# Plant traits and drought tolerance in the Savanna: A Kruger National Park case study

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## Abstract

One of the central goals of plant ecology is to understand the factors that control the local distribution of plant species and thus the composition of communities. The aim of this study is to determine plant functional traits that can be associated with drought tolerance/avoidance and to test whether wood density is a good indicator of drought tolerance. The study was carried out in Kruger National Park in the month of June. A number of plant traits including wood density, leaf thickness, leaf life span/longevity and water potential were measured along a rainfall gradient (from south to north of the park). Wood density and water potential did not show any significant differences between the wet and dry sites. Leaf thickness and percent leaf cover showed significant correlations with the rainfall gradient ($p = 0.00$ and 0.02 respectively). Wood density may not be the single most important factor that confers fitness during drought. Tolerance in plants may come about as a result of the interplay between plant traits and site characteristics that may result in the differential response even in plants that may be deemed drought tolerant.

## Introduction

One of the central goals of plant ecology is to understand the factors that control the local distribution of plant species and thus the composition of communities (Barton 1993). Within the tropics, water availability is one of the most important environmental factors determining tree species richness, composition and distribution (McDowell *et al.* 2008; Poorter and Markesteijn 2008). In the tropics, drought related tree mortality can produce important compositional shifts by removing drought sensitive species (Suarez *et al* 2004). Drought can/may produce instantaneous large scale water shortage and can thus have adverse effects on growth. In semi arid woodlands drought has been identified as the cause of massive die-off (van Nieuwstadt and Sheil 2005; Vesk and Westoby 2003) that contributes to low tree cover along moisture gradients.

There are several alternative strategies that plants use to cope with drought (Valladares and Sánchez-Gómez 2006) broadly classified as drought tolerant or drought avoidance strategies. These manifest themselves as behavioural and morphological traits (Dixon 1986) which come about as a result of the ecophysiological traits (Valladares and Sánchez-Gómez 2006) of the plant primarily in response to water limitation. Diaz *et* al. (2004) suggests that there is growing evidence that plant traits can be used to 'measure'/predict plant responses to change. They reason that there is a need to devise general predictors of plant responses to impacts such as drought as there is often no detailed knowledge of how the species in a particular ecosystem would respond. Various traits such as stem characteristic (e.g. woody density, vessel diameter, stem diameter), (van Gelder *et al.* 2006; Preston *et al.* 2006), leaf characteristics (e.g. leaf longevity, leaf size, sclerophylly, type: simple or compound and thickness), (Poorter and Markesteijn 2008; Sack *et al.* 2003; Lo Gullo and Salleo 1988) and plant height are among the traits that can be used to predict plant response to drought.

Among the plant traits, wood density is considered to be centrally important to the ecology of woody plants because it reflects carbon allocation to structural support, is correlated with growth rate and longevity, (van Gelder *et al.* 2006; Preston *et al.* 2006), and has been suggested to be a good predictor of plant response to drought. The reason for this as explained by van Gelder *et al.* (2006) is that low density wood is cheap to construct allowing for rapid growth in stem dimensions whereas high density wood results in persistent structures that allow high survival rate and a long life span. Wood density is correlated with the mechanical safety of stems (e.g. drought-induced xylem cavitation) and branches and influences the growth and survival of trees, inlcuding resistance to pathogens. One of the ways in which plant traits differ in response to drought conditions is the stomatal sensitivity to drought. This is widely different from one plant species to the next and it is partly due to the existence of drought adaptations based on drought avoidance (generally found in species with high stomatal sensitivity to drought with shallow root systems) or drought tolerance (in species with lower stomatal sensitivity but displaying structural and functional adaptive traits such as osmoregulation, deep root systems) (Picon *et al.* 1996; Schwinning and Ehleringer 2001). It was suggested in a study by Tobiessen and Kana (1974) that leaf water deficit at which stomata close was correlated with relative drought resistance of populations of *Calluna*. It was found that plants from drier sites closed their stomata at lower leaf relative turgidities than those from wetter sites.

Southern Africa faces significant environmental and economic challenges as a consequence of predicted global climate change (Meadows 2006). Under current climates, periodic severe droughts occur at decadal intervals in South African savannas. These create stressful conditions that create significant deviations from the optimal life conditions inducing changes and responses that may be permanent (Dorantesa and Sánchez 2006). Drought frequency and severity may increase under global climate change (Meadows 2006). It is therefore important to know how woody vegetation will respond to droughts, not least because they produce long lasting effects on ecosystems and landscapes (Suarez *et al* 2004). Droughts are increasingly recognized as a significant component of the savanna dynamics but detailed large-scale assessments of such events are scarce (van Nieuwstadt and Sheil 2005). It is for this reason that I conducted this study following up on the work of Viljoen (1995) in Kruger National Park (KNP) who documented tree mortalities as a result of the early 1990s drought. Some of the sites surveyed at the time were surveyed again to determine if there had been any changes in the woody vegetation surveyed then. In his study, Viljoen found that woody vegetation north of the Oliphants River in the more arid regions of Kruger National Park appeared to be more adapted to drought than those in the more mesic south. The aim of my study was to identify functional traits associated with drought tolerance/avoidance strategies and sensitivity in woody vegetation in the areas surveyed (north, central and south Kruger National Park) by Viljoen (1995). I wished to test whether there were any trait differences between plants found near rivers and away from rivers and whether wood density is a good indicator of drought tolerance. Following Viljoen's (1995) observations, I hypothesised that woody vegetation from north of the Oliphants River in KNP is more drought tolerant than that in south of the Oliphants River as plants are exposed to more droughty conditions than those in the south.

## Methods

### The study area

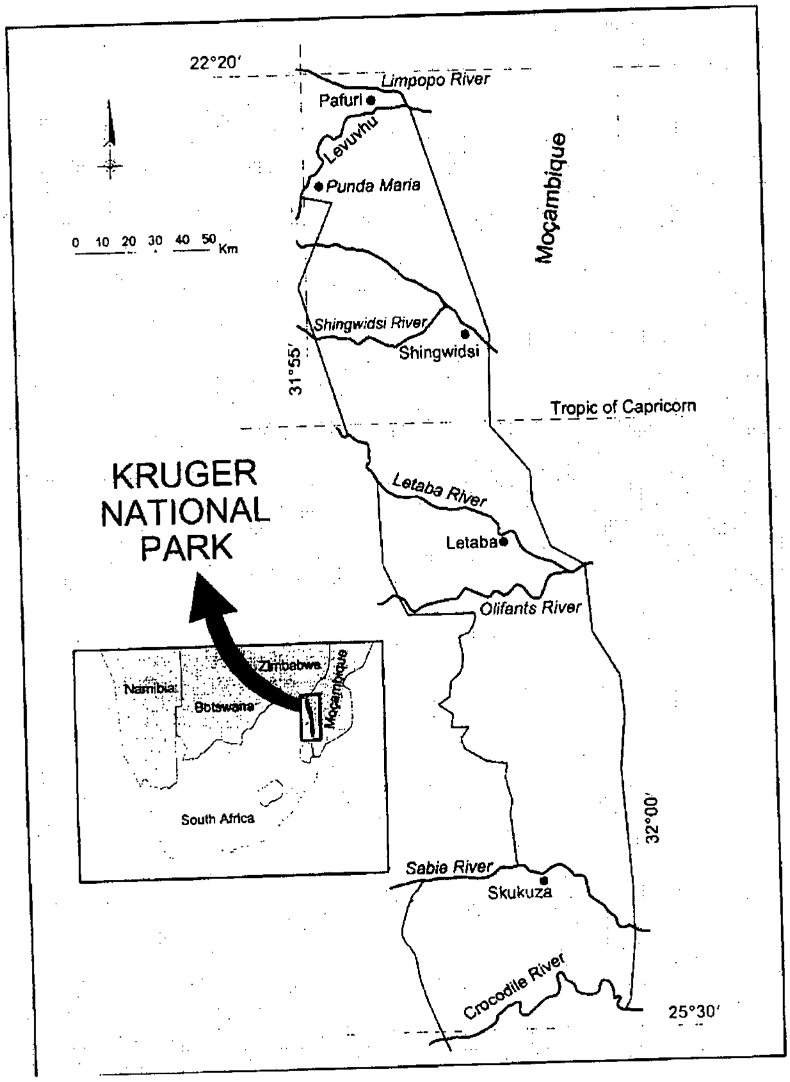


**Figure 1.** A map of South Africa showing the location of Kruger National Park (van Wilgen *et al.*, 2000).

The Kruger National Park was established in 1926 and it is situated in the eastern part of the Limpopo and Mpumalanga Provinces bordered on the east by Mozambique and Zimbabwe on the north (**Figure1**). The park covers 1 948 528 ha with an elevation range of 260-839 m above sea level (van Wilgen *et al.*, 2000). The park recieves about 537 mm mean annual rainfall ranging from 737 mm in the south to about 515 mm in the north (Zambatis 2005) as is depicted in **Figure 2**. The Kruger National Park has several rivers running through it from west to easterly direction with the Crocodile and Sabie Rivers in the south; Olifants in the central and the Letaba, ? Shingwezi, Levuvhu and Limpopo rivers in the north. The study sites were taken from the southern, central and northern part of the park. The study sites are shown below in **Table 1**

see map

**Table 1**. The study sites and their GPS location points

| Site | GPS points | |
|---|---|---|
| | S | E |
| Pretoriuskop | 025.11790 | 031.39978 |
| | 025.02665 | 031.32640 |
| Lower Sabie | 025.11429 | 031.91031 |
| Skukuza | 024.98733 | 031.62009 |
| | 024.98568 | 031.60153 |
| Tshokwane | 024.70435 | 31.79635 |
| Satara | 024.40785 | 031.77097 |

Show these on map

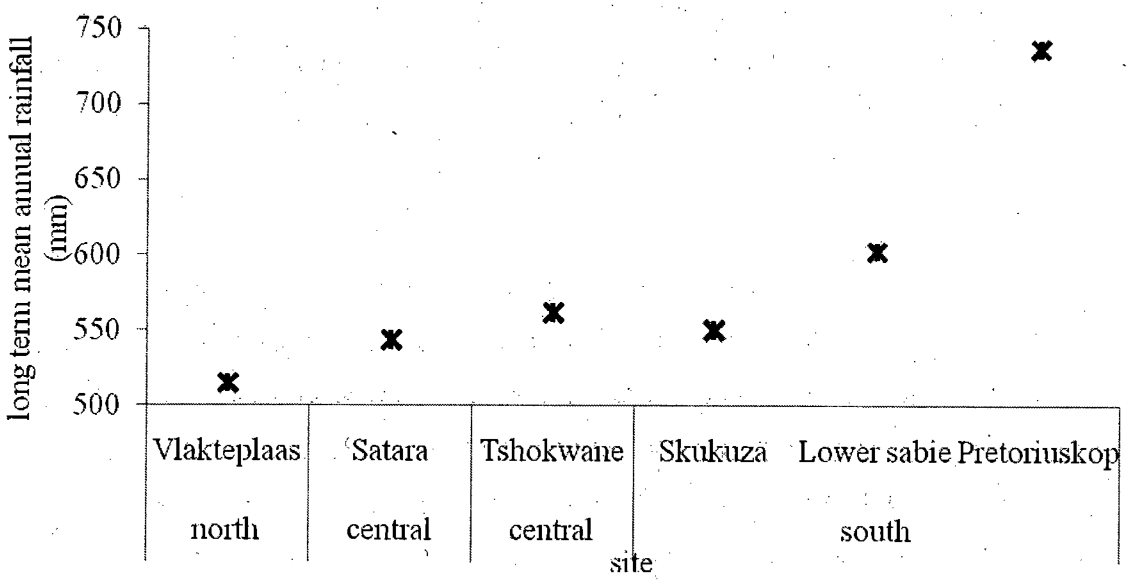


**Figure 2**. The rainfall gradient along the study sites in the Kruger National Park. Rainfall values from Zambatis (2005)

**Table 2.** . List of species that were used in the study and where they were found. Codes NR and R refer to non riparian and riparian species respectively. Drought index ranges from 1, most affected to 3, least affected by mortality in the early 1990s drought (ex Viljoen 1995).

| Family | Species name | Species code | Site | Drought index |
|---|---|---|---|---|
| Mimosoideae<br>Subfamily | | | | |
| | *Acacia nigrescens* | AN | Skukuza, Satara and Pretoriuskop (NR) | 2 |
| | *Dichrostachys cinerea* Africana | DCA | Lower Sabie (R)and Skukuza (NR) | 1 |
| | *Acacia tortilis* | AT | Skukuza (NR) | 1 |
| | *Albizzia versicolor* | AV | Tshokwane (R) | 2 |
| Loganiaceae | | | | |
| | *Strychnos madagascariensis* | SM | Pretoriuskop (NR) | 1 |
| Combretaceae | | | | |
| | *Combretum apiculatum* | CA | Skukuza (NR) and Pretoriuskop (NR) | 3 |
| | *Combretum hereroense* | CH | Lower Sabie (R) | 3 |
| | *Combretum imberbe* | CI | Lower Sabie (R) and Satara (NR) | 3 |
| ? | *Terminalia sericea* | TS | Pretoriuskop (NR) | 1 |
| Celastraceaea | *Gymnosporia heterophylla* | GH | Lower Sabie (R) | 2 |
| | *Gymnosporia senegalensis* | GS | Tshokwane (R) and Lower Sabie (R) | 2 |
| Ebenaceae | *Euclea divinorum* | ED | Skukuza (R) and Lower Sabie(R) | 1 |
| Zygophyllaceae | *Balanites maughamii* | B | Skukuza (R) | 1 |
| Caesalpinioideae | *Colophospermum mopane* | CM | Vlakteplaas (NR) | 3 |
| Anacardiaceae | *Sclerocarya birrea* | SB | Skukuza (NR)and Pretoriuskop (NR) | 1 |
| Papilionoideae | *Philenoptera violaceae*<br>*(Lonchocarpus capassa* Rolfe) | PV | Lower Sabie (R) and Tshokwane (R) | 1 |
| | Bolusanthus speciosa | BS | Pretoriuskop (NR) | 1 |

↑ Scientific names must be accompanied by authority. For DCA, what source for africana?

**Table 3**.The study species and the places they were found at. Scores of 0-5 are given where 0 is absent, 1 is rare and 5 is the most common.

| species | Site<br>Pretoriuskop | Lower Sabie | Skukuza | Tshokwane | Satara |
|---|---|---|---|---|---|
| ED | 0 | 0 | 2 | 3 | 0 |
| B | 0 | 0 | 3 | 0 | 0 |
| CM | 0 | 0 | 0 | 0 | 0 |
| SB | 5 | 0 | 0 | 0 | 0 |
| **PV** | **0** | **4** | **0** | **4** | **0** |
| **BS** | **4** | **0** | **0** | **0** | **0** |
| **AV** | **0** | **0** | **0** | **4** | **2** |
| **GS** | **0** | **0** | **0** | **3** | **0** |
| **GH** | **0** | **3** | **0** | **0** | **0** |
| **TS** | **5** | **0** | **0** | **0** | **0** |
| **CI** | **0** | **4** | **0** | **0** | **0** |
| **CH** | **0** | **3** | **0** | **0** | **1** |
| **CA** | **4** | **0** | **0** | **0** | **0** |
| **SM** | **4** | **0** | **0** | **0** | **0** |
| **AT** | **0** | **1** | **5** | **5** | **5** |
| **DCA** | **0** | **5** | **5** | **5** | **5** |
| **AN** | **5** | **1** | **5** | **0** | **3** |

Why use code?

## Results

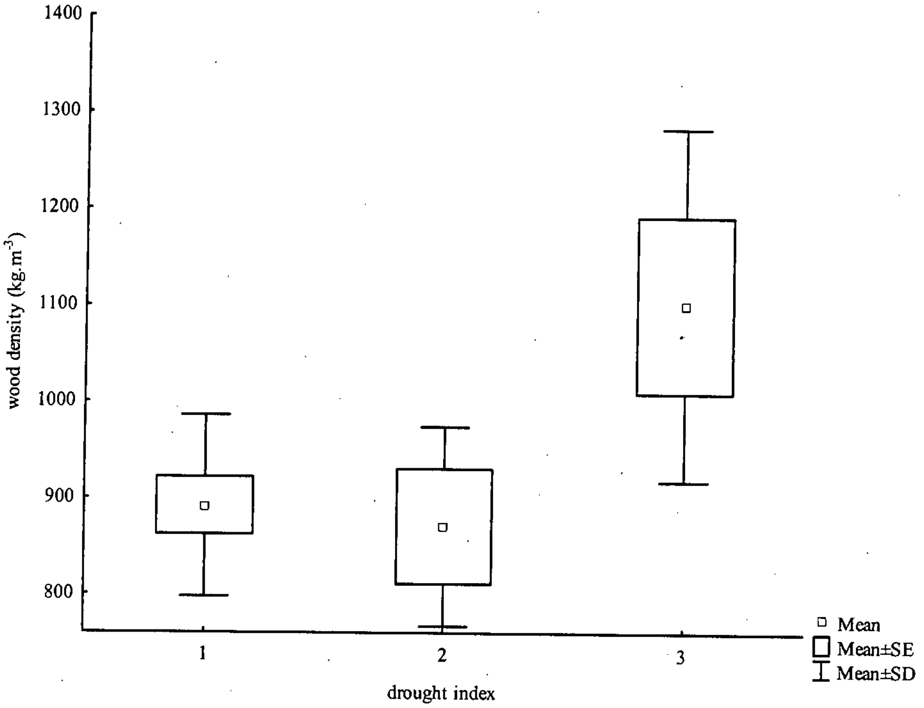
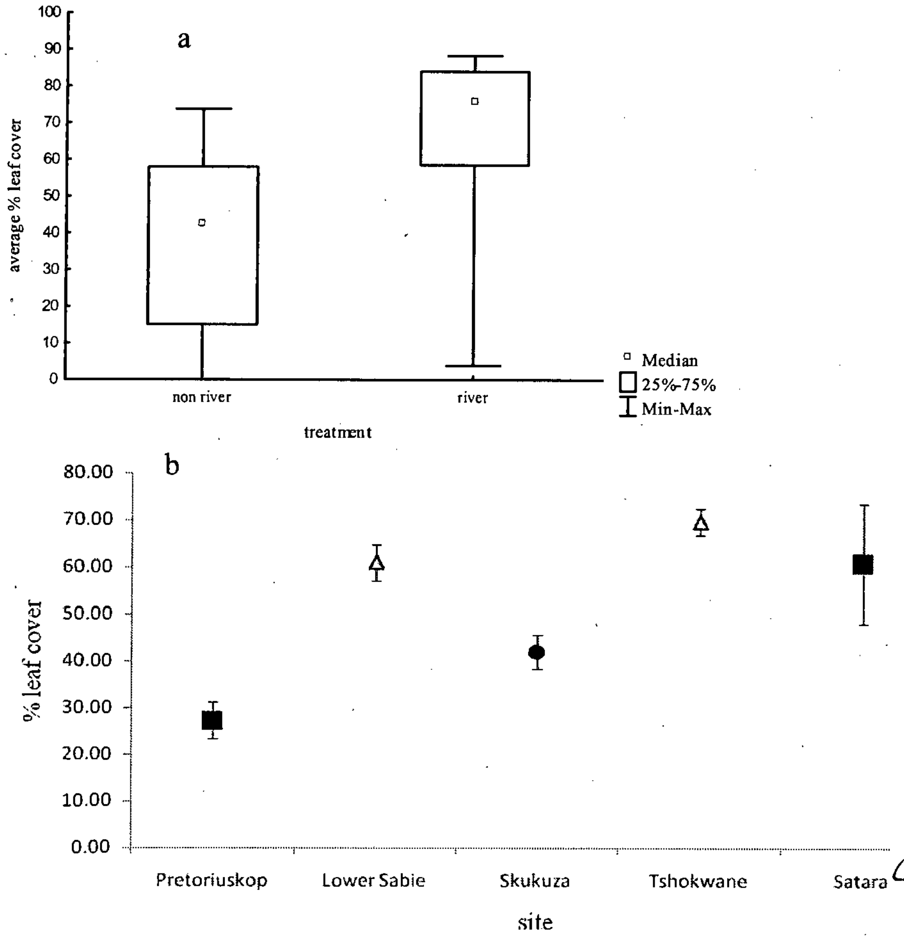


**Figure 3**. Wood density relationship with drought index. Drought index 1 is drought sensitive while drought index 3 is the most drought tolerant.

Wood density showed no significant difference between the treatments (non river/river sites) and among the individual sites involved in the survey (p>0.05). When the wood densities calculated in this study were compared with wood densities from other sources such as van Wyk (1972 and 1974). The Trees of Kruger National Park) (in this study referred to as van Wyk wood density), no relationship was apparent for most of the tree species with big deviations between the two. However, the combined wood density of this study and that of van Wyk showed a positive trend with high wood density for the most drought-tolerant species (**Figure 3**).

Of the traits examined in the survey of vegetation in KNP, the percentage leaf cover of plants in the riparian zone and those away from rivers was significantly different (p=0.02). Most of the tree species on the riparian zones (50%) had an average percent leaf cover between 60% and 80% with a maximum and minimum cover of 90% and 5% respectively (**Figure 4a**). For the sites that were away from rivers (non river), 50% of the tree species had an average percent leaf cover between 60% and 15% with a maximum and minimum cover of 75% and 0% respectively (**Figure 4a**).



why not rainfall on x axis?

**Figure 4**. (a) Percent leaf cover at river and non river sites,(P=0.02, n= 197), (b) average percent leaf cover by site. The difference lies between Pretoriuskop and all the sites (p<0.05) and Skukuza, Lower Sabie and Tshokwane (p<0.05). The vertical bars are the standard error bars. The solid squares represent non riparian sites, triangles the riparian site and the solid circle the both riparian and non riparian sites

Analyzing the river site and non river sites by the specific sites of survey showed a lot of variation along the rain fall gradient from Pretoriuskop to Satara (increasing from south to north) (**Figure 4b**). Skukuza had sites that were near and away from a river whereas Lower Sabie and

Tshokwane had riparian sites only. There was a lower mean percent leaf cover at Skukuza than at Lower Sabie and Tshokwane as shown in **Figure 4b**. The Skukuza sites had a combination of both highly deciduous and ever green trees. Satara and Pretoriuskop were the only regions with the survey sites away from rivers. However, more of the highly deciduous plants were found in Tshokwane than in Satara. The degree of plant cover in the regions varied with the deciduousness of the plants found in that region. The most highly deciduous plants were *Sclerocarya birrea* and *Dichrostachys cinerea* as shown in **Figure 5**. *Euclea* divinorum, *Philenoptera violaceae*, *Combretum imberbe* and *Gymnosporia heterophylla* and *senegalensis* were the most evergreen plant species found during the survey (**Figure 5**). *Sclerocarya birrea*, *Strychnos madagascariensis Terminalia sericea* were mostly found in the Pretoriuskop region in high abundances compared to other regions in this study. *Dichrostachys cinerea* was the most widely distributed of all the plant species in the survey.

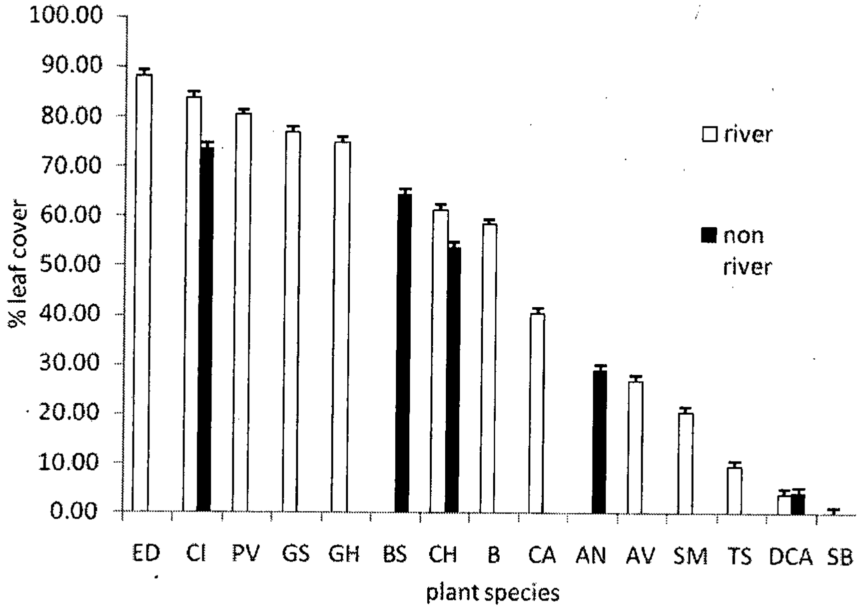


**Figure 5.** Percent leaf cover of the species from the survey. The black columns indicated species that were sampled on the riparian zone of the river and the open columns indicate the species that were sampled away from rivers (not near a river). The vertical bars denote the standard error bars.

Leaf cover data biased by time of study
when deciduous plants at no-leaf stage

Thicker leaves have got lower specific leaf area and the two have a positive correlation. In this study leaf thickness was used in this study as an indicator of specific leaf area (SLA). Sites with plants that had thicker leaves were those on the riparian zones (Lower Sabie and Tshokwane) as shown in **Figure 6**. Skukuza had the most plants with thinner leaves and very few with thicker leaves as is indicated by the longer confidence interval bars. The plant leaf thickness at the sites were significantly different from each other (p=0.00). With Pretoriuskop and Satara receiving the highest and lowest rainfall respectively as shown in **Figure 2** neither leaf thickness nor any of the other traits showed significant correlation with rainfall (p>0.05).

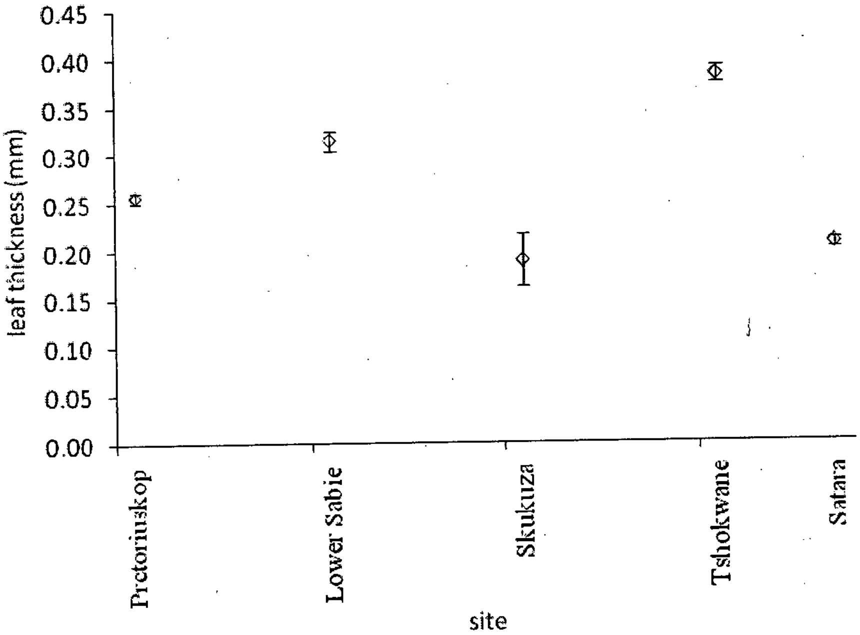


**Figure 6**. Leaf thickness variation among the sites, F (2,693) =9.01, p= 0.00014. The vertical bars denote 0.95 confidence intervals.

As an indicator of plant stress, mid-day water potential (Ψ) was measured at the sites for some plant species. There was no significant difference between the river and non river sites and among the sites and along the rainfall gradient. Of the plant species that were measured *Combretum apiculatum* was the most water stressed plant species while *Sclerocarya birrea* was the least water stressed of all the plant species (**Figure 7**). There was a variation of water potential for plant species in the family Combretaceae with *Combretum imberbe* being the least water stressed in the family.

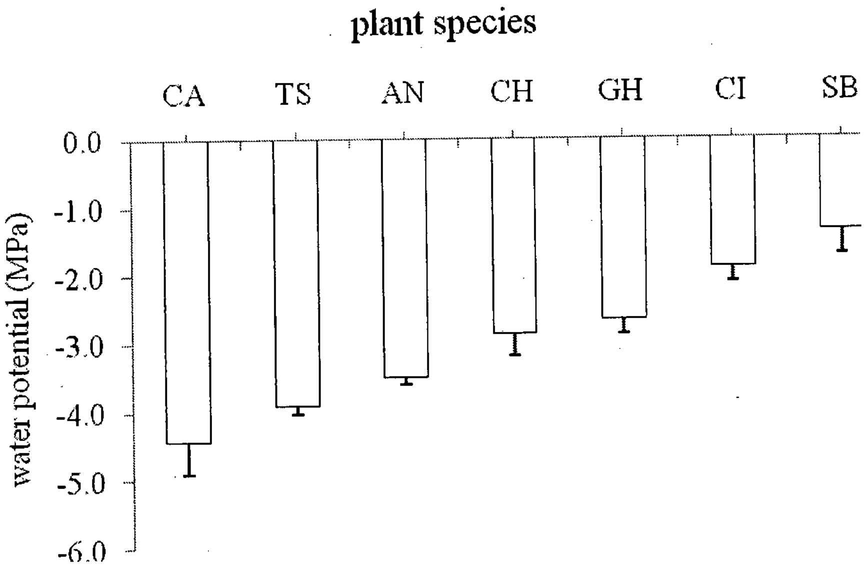


**Figure 7**. Water potential of the species tested. The vertical bars are the standard error bars.

## Discussion

Here I found that wood density had no correlation with water availability i.e. with rain fall and proximity to water sources such as rivers. However, there was a correlation between wood density and an index of drought tolerance derived from observations of tree responses to the early 1990s drought (Viljoen 1995). The most drought-tolerant trees were from the region of low rainfall. Trees near rivers that presumably had access to water most of the time had significantly more leaves than trees away from rivers (p=0.02), however, no pattern of leaf cover (deciduousness) with rainfall was established. Plant leaf thickness was significantly different among the study sites (p=0.00014) and trees near rivers had thicker leaves than those far form rivers, but this difference was not statistically significant.

This study suggests that no single trait will predict drought response in this savanna. It seems that an interaction of more plant traits will lead to drought tolerance in some species. Some plant traits that have been suggested to possibly play a role in plant drought tolerance include root length. Some plants have been found to posses the ability to adjust their root to shoot ratio based on the availability of water (Bonalt *et al.,* 2001; Niinemets 2001). However, this alone is not enough as the roots themselves also have to be able to withstand very low soil water potentials by producing cavitation resistant roots (Ewers *et al.,*2000). At the core of this paper has been the influence of wood density on drought tolerance. High wood density is associated with safer xylem vessels as there is reinforcement to withstand very low water potential compared to low density wood.

It has been suggested that stomatal closure or leaf loss can prevent embolism-inducing xylem tension during drought. However, plants may die either because of decreased photosynthesis (starvation) or failure to recover following hydraulic failure (McDowell *et al.* 2008; Valladares and Sánchez-Gómez 2006). Also linking carbon gain and starvation to drought tolerance is water use efficiency, a trait that has been found to increase with increasing drought stress (Juenger *et al.,* 2005). However, even though water use efficiency confers fitness during drought, the collective interaction of plant traits with the environment may determine fitness. For example even in favourable conditions, fitness may come at a cost to the plant such as reduced growth rate and delayed phenology.

During drought plant mortality does not always come as a result of traits that render the plant unfit in drought conditions. There are other factors that that may indirectly or directly influence plant mortality (Suarez *et al* 2004). Fires are usually very prevalent during drought especially in xeric environments and these may predispose trees that survive the fire to pathogens and herbivorous insects thus increasing the plant's susceptibility subsequent drought stress. In a study by Suarez *et al.,* (2004) it was found that infections by bark beetles (*Dendroctonus* spp. e *Ips* spp) was an important predisposing factor for the death of *Pinus ponderosa* during the mid-1950s New Mexico drought. Other factor that may contribute to die backs during drought may include herbivore load in the environment (e.g. elephants), the influence of previous droughts on the environment, age of trees, edaphic characteristics and slope and the timing of heat shock.

## Conclusion

Given that southern Africa contains two the world's top 25 hotspots (Meadows 2006) and in light of the current climate change predictions that most of the South African biomes will shrink by 2050 based on the HadCM2 model (Meadows 2006), it is important to focus future research on plant trait interactions and how they confer drought fitness/tolerance. In this study I have shown that wood density is not the single most important factor predicting drought mortality as it could not be related to moisture availability. However drought tolerance in plants may come about as a result of the interplay between plant traits and site characteristics which may lead to patchy mortality of a single species in different environments. Since drought events are all not similar to each other in terms of intensity and duration, the timing of individual events during drought may result in the varied response, even in plants that may be deemed drought tolerant.

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to branch). The lengths of ten mature leaves were measured on each branch sampled. The length of the longest branch was measured, and also the total length of branches in the sample.

Fifty spines of *A. grandicornuta* and seventy hooks of *A. burkei* were weighed in order to ascertain whether there is any correlation between length and base of spines and their mass, and the length, base and gape of hooks and their mass. Such a relationship would allow for the extrapolation of the mass of all thorns for which those dimensions had been measured.

*Feeding simulations*

Three feeding simulations were performed. The sock test (Figure 2) involved throwing a tennis ball in a sock into each of the study individuals. This was then pulled out of the tree using a spring scale (10kg Persola scale in the Kruger National Park, and a 50kg digital Bonso handy scale in the Hluhluwe-Umfolozi Game Reserve), and the force required recorded. This test is aimed at quantifying defence against an animal pulling its head and ears or even whole body out from the low branches it was feeding on. On a smaller scale it also simulates leaf stripping. This test was performed ten times on each individual.

The muzzle test (Figure 3) involved pushing a wooden block (6cm x 6cm x 8.5cm) covered in plasticine in and out through the outer branches of each individual five times. The total number of scratches in the plasticine was recorded, as well as the number of scratches deemed to potentially be inflicting serious damage to the simulated herbivore (Figure 3). This test is designed to try and imitate a browser moving its muzzle in and out of the tree as it feeds. Not all contact with thorns is going to effectively deter a browser, but it is argued that more severe stabbing and gouging will impede its feeding. Scoring this test as a ratio of serious scratches: total number of scratches, is based on the idea that it is not only about thorn density, but that their design and presentation are also very important in determining their effectiveness as physical defences. This test was performed three times on each individual.