep, permanent water source such as groundwater in aquifers makes it possible for some plants to survive long periods without rain (Jennings 1974; Schachtschneider and February 2010). In the more arid parts of southern Africa, ephemeral rivers are populated by trees exploiting these deep water sources (Schachtschneider and February 2010). For the savanna regions of southern Africa however, climate predictions suggest that rainfall is decreasing and will become more erratic over the next few decades, increasing drought frequency and/or duration (Hulme *et al.* 2001; Batisani and Yarnal 2010; Kusangaya *et al.* 2014). In these regions, quantifying how and where plants access their water and the anthropogenic effect on this water is of some concern. It is therefore extremely important to develop a better understanding of the potential impacts such predictions may have on vegetation structure in arid environments such as at my study site in the Kgalagadi Transfrontier Park.

Plants may either close stomata in response to drought or maintain transpiration at the risk of xylem cavitation through high negative pressures (McDowell 2011). With persistent drought however plants may die either through carbon starvation if stomata are closed for extended periods or hydraulic failure with cavitation of the xylem through increasing negative pressures (McDowell *et al.* 2008; West *et al.* 2008; McDowell 2011). Several studies have now shown that plants with deep root systems maintain gas exchange at the cost of declining xylem pressure potentials (Schwinning *et al.* 2004; McDowell *et al.* 2008; West *et al.*2008, 2012).

In arid savannas such as at my study site there is no surface water and as such all water for animals and any new tourism development (such as is planned for 2015) has to come from groundwater abstraction (Mills and Retief 1984; van Wyk and le Riche 1984; SANParks 2008). Such abstraction has to be monitored, as several studies in Arizona in the USA and Western Australia have shown both short- and long-term water table declines as a result of groundwater draw-down (Stromberg 1993; Groom *et al.* 2000; Lite and Stromberg 2005; Barron *et al.* 2014). In these studies trees are able to withstand small fluctuations in water level but cannot put down roots fast enough to adjust to large drops of between 1.2 m - 2.4 m (e.g. Cooper *et al.* 2006). In contrast, some trees such as *Tamarix* (an aggressive riparian invader) can grow roots very quickly (~15mm/day root growth) to follow a declining water table (Nippert *et al.* 2010).

Using hydrogen ($^2H/^1H$) and oxygen ($^{18}O/^{16}O$) isotope ratios of xylem water extracted from suberized wood it is possible to show the water source of a plant (Dawson *et al.* 2002; Schachtschneider and February 2010). The method is based on the expectation that the stable isotope ratio of the source water does not change when taken up by the plant. Using this method Schachtschneider and February (2013) demonstrated that the trees growing in a river system similar to the one at my study site were using deep groundwater (up to 56 m). The two most common tree species, *Acacia erioloba* and *Acacia haematoxylon* at my study site are both considered keystone species because they provide nesting sites, shade, food resources, increased soil water availability and soil nutrients for a variety of other plants and animals (Milton and Dean 1995; Dean, Milton and Jeltsch 1999; Ludwig *et al.* 2004). They can also send their roots very deep to source water (Schachtschneider and February 2010) and, while there has been no research on this, the two species could be hydraulically redistributing water in the upper layers of the soil, facilitating the water use of shallow rooted species such as grasses (Caldwell, Dawson and Richards 1998; Burgess *et al.* 2001; Ludwig *et al.* 2004).

Here I examine the effects of groundwater abstraction from two boreholes on the tree species *A. erioloba* and *A. haematoxylon* in the Auob where water abstraction is low, and the Nossob where abstraction is higher. The two boreholes service the Urikaruus Wilderness Camp and Nossob Rest Camp on the Auob and Nossob rivers respectively. Urikaruus Wilderness Camp holds a maximum of eight guests at a time and is occupied throughout the year (92.4 % annual unit bed occupancy in 2008; SANParks 2008). Nossob Rest Camp is much larger with the possibility of holding ~120 guests and also has high occupancy each year (79.3 % annual unit bed occupancy in 2008; SANParks 2008).

I hypothesise that the trees and humans in both rivers are using the same water source. The humans are accessing this water through boreholes while the trees are using deep root systems. I examine this hypothesis by firstly determining the depth of the water source for both *A. erioloba* and *A. haematoxylon* using hydrogen and oxygen isotope ratios of both xylem and borehole water. I also determine the extent to which the two species are near the threshold of physiological stress by using leaf $\delta^{13}C$ values, midday xylem pressure potentials and specific leaf area to show water-use efficiency and stomatal regulation, the amount of tension the water column is under and the efficiency of resource use respectively. I expect that trees upstream of the active borehole in the Auob and Nossob will have more positive midday xylem pressure potentials (XPP), higher specific leaf areas (SLA) and more negative leaf $\delta^{13}C$ values, while below the borehole trees will have more negative midday XPPs, lower SLAs and more positive leaf $\delta^{13}C$ values due to the effects of anthropogenic water abstraction increasing water stress in the trees. I expect to find similar trends in both the Auob and the Nossob but with greater differences between upstream and downstream in the latter river system due to more water stress as a result of higher rates of abstraction being used to supply the larger camp at Nossob.

Methods

Description of the study area

The 38 000 km^2 Kgalagadi Transfrontier Park is situated in the south-western Kalahari (between latitude -24.10° to -26.67°, longitude 20.00° to 21.84°) and is characterized as an arid savanna with a sandy subsurface, deep groundwater and an annual rainfall between 180 and 210 mm, increasing from Nossob (-25.4212°, 20.5968°) in the northeast to Twee Rivieren (-26.4721°, 20.6116°) in the southwest. The wet season rainfall (late November to early April) occurs as erratic and highly localised thunderstorms usually peaking in February/March (van Rooyen and van Rooyen 1998; SAWS 2015), with mean monthly minimum and maximum temperatures of 0.1 °C and 36.7°C for July and December respectively (SAWS 2015). Potential annual evaporation in summer (January) can reach more than 3 000 mm around Nossob (Rutherford *et al.* 2006). Thirty years of South African Weather Service (SAWS 2015) data reflects this strong seasonal change (Fig. 1).

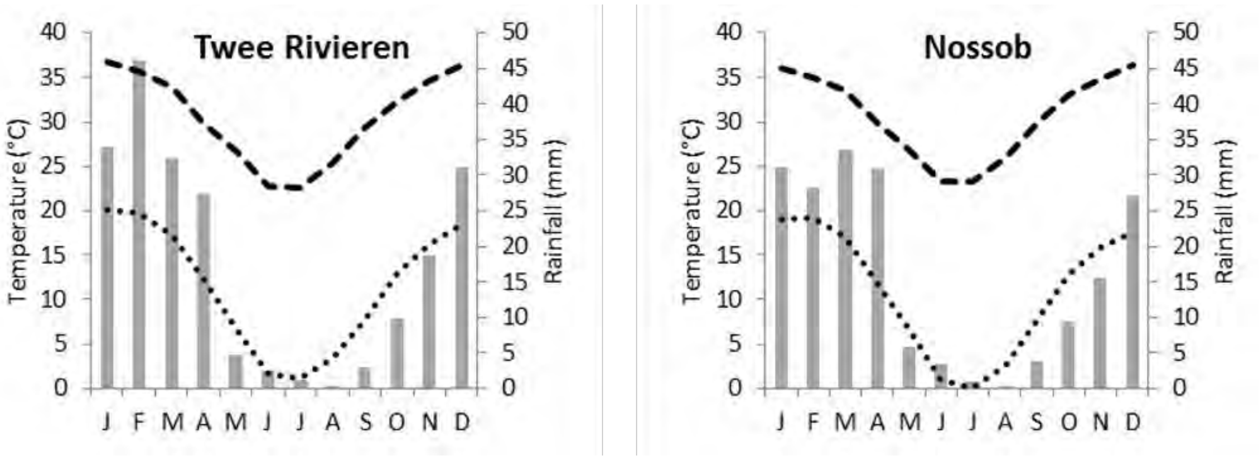

Figure 1: *Average monthly rainfall (bars) and average maximum (--) and minimum (…) temperatures from 1984 to 2014 for Twee Rivieren [Station No. 0461208 4] and Nossob [Station No. 0535175 5] (SAWS 2015).*

My two sampling areas were situated in the Auob and Nossob river beds on the South African side of the Kgalagadi Transfrontier Park (Fig. 2). In the Auob, *A. erioloba* and *A. haematoxylon* (biogeographically endemic to the Kalahari) are the dominant tree species, with *Acacia mellifera* and *Rhigozum trichotomum* being common shrubs. Grasses such as the annual *Schmidtia kalahariensis* and perennial *Stipagrostis obtusa* occur in sparse clumps (Leistner 1959; Rutherford *et al.* 2006). The vegetation in the Nossob is very similar to that of the Auob, but with no *A. haematoxylon*, only large *A. erioloba* trees. Common grasses here are the perennial *Panicum coloratum* var. *coloratum* and *Eragrostis bicolor* (Bothma and de Graaf 1973; Rutherford *et al.* 2006).

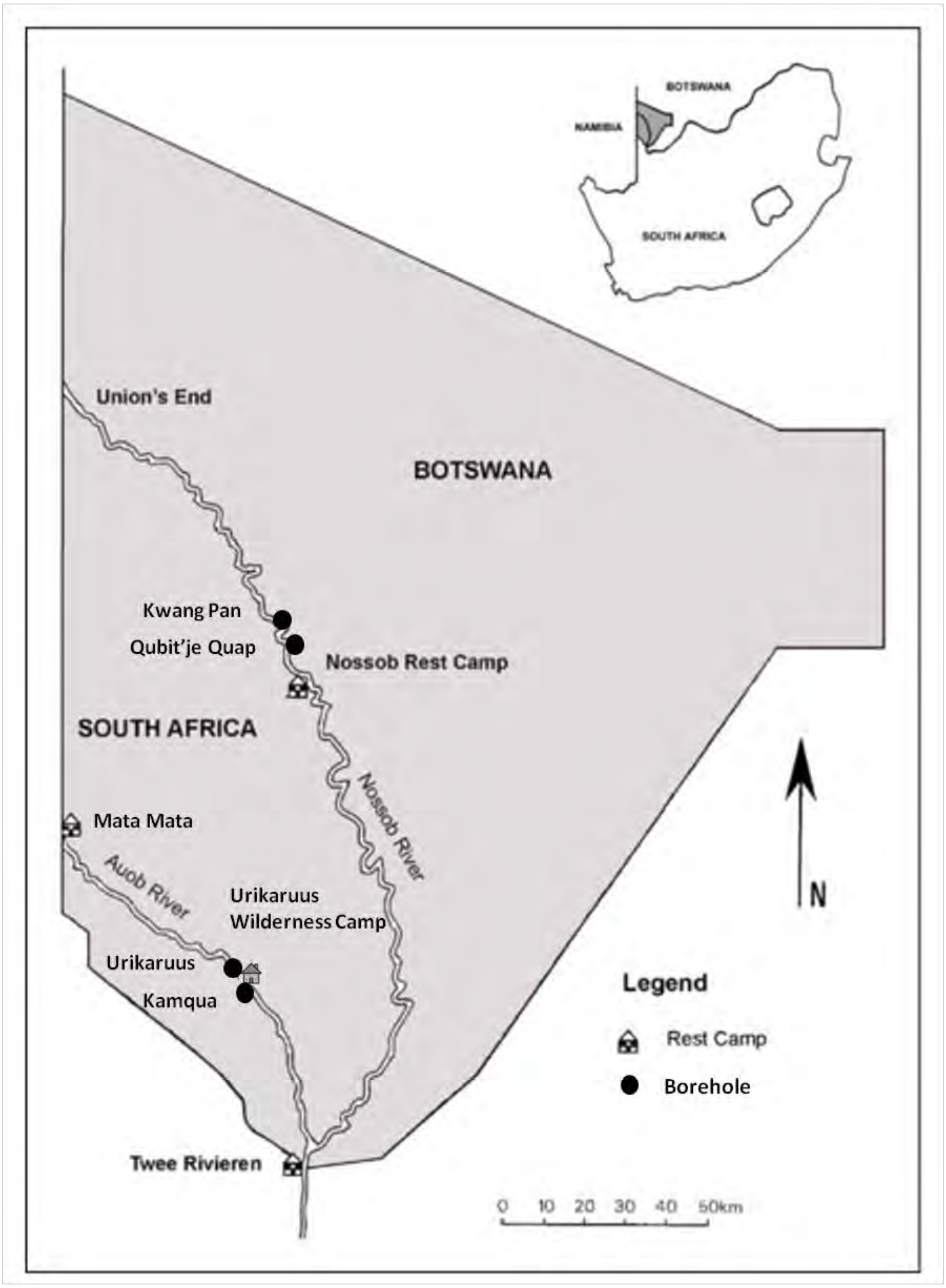

Figure 2: *Location of the Kgalagadi Transfrontier Park (shaded area) in southern Africa with the location of the boreholes depicted at Urikaruus and Kamqua in the Auob and Kwang Pan and Qubit'je Quap in the Nossob rivers (Map adjusted from van Rooyen* et al. *2008).*

Groundwater sampling: Tree Water Source

Of the estimated 88 boreholes drilled in the Park since the early 1930s, less than half are active today. These boreholes provide water for the nine permanent camps, four picnic sites and 41 artificial waterholes (Mills and Retief 1984; van Wyk and le Riche 1984; SANParks 2008). Out of these I sampled four boreholes (Table 1): Urikaruus and Kamqua boreholes upstream and downstream respectively of the Urikaruus Wilderness camp borehole (-26.010832°, 20.349627°) in the Auob; and Kwang Pan and Qubit'je Quap boreholes upstream and downstream respectively of the Nossob camp borehole (-25.287383°, 20.537513°) in the Nossob.

Table 1: *The four sampled boreholes upstream or downstream of an actively pumped borehole, Urikaruus Wilderness camp borehole (-26.010832°, 20.349627°) on the Auob and the Nossob camp borehole (-25.287383°, 20.537513° on the Nossob.*

Position	**Borehole**	**Latitude**	**Longitude**
Auob Upstream	Urikaruus	-25.995517°	20.339600°
Auob Downstream	Kamqua	-26.010850°	20.399750°
Nossob Upstream	Kwang Pan	-25.287933°	20.536950°
Nossob Downstream	Qubit'je Quap	-25.321483°	20.547150°

The sampled boreholes in the Auob were 6 km apart as the crow flies and 7.7 km following the riverbed. Between these is the actively pumped borehole supplying the small Urikaruus Wilderness Camp. In the Nossob the boreholes were 4 km apart as the crow flies and 10 km following the riverbed with the active borehole supplying the large Nossob Rest Camp in-between. In 2013, the active borehole pumped ~24 000 l (when the camp was quiet) to ~30 000 l (busy) per day, 7 days a week, supplying on average ~120 people, and was rested only for refuelling and maintenance (G. Ellis, *pers comms*).

The sampled boreholes were monitored to determine seasonal fluctuations in the water table by inserting piezometers (Solinst-Levelogger, Johannesburg, South Africa) in the Auob boreholes from 25/08/2012 to 30/01/2014, and in the Nossob boreholes (Schlumberger - Diver, Delft, The Netherlands) from 26/08/2012 to 31/01/2014. The data were recorded at hourly intervals and downloaded every six months.

Water Relations

To determine the water relations of my study trees, I took samples for both water and carbon isotopes, midday xylem pressure potentials, and specific leaf area and estimated canopy death. In the Auob I sampled both *A. haematoxylon* and *A. erioloba* between 2 and 375 m from the Urikaruus and Kamqua boreholes. As there are no *A. haematoxylon* in the Nossob I only sampled *A. erioloba,* between 19 and 412 m from the Kwang Pan and Qubit'je Quap boreholes (Fig. 2).

Stable isotope analysis

Sampling for stable oxygen and hydrogen isotope ratios on twelve trees of both species above and twelve trees below the active borehole for the Auob River and eight *A. erioloba* trees above and eight below the active borehole in the Nossob was done for three seasons (January 2013 - wet, July 2013 - dry and January 2014 - wet). For this, two non-photosynthesizing twig sections (0.5 - 1cm in diameter and 5 - 7cm in length) were cut from each tree using a pair of secateurs. These sections were immediately placed into borosilicate screw-top vials (Kimax–Kimble, New Jersey, USA) and sealed with Parafilm (Pechiney Plastic Packaging, Chicago, IL, USA) to reduce any evaporative enrichment of the xylem water (West *et al.* 2008; Schachtschneider 2010). The samples were frozen as soon as possible and kept at - 4 °C until the water was separated out through cryogenic vacuum extraction in the laboratory. Twig samples yielded between 1.5 – 4.5 ml of water during extraction. Borehole water samples from the four boreholes (Urikaruus, Kamqua, Kwang Pan and Qubit'je Quap) were collected at the same time as the twig samples. These were stored in small (20 ml) glass screw-top bottles (Wheaton Liquid Scintillation Vials, Millville, NJ, USA) sealed with Parafilm (Pechiney Plastic Packaging, Chicago, IL, USA) and kept as cool as possible without freezing until analysis. Following the methods of Schachtschneider and February

(2010) I calculated a local meteoric water line (LMWL) specific for my study site. As it was unknown where the trees were sourcing their water at the time, this measure allowed the distinction of deep groundwater signals from those of local rainfall and hence shallow soil water and to determine if humans and trees in the Park were utilising the same water. Rain water samples were collected opportunistically at Twee Rivieren on 5/07/2013, between the 19th and 28th of January 2014 as well as between Kwang Pan and Nossob on the 4/07/2013.

The water samples (borehole, rain, plant) were analysed for $^{18}O/^{16}O$ ratios following the CO_2 equilibrium method of Socki *et al.* (1992), while $^{2}H/^{1}H$ ratios were obtained using a variation of the zinc closed tube reduction method of Coleman *et al.* (1982) as modified by Schachtschneider and February (2010).

As an indication of changes in water-use efficiency and stomatal regulation, ten mature leaves were picked from each study tree in the 2013 wet season (January) for stable carbon isotope analysis ($^{13}C/^{12}C$). The leaves were oven-dried at 70 °C for 24 hours in a Thermo Oven (Scientific Series 2000 model 278, South Africa), and ground to a fine powder using a Retsch MM200 ball mill (Retsch Inc. GmbH & Co KG, Haan, Germany) .

Oxygen, hydrogen and carbon isotope ratios were determined using a Thermo Finnigan Delta Plus XP Mass Spectrometer (Thermo Finnigan, Hamburg, Germany). The laboratory's own internal standards were run to calibrate the results relative to Vienna-Standard Mean Ocean Water (V-SMOW) for oxygen and hydrogen and Pee Dee Belemnite for carbon. The deviation from the standard is denoted by the term δ and results are expressed as parts per mil (‰) using the equation:

$$\delta^{x}\mathrm{E} = \left(\frac{\mathrm{R}_{sample}}{\mathrm{R}_{standard}} - 1\right) \mathrm{x}\ 1000$$

where $\boldsymbol{\delta^{x}E}$ is the respective element (^{2}H, ^{18}O or ^{13}C), **x** is the mass of the heavier isotope in the abundance ratio, and $\mathbf{R}_{\boldsymbol{sample}}$ and $\mathbf{R}_{\boldsymbol{standard}}$ are the ratios of the heavy to light isotope of sample and standard respectively (Dawson *et al.* 2002). The analytical uncertainty is approximately 0.1 ‰ for $\delta^{13}C$, 2 ‰ for $\delta^{2}H$ and 0.2 ‰ for $\delta^{18}O$.

Xylem pressure potentials

Xylem pressure potentials (XPPs) are a relative indicator of the amount of water available to the plant through a determination of the amount of tension the water column is under (Scholander *et al.* 1965; Hempson *et al.* 2007). Midday XPPs were taken in both the wet and dry season of 2013 using a Scholander-type pressure chamber (PMS Instrument Company, Corvallis, OR, USA). I specifically used midday rather than predawn XPP because of the hazards related to working in the dark with large carnivores present in the area and long travel distances. I also assumed that midday readings in the middle of both the wet and dry seasons should sufficiently illustrate the reliance of individual trees on seasonal (rain) or deep groundwater. Terminal twigs with intact leaves (~0.5cm diameter) were cut from each tree with secateurs, immediately inserted into the pressure chamber and the pressure value read when water droplets began to form on the bisected stem.

Specific Leaf Area

Ten leaves were picked from each tree in both dry and wet seasons of 2013. All ten leaves were placed together on a white background and photographed immediately after picking with a Canon PowerShot SX240 HS (Canon, Tokyo, Japan). The background had a pre-drawn 5 x 2.5 cm block on it to enable calibration during analysis. The area of each individual leaf from the JPEG photograph was determined by the sum of pixels of a particular colour covered by the leaves (converted into cm^2 through calibration) using open-source image software (ImageJ®). In the laboratory the leaves were oven dried at 70° C for 24 hours in a Thermo Oven (Scientific Series 2000 model 278, South Africa) and weighed to determine dry weight. Specific leaf area (SLA) was calculated for each tree using;

$$SLA = \frac{\text{leaf area (cm}^2\text{)}}{\text{dry weight (g)}}$$

Canopy Dieback

Semi-deciduous species such as *A. erioloba* and *A. haematoxylon* are very rarely leafless in the dry season due to synchronised leaf fall and new leaf emergence (Sekhwela and Yates 2007; Schachtschneider and February 2013). Twigs and branches with no leaves were therefore attributed to canopy dieback. Photographs of each tree's canopy were taken in each site once per season (wet and dry 2013) to score canopy dieback as a percentage of dead/woody material relative to the remainder of the canopy.

The photographs were taken when the entire tree canopy was just inside the field of view through a 18-200 mm f/3.5 - 6.3 HSM DC lens (Sigma, Fukushima, Japan) fixed at 52 mm, F8 aperture and through a PRO1 D UV (W) filter (Kenko, Tokyo, Japan) on a D60 Nikon camera (Nikon, Ayuthaya, Thailand) set upon a tripod (290 Series; Manfrotto, Cassola, Italy) 1.5 m off the ground. The distance between camera and tree was measured from the mid-point of the tripod to the base of the tree in a straight line using a100 m tape measure. These photographs were taken between 10 am and 4 pm in two directions, east to west and north to south, unless obstructed in which case the direction was switched through 180°. The angle of the tripod head (with attached camera) was adjusted using the spirit level set into the tripod, so that the camera was always horizontal (relative to the ground) and tilted vertically keeping the entire tree canopy just inside the field of view. For the calibration of each photograph, a retractable 5 m aluminium ranging rod (levelling staff; Leica Geosystems, St. Gallen, Switzerland) was held vertically at the edge of the canopy in the field of view (Fig. 3).

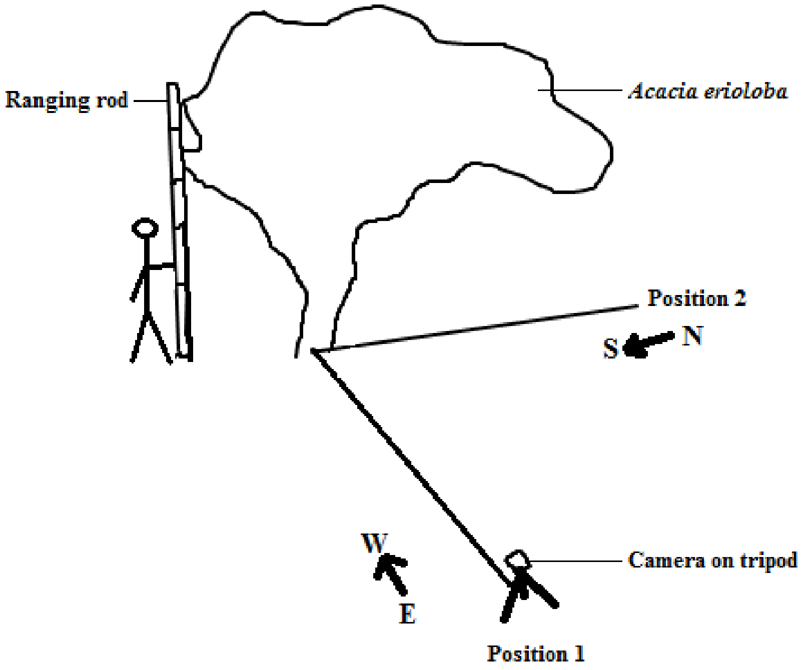

Figure 3: *Illustration of photography setup showing orientation the two photographs were taken from for each tree and the placement of the ranging rod for Position 1.*

The photographs were taken in RAW format and adjusted into TIFF images when analysed in Adobe Photoshop CS5 v12.0 x 32© (Adobe Systems Software Ltd, Ireland). Each photograph was overlaid by a calibrated grid (50 cm boxes, subdivided by 10), the ranging rod enabling calibration. To determine canopy dieback living (leaf) and dead material (twigs < 5 cm thick) were noted at each grid intercept around the outer 15 cm edge of the canopy (Fig. 4).The method was repeated for both angles of each tree (two photographs). From the total number of intercepts (dead + live), the percentage of canopy dieback was calculated for each photograph and then averaged per tree.

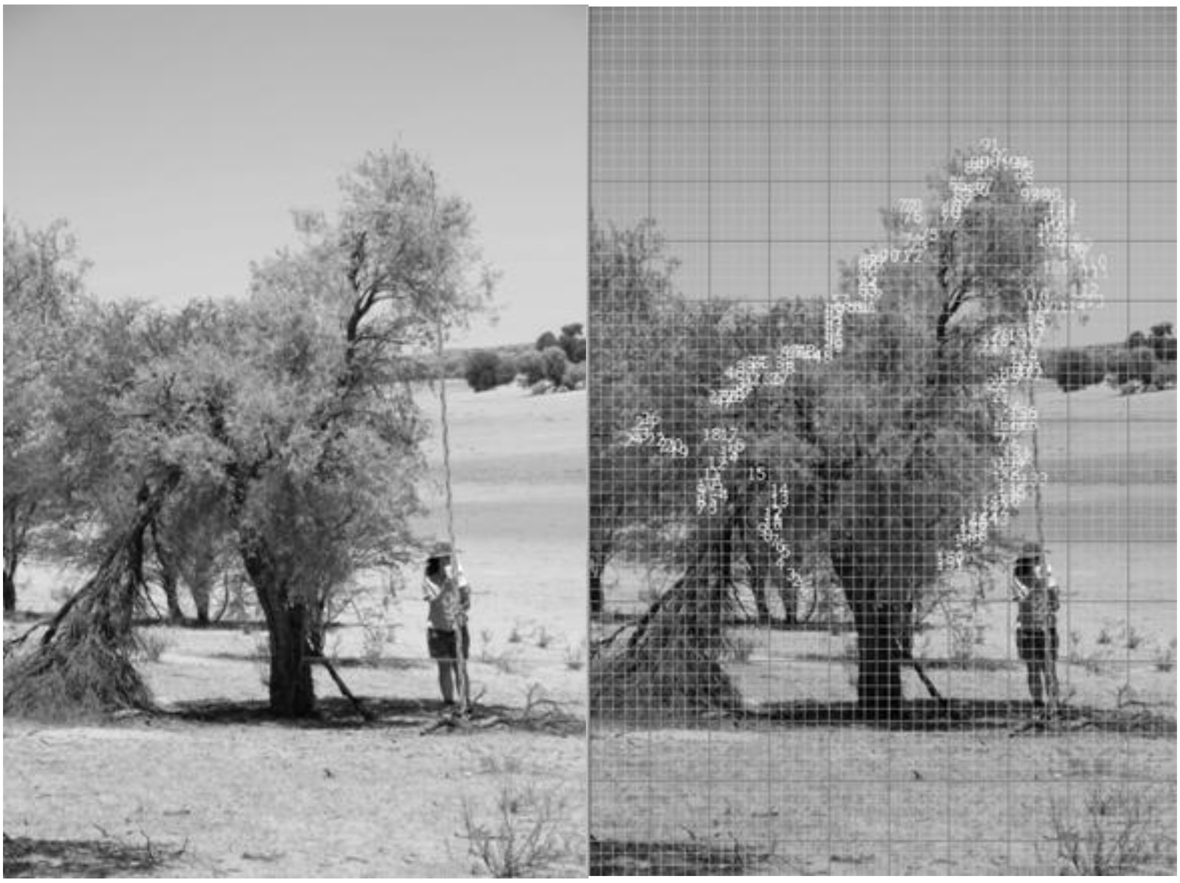

Figure 4: *Illustration of the grid overlay and intercept counting (numbers) method implemented to determine canopy dieback from photographs.*

Statistics

The data were split into three sets according to river and species: *A. haematoxylon* and *A. erioloba* in the Auob; and *A. erioloba* in the Nossob. The differences between upstream and downstream for six dependent variables were assessed: Wilcoxon Sum Rank tests for leaf

$\delta^{13}C$ values, linear mixed effects models for $\delta^{18}O$ and $\delta^{2}H$ values and midday xylem pressure potentials, linear models for specific leaf area and Kruskal-Wallis Rank Sum tests followed by a Pairwise Wilcoxon with Bonferroni correction for canopy dieback. The models were developed using 'season' (wet/dry), 'position' (upstream/downstream) and the interaction between these with individual trees as the random effect (the same trees were sampled in both seasons). All tests on the data were assessed in R© v3.1.2 (R Core Development Team 2014) and a value of $p < 0.05$ required for significance.

Results

Borehole water level

Instrument malfunction affected recordings, so only those of which I am certain were considered for comparison, as in the Nossob upstream borehole for which I only obtained August and September 2012 readings. In both the Auob and Nossob Rivers, the water table at the upstream borehole was lower than the downstream borehole (Fig. 5). This was unexpected, but I speculate that this was due to calcrete layers lying closer to the surface under the water table for the downstream boreholes in both rivers. Both the Auob boreholes show a similar pattern in groundwater flux through time: a steady drop in water level of ± 4 m soon after the peak of the dry season (July/August), and a subsequent rise of ± 4 m matching the peak of the wet season rains (January/February). The Nossob downstream water level showed a 6 m drop two months after the peak of the dry season, but only a 2 m rise during the peak of the wet season rains (Fig.5). The water level here asymptotes unusually low early on from February 2013.

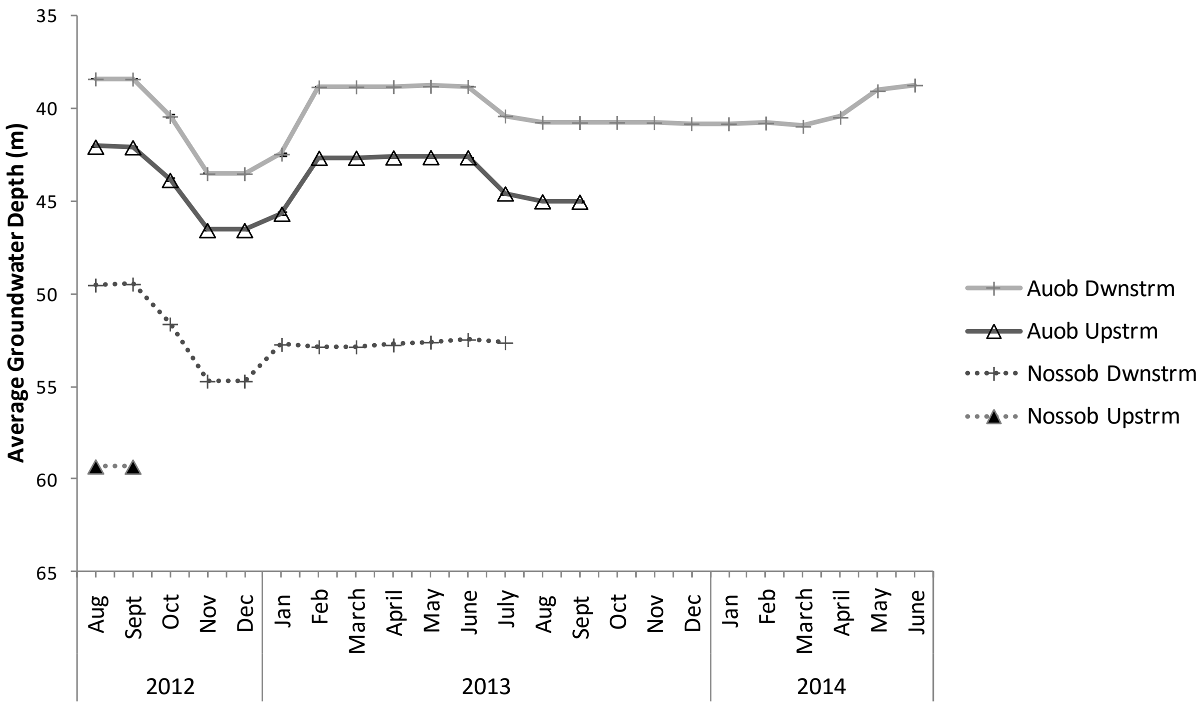

Figure 5: *Average monthly groundwater depths for the Auob River and the Nossob River upstream and downstream monitored boreholes over the study period.*

Water Source of trees

Sampled tree heights ranged from 2.5 – 7.2 m for *A. haematoxylon* and 3.4 – 11.1 m for *A. erioloba* in the Auob, and between 2.9 – 12.8 m for *A. erioloba* in the Nossob.

Oxygen and Hydrogen Stable Isotopes

Meteoric waters worldwide follow a Rayleigh distillation process that results in a linear relationship between $\delta^{18}O$ and $\delta^{2}H$, termed the global meteoric water line (GMWL; $y = 8x + 10$) (Craig, 1961; Gat, 1996). For plant water source studies in arid environments these linear relationships (essentially representing evaporation) are extremely useful as deep (non-evaporatively enriched) and shallower moisture sources (evaporatively enriched) can be readily distinguished, with deep water plotting more negative values and shallow water more positive values (February *et al.* 2007; West *et al.* 2012). I constructed my own local meteoric water line (LMWL; $y = 5.06x - 6.75$) from rain water samples collected at Twee Rivieren between the 19th and 28th of January and the 3rd and 5th of August 2013 and between Kwang Pan and Nossob from the 3rd to the 4th of August 2013 (Fig's. 6, 7). Rainfall at my study site is extremely seasonal and, even after no rainfall for several months, with mean midday temperatures between 30°C and 40°C my study trees are not deciduous and tree water isotope ratios are indistinguishable from that of groundwater (Fig's. 6, 7).

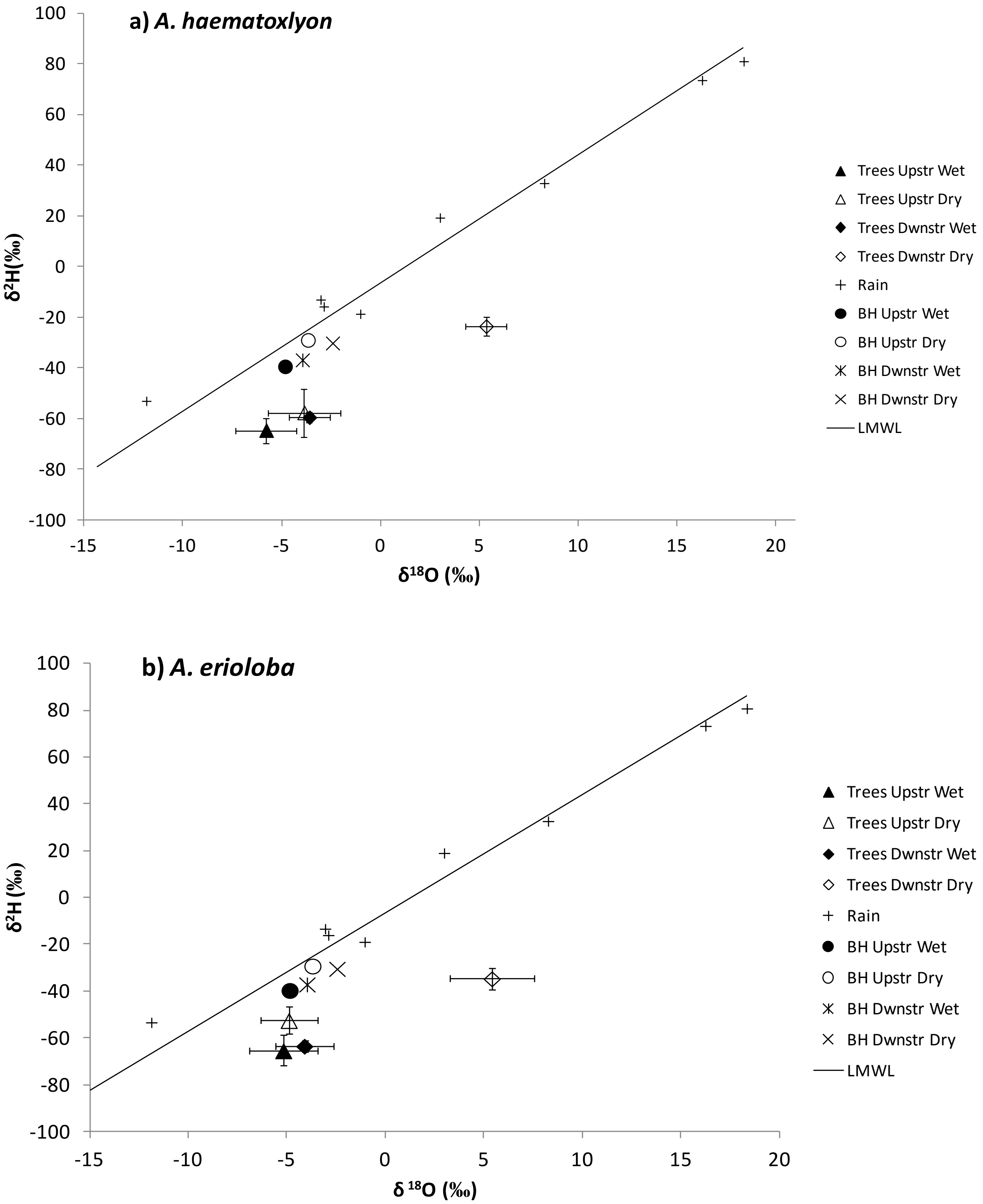

Figure 6: *The relationship between stable oxygen ($\delta^{18}O$) and hydrogen ($\delta^{2}H$) isotope ratios for two seasons (wet and dry) of average (±SE) xylem water values for a)* Acacia haematoxylon *and b)* Acacia erioloba *with related borehole water samples upstream and downstream in the Auob River. The local meteoric water line (▬ LMWL) is plotted using collected rain water samples.*

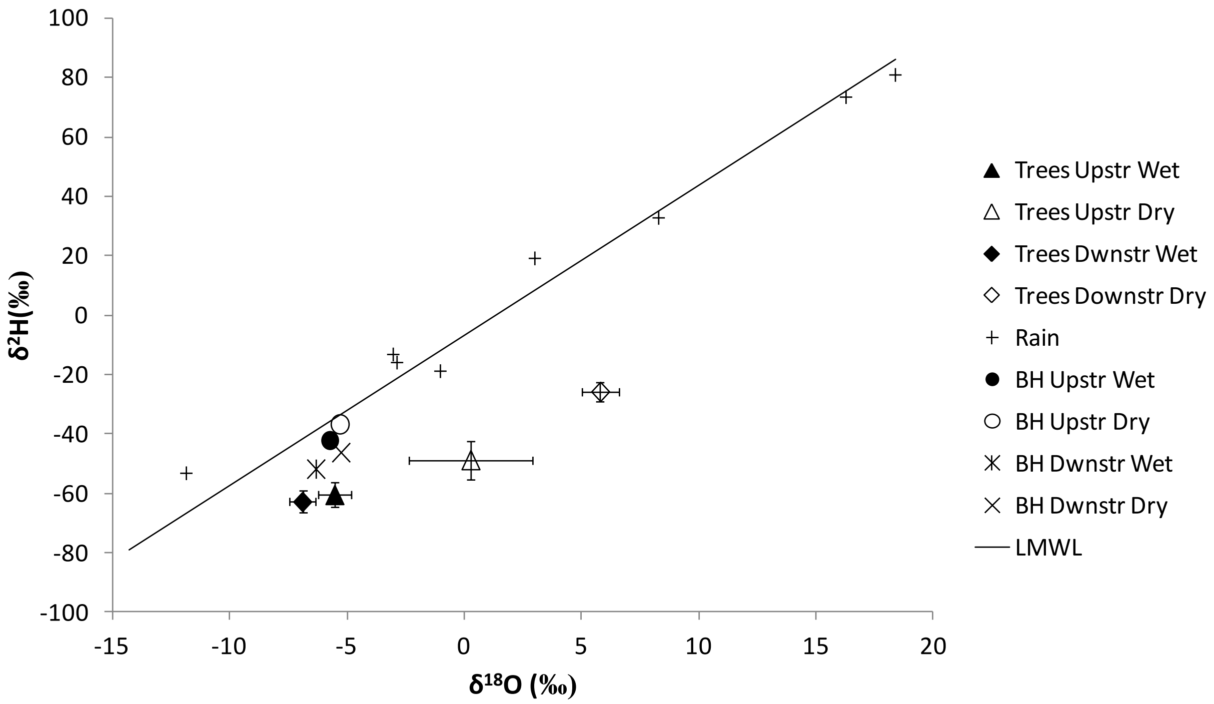

Figure 7: *The relationship between stable oxygen ($\delta^{18}O$) and hydrogen ($\delta^{2}H$) isotope ratios for two seasons (wet and dry) of average (±SE) xylem water values for* Acacia erioloba *trees and related borehole water samples (circled) upstream and downstream in the Nossob River. The local meteoric water line (— LMWL) is plotted using rain water samples.*

The results for all xylem water samples for both *A. erioloba* and *A. haematoxylon* plotted below the LMWL with values similar to that of the groundwater values (Fig.'s 6, 7; Table 2). In the Auob upstream of the abstraction point, xylem water δ^{18}O values for both species are significantly different from the groundwater δ^{18}O values but only in the dry season (Fig 6; Tables 2, 3). In the Nossob, δ^{18}O values are similar to that of the Auob in the wet season in that xylem water δ^{18}O values are similar to that of the groundwater (Fig 7; Tables 2, 3). In the dry season however, δ^{18}O values for xylem water in trees both upstream and downstream of the abstraction borehole are significantly different from the groundwater (Fig 6; Tables 2, 3).

Table 2: *Summary of ANOVA results comparing xylem and borehole water $\delta^{18}O$ isotope ratios, df = 1 for each factor. Significant differences at $p < 0.05$ indicated by **. 'Sample' is borehole/tree; 'season' is wet/dry and the interaction between the two factors is shown.*

Area	Species	Factor	Mean sq	F-Statistic	P-value
Auob	*Acacia haematoxylon*	Sample	5.10	0.45	0.51
		Season	104.25	9.23	0.00**
		Sample*Season	23.31	2.07	0.16
Auob	*Acacia erioloba*	Sample	10.68	0.55	0.46
		Season	125.33	6.50	0.02 **
		Sample*Season	29.72	1.54	0.22
Nossob	*Acacia erioloba*	Sample	99.1	6.39	0.02 **
		Season	516.6	33.32	0.00 **
		Sample*Season	106.5	6.87	0.02 **

Table 3: *Summary of linear mixed effects model results for xylem water $\delta^{18}O$ isotope ratios. Significant differences indicated by ** for $p < 0.05$ and $df = 10$. 'Position' (upstream/downstream of the active borehole), 'season' (wet/dry) and the interaction between the two factors are indicated.*

Area	Species	Factor	Estimate (2.5, 97.5% CI)	t-value	P-value
Auob	*Acacia haematoxylon*	Position	-5.02 (-9.82, -0.21)	-2.32	0.04 **
		Season	-6.29 (-8.96, -3.61)	-5.31	0.00 **
		Position*Season	3.89 (-0.05, 7.83)	2.23	0.05 **
Auob	*Acacia erioloba*	Position	-10.47 (-14.93, -6.01)	-5.23	0.00 **
		Season	-9.77 (-13.95, -5.59)	-5.21	0.00 **
		Position*Season	9.43 (3.52, 15.35)	3.55	0.01 **
Nossob	*Acacia erioloba*	Position	-4.89 (-9.26, -0.52)	-2.40	0.03 **
		Season	-12.16 (-15.99, -8.32)	-6.80	0.00 **
		Position*Season	6.71(1.29, 12.13)	2.66	0.02 **

Water Relations

Stable Carbon Isotopes

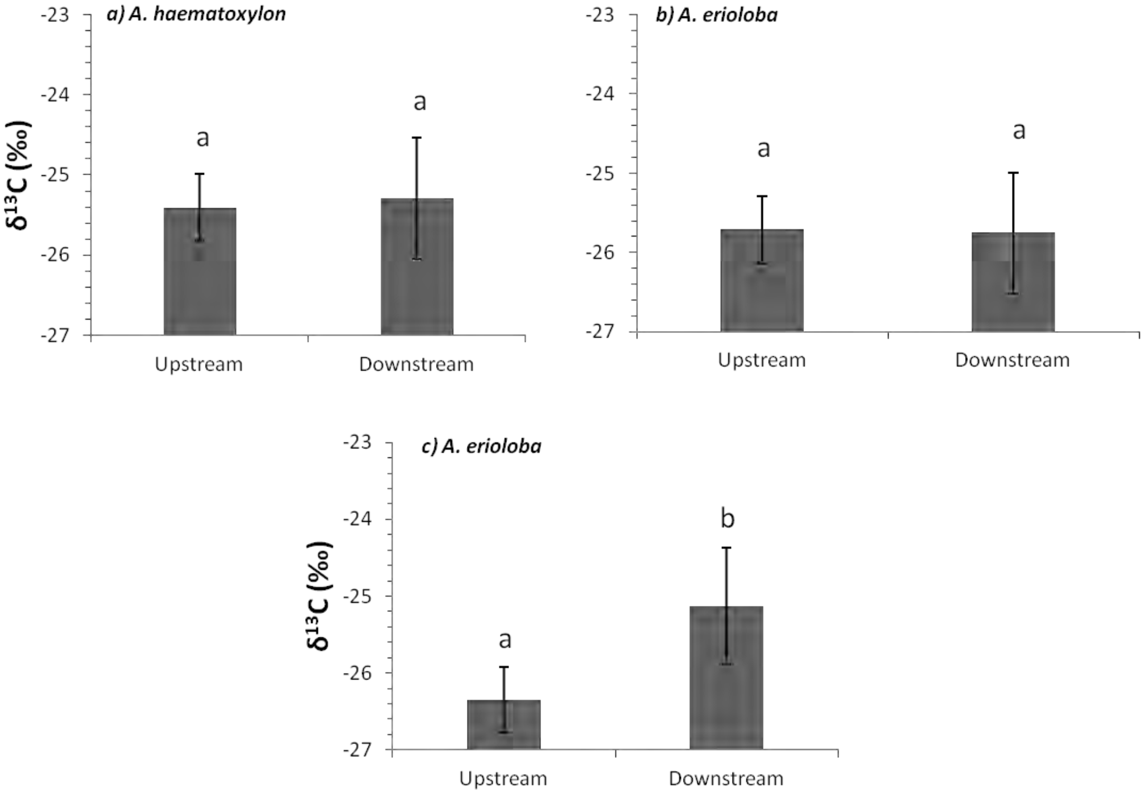

Figure 8: *Upstream and downstream leaf $\delta^{13}C$ values (±SE) for a) Auob* Acacia haematoxylon*, b) Auob* Acacia erioloba *and c) Nossob* Acacia erioloba*. Different letters indicate significant differences at $p < 0.05$ (Wilcoxon Rank Sum Test, unpaired) between upstream and downstream.*

In the Auob, there were no significant differences in leaf $\delta^{13}C$ values for either upstream or downstream *A. haematoxylon* or *A. erioloba* (Fig. 8*a, b*). In the Nossob (Fig. 8*c*) however, *A. erioloba* values downstream (-24.72 ± 0.4 ‰) were significantly more enriched ($W = 52$, $p = 0.04$) relative to upstream $\delta^{13}C$ values (-26.35 ± 0.37 ‰).

Xylem pressure potentials

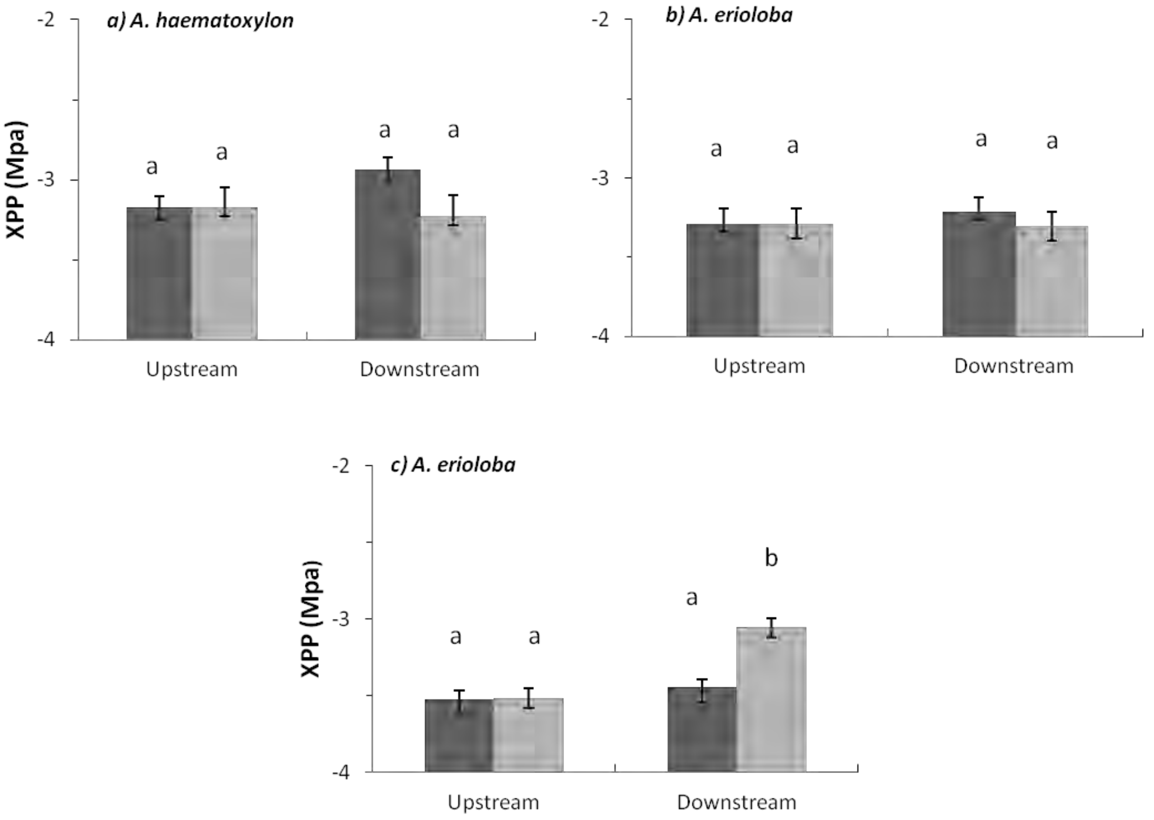

Figure 9: *Midday Xylem pressure potential (XPP) measurements for upstream and downstream values (±SE) of both wet (dark) and dry (light) seasons for a) Auob River* Acacia haematoxylon, *b) Auob River* Acacia erioloba *and c) Nossob River* Acacia erioloba. *Different letters indicate significant differences at $p < 0.05$ (linear mixed effects model, Simultaneous tests for generalised linear hypotheses) between upstream and downstream trees within and between seasons.*

In the Auob, midday Xylem pressure potentials (XPP) for both species were very negative (ranging between -2.5 and -3.9 Mpa) and lower for the downstream trees relative to the upstream trees during the dry season (Fig 9 *a, b*). In the Nossob the downstream trees in the dry season (average -3.1 Mpa) had significantly higher values than upstream trees during both the dry and wet seasons (average -3.5 and -3.4 Mpa respectively; Fig 9*c*; Table 4).

Table 4: *Summary of linear mixed effects model results for midday Xylem pressure potential measurements, df = 10 for each factor. Significant differences at $p < 0.05$ indicated by **. 'Position' = upstream or downstream of the active borehole, 'season' = wet or dry and the interaction between the two factors is indicated.*

Area	**Species**	**Factor**	**Estimate (2.5%, 97.5% CI)**	**t-value**	**P-value**
Auob	*Acacia haematoxylon*	Position	0.05 (-0.43, 0.53)	0.23	0.82
		Season	0.29 (-0.14, 0.72)	1.49	0.17
		Position*Season	0.10 (-0.51, 0.71)	0.34	0.73
Auob	*Acacia erioloba*	Position	0.02 (-0.4, 0.43)	0.09	0.93
		Season	0.09 (-0.29, 0.48)	0.53	0.61
		Position*Season	0.28 (-0.27, 0.82)	1.13	0.29
Nossob	*Acacia erioloba*	Position	-0.46 (-0.77, -0.15)	-3.21	0.01 **
		Season	-0.39 (-0.62, -0.16)	-3.71	0.00 **
		Position*Season	0.39 (0.07, 0.71)	2.60	0.02 **

Specific Leaf Area

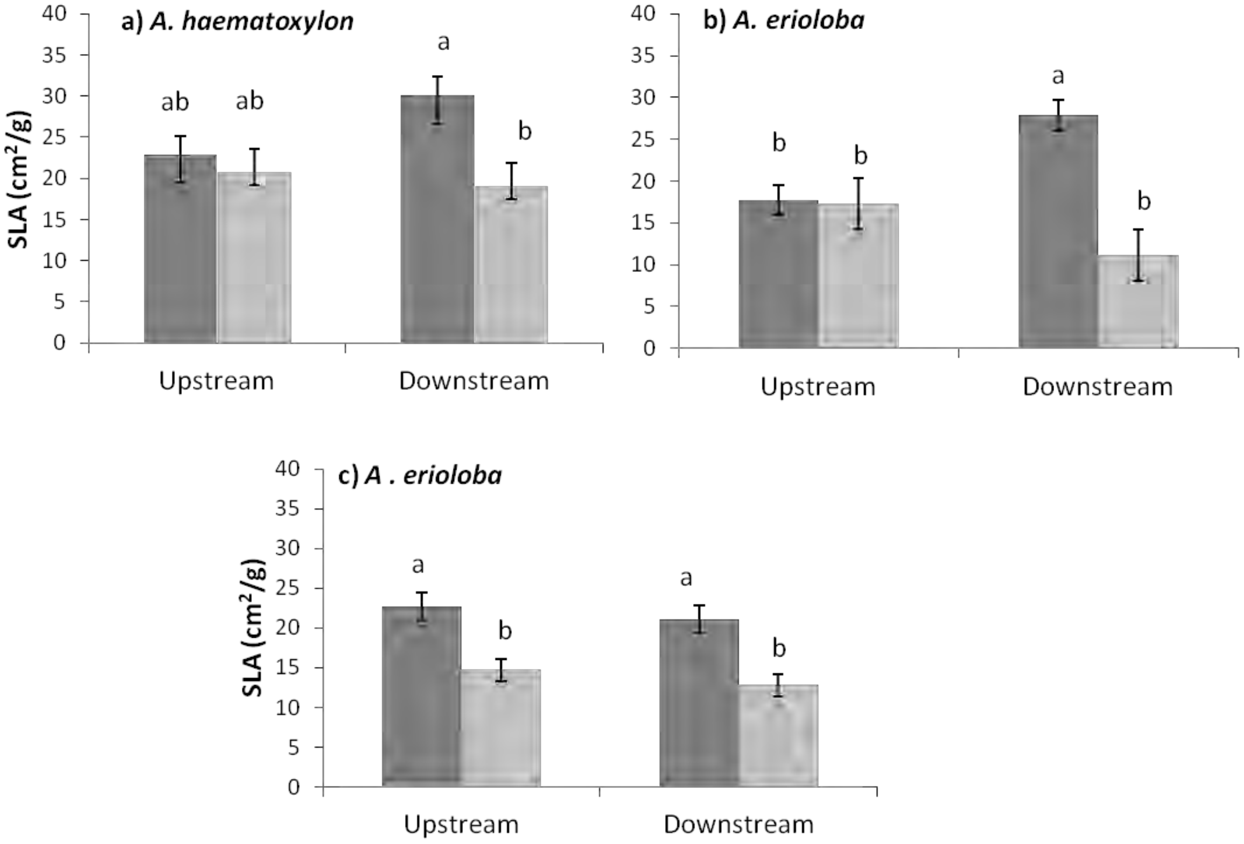

Figure 10: *Specific Leaf Area (±SE) measurements for upstream and downstream of both wet (dark) and dry (light) seasons for a) Auob* Acacia haematoxylon, *b) Auob* Acacia erioloba *and c) Nossob* Acacia erioloba. *Different letters indicate significant differences at $p < 0.05$ (ANOVA, Tukey HSD) between upstream and downstream within and between seasons.*

In the Auob, trees downstream of the active borehole had significantly lower SLA values in the dry season compared to the wet season (Fig. 10*a, b*; Table 5). For the Nossob, SLA values were significantly lower in the dry season compared to the wet season (Fig. 10*c;* Table 5).

Table 5: *Summary of ANOVA statistical results for Specific Leaf Area measurements, df = 1 for each factor. Significant differences at p < 0.05 indicated by **. 'Position' is upstream or downstream of the active borehole, 'season' is wet or dry and the interaction between the two factors is indicated.*

Area	Species	Factor	Mean sq	F-Statistic	P-value
Auob	*Acacia haematoxylon*	Position	44.2	0.95	0.34
		Season	264.4	5.66	0.03 **
		Position*Season	120.7	2.59	0.12
Auob	*Acacia erioloba*	Position	23.8	1.35	0.26
		Season	443.2	25.1	0.00 **
		Position*Season	394.4	22.33	0.00 **
Nossob	*Acacia erioloba*	Position	24.1	1.36	0.25
		Season	527.6	29.79	0.00 **
		Position*Season	0.1	0.01	0.93

Canopy dieback

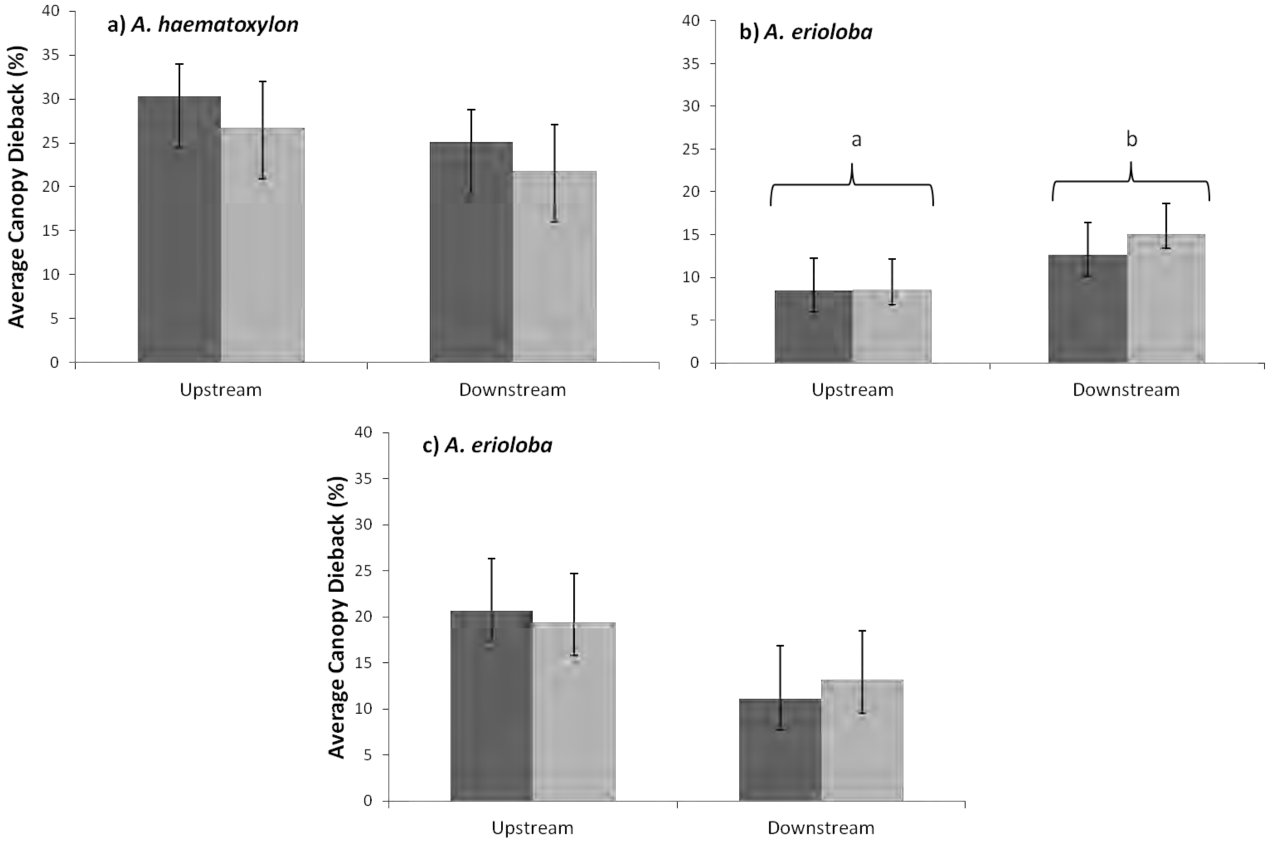

Figure 11: *Average percentage (±SE) canopy dieback for upstream and downstream values of both wet (dark) and dry (light) seasons for a) Auob* Acacia haematoxylon*, b) Auob* Acacia erioloba *and c) Nossob* Acacia erioloba*. Different letters indicate significant differences at* $p < 0.05$ *(Kruskal-Wallis Rank Sum test followed by a Pairwise Wilcoxon with Bonferroni correction) between upstream and downstream.*

There were no significant differences in average percentage canopy dieback for *A. haematoxylon* in the Auob and *A. erioloba* in the Nossob upstream or downstream of the abstraction boreholes (Fig. 11*a, c*; Table 6). In the Auob, *A. erioloba* showed significantly more dieback downstream in both seasons (Fig.11*b*; Table 6). Average canopy dieback was higher in *A. haematoxylon* (between 26 – 30 %) relative to *A. erioloba* (between 12 – 20 %).

Table 6: *Summary of Kruskal-Wallis Rank Sum tests followed by a Pairwise Wilcoxon with Bonferroni correction for percentage canopy dieback measurements. Significant differences at p < 0.05 indicated by **. 'Position' is upstream or downstream of the active borehole, 'season' is wet or dry and the interaction between the two factors is indicated.*

Area	Species	Factor	Chi-squared value	df	P-value
Auob	*Acacia haematoxylon*	Position	0.96	1	0.33
		Season	0.33	1	0.56
		Position*Season	1.3	3	0.73
Auob	*Acacia erioloba*	Position	5.33	1	0.02 **
		Season	0.21	1	0.64
		Position*Season	5.76	3	0.12
Nossob	*Acacia erioloba*	Position	1.84	1	0.17
		Season	0.07	1	0.79
		Position*Season	2.08	3	0.56

Discussion

The first deep boreholes in the Kgalagadi Transfrontier Park were drilled in the early 1930s (Mills and Retief 1984; van Wyk and le Riche 1984). As there is no surface water, the Park is reliant on the ~44 active boreholes to provide water for the permanent camps, picnic sites and artificial waterholes for the animals (Mills and Retief 1984; van Wyk and le Riche 1984; SANParks 2008). Testing the depth of water in the boreholes shows that groundwater is between 38 – 59 m under the surface. With mean annual rainfall at Nossob of 180 mm and at Twee Rivieren of 210 mm (van Rooyen and van Rooyen 1998), recharge for the Auob and the Nossob are mainly dependent on seasonal rainfall in their upper catchment in Namibia (374 mm per year; Climate Data 2015). Recent development in the tourist camps at Nossob, Kieliekrankie and Urikaruus suggests that abstraction of groundwater is going to intensify (SANParks 2016).

My results are in agreement with research showing that both *A. erioloba* and *A. haematoxylon* are using deep groundwater (Schachtschneider and February 2010, 2013). They also show that there are differences between the low water use site in the Auob and the high water use site in the Nossob. In the Auob the trees upstream and downstream of the active borehole are using deep groundwater in the wet season. In the dry season however, they are using groundwater upstream and more isotopically enriched soil water downstream. Less negative midday xylem pressure potentials and significantly lower specific leaf area values for both species downstream in the dry season indicate that trees downstream are closer to the threshold of physiological stress than upstream. In the Nossob, trees upstream and downstream of the active borehole are using deep groundwater in the wet season, but in the dry season, trees in both positions are using more isotopically fractionated soil water. Significantly more positive leaf $\delta^{13}C$ values for downstream trees indicate that these trees are starting to use stomatal regulation to improve their XPPs compared to the upstream trees (van der Water *et al.* 2002; McDowell *et al.* 2008). Lower average percentage canopy dieback in downstream trees and lower specific leaf area values and less negative midday xylem pressure potentials for both upstream and downstream in the dry season would however suggest that while the trees may be dealing with lower water levels, there is no water ‘stress’ reflected in canopy dieback as yet.

My results show that in the dry season, both species are physiologically adapting further by using stomatal regulation because of less water available than usual downstream of an active borehole in both rivers. The high potential for water stress in this system is there. The trees continue to transpire in the dry season suggesting that they are physiologically able to adapt to fluctuations in the water table of between 4.5 – 5.2 m between the wet and dry season. In the Northern Cape, South Africa, van Dyk *et al.* (2008) found that seasonal fluctuation of the water table ranged from 0 - 2 m during recharge and recession and attributed a flux of 5 m to abstraction which developed over many years (van Dyk *et al.* 2008). This emphasises how much natural flux the ecosystem goes through. Combined with its extensive rooting system (~56 m; Schachtschneider and February 2013), the xylem anatomy of *Prosopis*, an exotic invasive competing with *A. erioloba* in the Kuruman river system near the Park, is able to withstand a wide range in xylem pressure potentials which allows these trees to grow in environments with seasonal fluctuations in the water table of more than 4 m (Schachtschneider and February 2013). Stable water isotope ratios from the Kuruman River indicate that both *A. erioloba* and *Prosopis* are competing for the same water source as both species use evaporatively enriched water during the wet season and deeper ground water during the dry season when shallow water is depleted (Schachtschneider and February 2013). At my study site the trees in the Nossob which are near a borehole with a higher extraction rate are showing signs of adjusting to more water scarcity (over a season) than trees in the Auob where water abstraction is lower. My results show that the Nossob trees are losing contact with groundwater during the dry season and have to rely on some as yet unmeasured water source in the soil profile. This interesting result has clear implications for tourist camp development and further groundwater abstraction. While these trees may be physiologically tolerant of the current seasonal fluctuations in the water table this could change with drought. It would be possible to quantify these deaths with a longer term study as I observed more dead *A. erioloba* in the Nossob compared to the Auob. I did not quantify these differences but it is possible that these deaths may have occurred in a previous drought.

This study shows that *A. erioloba* and *A. haematoxylon* trees are nearing the threshold for physiological stress and that this stress will first appear for trees downstream of the active borehole in the Nossob. While this stress is as yet not reflected in canopy dieback, it is seen that water relations in estimates of specific leaf area, leaf stable carbon isotope ratios and midday xylem pressure potentials will help to assess the overall effect of water abstraction. The long-term measurements of water relations (specific leaf area and percentage canopy dieback) show the seasonal trends and natural flux of the ecosystem which is quite substantial when compared to similar ecosystems. Although the *Acacia* species are adequately adapted physiologically to large fluctuations in the water table, there is the potential for death of some trees with drought. My study would suggest that the trees in the Nossob are particularly prone to drought and it is this system that has recently seen an increase in tourism infrastructure and water abstraction.

Conclusion

Aquifer management is based on abstraction of the same amount of water as is replenished and such abstraction should take into account the ecological reserve as set out in the RSA

National Water Act (Act 36; RSA 1998). This Water Act allows for an adequate amount of water for the terrestrial plants and animals that are reliant on the aquifer (Baron *et al.* 2002). The managers of the Kgalagadi Transfrontier Park have to allow for an adequate ecological reserve (enough water) which is necessary to maintain and conserve biodiversity. My study would suggest that it is imperative to develop a strategic adaptive management approach for groundwater use in the Park. Such an approach would develop thresholds for potential concern (Biggs and Rogers 2003) that would allow for an adequate ecological reserve as my study suggests that trees in the Park, and in particular the Nossob, are nearing the threshold for physiological stress. Previous research has demonstrated that these trees have a keystone function and as such the system will collapse if they start disappearing (Milton and Dean 1995).

The Park could also adopt a more aggressive approach to developing new water use strategies to reduce the amount of water extracted from the aquifer. This could include catchment/harvesting of rainwater off the roofs of houses and paved surfaces (Mathias and Wheater 2010) and emphasis on social recognition of water scarcity i.e. visitors made aware of what their water-usage means and how to adjust it while in the Park. Long-term monitoring of all underground water use in the Park but especially in the Nossob would be of tremendous advantage to understanding and avoiding potential non-returnable negative effects of unsustainable use on the large keystone species *A. erioloba* and *A. haematoxylon*. Further investigation would be warranted to establish rates of root growth for *A. haematoxylon* and *A. erioloba* to map how they respond to changes in water level. With the realisation of climate change and its effects currently being felt, the dramatic altering of the ecosystem through the loss of these trees would be devastating.

CHAPTER 4:

Synthesis

Rationale for the study

Acacia erioloba and *Acacia haematoxylon* are two tree species occurring in the more arid regions of southern Africa. These two species are the dominant large trees in the Kgalagadi Transfrontier Park occurring primarily in the ephemeral Auob and Nossob river beds. This is also the only area where the tree growth form of *A. haematoxylon* is found. These large trees are considered keystone species due to their pivotal role in providing many resources to other plant and animal species (Milton and Dean 1995). Preliminary observations of altered canopy structure of the trees in the Auob suggested that giraffe browse may be affecting both vegetation structure and reproductive output. With no naturally occurring surface water and new tourist infrastructure proposed in the Nossob, there has also been some concern around the effect of increased groundwater abstraction on large trees.

Despite the demand to increase both tourism infrastructure and throughput in the Kgalagadi Transfrontier Park, there has been very little research conducted on the effect that an increase in tourism may have on the natural environment in the Park. In this study, I first ask if browsing by giraffe, an introduced megaherbivore, is altering the canopy structure of both tree species to such an extent that they are reducing the reproductive potential of the trees. In the second data chapter I investigate whether trees and humans are using the same water source and whether constant and/or increasing levels of water abstraction are affecting the water source of the trees beyond a level they can cope with.

Summary of key findings

In biodiversity conservation, the mandate and priority for the national park system in South Africa is a functioning ecosystem. Humans are part of that ecosystem, but have a propensity to affect the environment to such extents that they may fundamentally change the functioning of that system. These changes need to be monitored carefully to maintain ecosystem health, especially under changing climatic conditions.

Giraffe were introduced into the Kgalagadi Transfrontier Park in the 1990's primarily because these are charismatic animals that tourists are excited to see. I determine the impact of giraffe on canopy structure and reproductive potential of the two tree species using a series of transects through the Auob River to determine both giraffe and tree density while also photographing several trees to determine change in canopy structure. My results show a significant negative impact of giraffe browse on canopy structure, specifically for *A. haematoxylon*. I did not find any significant differences in recruitment between the different giraffe density zones but a noticeable decrease in numbers of flowers and pods suggests that giraffe will have a negative effect on the *A. haematoxylon* population but not the *A. erioloba* population in the future. Such an impact on *A. haematoxylon* establishment and recruitment may already be evident. Future research should both monitor and determine the veracity of this.

Using stable hydrogen and oxygen isotope ratios of xylem water relative to borehole water I determine the water source for the two tree species. I also determine the potential for physiological stress the trees are under both upstream and downstream of active boreholes used for two tourist camps, one camp in the Nossob River abstracting at a higher rate than the other in the Auob. My results show that both *A. erioloba* and *A. haematoxylon* are using deep groundwater. My results also show that in the dry season, *A. erioloba* downstream of the Nossob borehole are closer to physiological stress with high rates of canopy dieback. The trees continue to transpire in the dry season suggesting that they are physiologically able to adapt to fluctuations in the water table of between 4.5 – 5.2 m between the wet and dry season but my results would suggest that they are prone to drought-induced carbon starvation. Future research should monitor transpiration and canopy health for trees downstream of all abstraction points and relate this to amounts of water abstracted.

Management implications & Future research

Achieving tourist satisfaction has become a strong driving goal in the management of many Protected Areas in South Africa, often at the expense of biodiversity objectives (Maciejewski and Kerley 2014). Economic returns from tourism appear to be the primary objective of the management of the Kgalagadi Transfrontier Park. This objective is framed in terms of "safeguarding the ecological integrity and pristine wilderness quality of the Kgalagadi Transfrontier Park" (SANParks 2008). If the environment is of real concern then management should determine exactly where arid savanna trees are sourcing their water from and what the effect of increasing abstraction may be on that water source. Such management should also develop a more complete and ecosystem-friendly water management plan beyond merely extracting continuously from the aquifer in the river. Such a management plan should consider the role of a keystone species in the environment and how the collapse of such a species may trigger the collapse of the entire system.

Conclusion

This study forms the foundation for monitoring the future impacts of giraffe browse and water abstraction on large trees in the Kgalagadi Transfrontier Park. The density of trees of relative height classes needs to be determined for each river system, with the inclusion of dead trees. This survey should be repeated every five years to monitor the populations of both large *Acacia* species, but specifically *A. haematoxylon* due to the greater negative effects from browse and water abstraction on this species found in this study. With regards to giraffe population numbers, Kruger (1994) suggests that the Park has a carrying capacity of between 40 and 50 giraffe. Official game counts and estimates of giraffe presence obtained from this study suggest that these numbers have been reached and therefore a management plan should be implemented to ensure that this number is not exceeded.

While tourism is beneficial to the economy, my results show that it can impact negatively on vegetation structure through both top-down and bottom-up effects such as the introduction of charismatic large herbivores and an increase in water abstraction. The managers of the Kgalagadi Transfrontier Park have a mandate to conserve biodiversity. To fulfil this mandate thresholds for potential concern related to groundwater abstraction have to be determined (Biggs *et al.* 2003). These thresholds have to allow for an adequate ecological reserve as our study suggests that water abstraction is already affecting the vegetation structure in the Park. Management should also develop a threshold for potential concern for giraffe as these too are affecting vegetation structure, which in turn will affect biodiversity.

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