The copyright of this thesis vests in the author. No quotation from it or information derived from it is to be published without full acknowledgement of the source. The thesis is to be used for private study or non-commercial research purposes only.

Published by the University of Cape Town (UCT) in terms of the non-exclusive license granted to UCT by the author.

University of Cape Town

Limitations of savanna trees in the Highveld grasslands of South Africa

Julia Leslee Wakeling

Thesis presented for the degree of Master of Science

Department of Botany, University of Cape Town, South Africa

Supervisors:

Professor William Bond

Associate Professor Michael Cramer

February 2009

University of Cape Town

"It's funny about these Bluegums growing like this by the side of the road when the rest of the veld is bare." (Oom Schalk Lourens to Adriaan Neil)

Dream by the Bluegums, Herman Charles Bosman

This thesis is dedicated to
my mother and grandmother for being eternally inspiring;
and to Sipho Zulu for having the ability but not the opportunity, and for making it happen.

University of Cape Town

Declaration

I, Julia Leslee Wakeling, hereby,

1. grant the University of Cape Town free licence to reproduce the above thesis in whole or in part, for the purpose of research;
2. declare that:
   i. the above thesis is my own unaided work, both in concept and execution,
   ii. neither the substance nor any part of the above thesis has been submitted in the past, or is being, or is to be submitted for a degree at this University or at any other university.

I am now presenting the thesis for examination for the degree of Master of Botany, Plant Ecology.

Julia Leslee Wakeling

University of Cape Town

Abstract

Many grassland areas throughout the world may support a woody biomass if fire is suppressed. It is puzzling that fire-tolerant savanna trees do not grow in these grasslands. The Highveld grasslands of South Africa are one such grassland. Hypotheses including fire, human intervention, grass competition and various attributes of soil have been proposed to explain the tree-less nature of the Highveld grasslands, but they have mostly been discounted. In this study it was hypothesised that cool temperatures or low nutrient availability would result in slow growth of saplings in grassland areas that would subsequently not be able to escape frequent fires. Alternatively, frost may exclude trees from grasslands. A seedling transplant experiment of savanna tree species of the *Acacia* genus, into grassland and savanna areas arranged across an altitudinal gradient, was used to compare growth in these varying climates over one growing season, and the influence of frost on seedlings in the following winter. Soils were collected from grassland and savanna regions to establish if nutrients varied between these areas, and seedling growth was measured in a pot experiment including these different soils. To minimise the effect of other variables, seedlings were watered and grass was excluded.

Higher altitude grassland areas were cooler, and the grassland soils that were collected were nutrient-poor, relative to the savanna equivalents, with the exception of one nutrient-poor low altitude soil. Growth was well correlated to both temperature and nutrient availability, and in general there was slower growth in grassland climates and grassland soils compared to in savannas. These seedling growth rates were extrapolated to the growth rates of saplings in natural environments and the time it would take saplings to reach a height above flame height was calculated. This showed that although there were significant differences between growth rates in grassland and savanna soils, the magnitude of these differences was not large enough to prevent saplings from growing into adults in grassland soils. Differences in growth due to temperature variations, however, were large enough to suggest that saplings in grassland climates would grow too slowly to ever reach escape height between frequent fires. Frost caused damage to seedlings and decreased seedling survival at

University of Cape Town

the highest elevation sites, but trees were absent well below the altitudinal limit of frost damage.

There has been much discussion about the tree-less nature of the Highveld grasslands, but very little experimental work to back it. Neither temperature nor fire alone can explain the lack of trees. This study provides empirical evidence that slow growth due to low temperatures in combination with frequent fire could exclude savanna trees from the grasslands. The effect of grass competition still needs investigation. The incorporation of fire is useful as it is a fundamental part of C_4 ecosystems; this, on top of a base of variable growth due to changes in resource availability. The barely recognised savanna tree-line deserves attention, as savannas continue to invade grasslands in a warming world.

University of Cape Town

Acknowledgements

I would firstly like to thank my supervisors, William Bond and Mike Cramer, for trusting me to carry out these experiments of mammoth proportions. William, for his exciting ideas and for being at the end of the phone with a practical solution; and Mike for being precise and thorough with everything from experimentation, to analysis and writing. I would like to thank both Mike and William for always being interested and excitable, and for their patience in teaching me how to think and write.

This project was hosted by Kwa-Zulu Natal Ezemvelo Wildlife in Hluhluwe-iMfolozi and to all the staff at the research station, I am extremely grateful, particularly Sue van Rensburg who kept us all on the straight and narrow.

This project would not have happened without the dedication of the Zululand Tree Project staff. A special thanks to An van Cauter for being a fantastic home base, and to Eric Khumalo, Vincent Mkhwanazi, Sakhile Nsukwini and Zanele Chonco. Sipho Zulu, Dumisani Mnomezulu and Phumlani Zwane in particular gave up many weekends and hours of hard work. To the ladies who helped sort leaves from stems: Nontabeko Maude, Gugu Mdluli, Nokukhanya Mdluli, Thobina Mavmbela, Khethukuthula Ntshongase, Agrineth Ngema and Sphesile Thabethe: you have more patience than me.

Many thanks to the staff of the UCT Botany Department, including Des Barnes, Ncumisa Thungela, Natalie Allies, Zama Jikulambo and particularly Sandy Smuts.

I am indebted to the people who lent me their land, cared for my plants, and hosted Sipho, Dumi, Phumlani and I time and time again: Robin & Sue Kirkwood; Johan Kriek; Emile Schmidt; Ian & Carol Goss; Henry & Ria Malan; Katy & Stephan Heitland; Clayton & Debbie Comins; Hendrick van Rensburg; Graham & Janine Ford, Richard & Rob; Nigel, Sue, Jen & Tracy Anderson; Mark & Ruth Armitage; Andrew & Amanda Shand; and Mark, Yvette, Michael & Andrew Hitchins. Thank you to the Department of Agriculture and Mr Kosy Dongo for hosting my project at

University of Cape Town

the Nooitgedacht and Athole Research stations, and to Jan Theron, Lesego Bodibe and Samuel Zulu. Duncan Ballantyne put me in contact with Mark Hitchins and Kevin Kirkman with the staff at the Nooitgedacht research station.

Thanks to Tim O'Connor, Kevin Kirkman, Ed Granger, Roger Uys, Colin Everson and Jeff Hughes for discussions right at the beginning and to Hans Lambers for suggesting a nutrient limitation hypothesis. Sally Archibald provided me with fire data. Danni Guo generated climate envelope maps and provided an initially terrifying thesis template. Thanks also to Nick and Thomas in the GIS lab.

And of course to my fellow students and support groups in Hluhluwe and Cape Town: Carla, Cleo, Jasper, Jan, Matt, Matt, Tarik, Geoff, Claire, Rob, Alex, Clelia, Christopher, Mel, Gareth, Ben, Heidi, Pete, Nick & Bruce, Tim, Mum, Dad and Fynn. Particular mention is required of the infamous writing group: Diane and Fiona, without whom there would be no words.

This project was made possible by funding from the Andrew W Mellon foundation and the National Research Foundation.

Thank you all for teaching me so much.

University of Cape Town

Table of Contents

University of Cape Town

Table of Contents

University of Cape Town

Chapter 1: Introduction

Many grassland areas of the world are fire-dependent, and in the absence of fire would be replaced by forest (Bond *et al.* 2005). Examples of these fire-dependent grasslands include the prairies (Knapp *et al.* 1999) and Appalachian balds of North America (Mark 1958, Lindsay & Bratton 1979b), the campos grasslands of South America (Behling *et al.* 2007, Overbeck *et al.* 2007), the balds of south east Australia (Webb 1964, Fensham & Fairfax 1996, 2006), and grasslands throughout Africa (Acocks 1953, White 1983) and Madagascar (Bond *et al.* 2008). All these grasslands burn regularly. Fire excludes forest species from establishing in grasslands and savannas (Bowman 2000). Given that savanna tree species are fire adapted, it is interesting that they do not grow in these grasslands.

University of Cape Town

Explanations of the tree-less nature of the tall-grass prairies include fire (Bragg & Hulbert 1976), fire and grazing (Knapp *et al.* 1999), climate, including drought (Weaver 1954), and grass competition (Walter 1979). The Appalachian balds are at an ecotone between deciduous and coniferous forest (Mark 1958). They originated when forest was removed by climate change and now cannot re-establish due to fire and grazing (Mark 1958). Other explanations include fire, clearing by humans, and herbivory (Lindsay & Bratton 1979b). It was originally thought that the balds of south eastern Australia were due to human caused fires (Herbert 1938), but Webb (1964) has since concluded that the balds were physiographically determined, with savanna *Eucalytpus* species seen to be at their climate limit, and are currently maintained by fire. Fensham & Fairfax (2006) showed more recently that eucalypt trees could encroach into these Australian grassy balds, but suggested that they do not as they are limited by seed dispersal. Savanna tree species have been seen to encroach into some of these grasslands in the warmer parts of their distributions (Webb 1964, O'Connor 1995, van Auken 2000, Jurena & Archer 2003).

A "savanna tree-line"

In South Africa, lower altitude savannas and higher altitude grasslands are adjacent in many areas (Acocks 1953, Mucina & Rutherford 2006) (Figure 1.1). The boundary between the tree-less grasslands and the wooded savannas is often narrow and abrupt, analogous to an alpine tree-line (pers. obs.; Figure 1.2), and could be termed a "savanna tree-line". The savanna tree-line marks the loss of savanna trees from a C_4 dominated grassy layer. In contrast to forest-grass boundaries with no fire versus frequent fire (Bowman 2000), the fire regime is continuous across the savanna grassland tree-line.

C_4 grasses occur in areas with a mean growing season temperature of 22°C or more, usually within 30°N and 30°S (Collatz *et al.* 1998, Ehleringer 2005). In areas cooler than this, examples of tree-grass boundaries usually involve C_3 grasses (for example Coop *et al.* (2007)). Alpine tree-lines occur at high altitudes and latitudes where the mean growing season air temperature is *ca.* 7 – 10°C (Grace 1987, Körner & Paulsen 2004) and trees cannot survive above the tree-line. The major difference between alpine and savanna tree-lines is that trees can survive and thrive above the savanna tree-line. Evidence for this is the presence of patches of indigenous forest (O'Connor & Bredenkamp 1997), exotic plantations (Fairbanks *et al.* 2000, O'Connor 2005), and indigenous trees such as *Leucosidea sericea*, and *Protea* and *Cussonia* species which occur in specific areas, such as on rocky outcrops, gullies, and steep slopes where moisture availability is higher (Acocks 1953, Mucina & Rutherford 2006). Woody invaders such as wattles, Australian *Acacia* species, are also common in grassland areas (Rutherford & Westfall 1986), in contrast to alpine tree-lines above which woody species cannot grow. Savanna tree-lines also occur at varying altitudes. In general, the transition from savanna to grassland biomes is at *ca.* 900m (Schulze 1997, Mucina & Rutherford 2006), but satellite grasslands also occur on hilltops within savanna areas, in areas as low as 300m or 400m above sea level (Mucina & Rutherford 2006).

University of Cape Town

The grassland biome in South Africa

In South Africa, the grassland biome is mostly on the high central plateau, the Highveld (Rutherford & Westfall 1986). The underlying geology includes the Karoo Supergroup, sedimentary sandstone, mudstone and slates interspersed with dolerite intrusions (Rutherford & Westfall 1986, Mucina & Rutherford 2006). The topology is mainly flat to rolling hills, but also includes mountainous areas and the Great

Escarpment in the east of South Africa (Mucina & Rutherford 2006). Grasslands also occur on more recently dissected land in cool areas south of Lesotho (Figure 1.1). Above *ca.* 2000m the grasses are predominantly C_3 and in lower areas, the grasses are C_4 (Mucina & Rutherford 2006). The higher altitude C_3 grasslands are not the focus of the present study. Grasslands and savannas are characterised by summer rainfall and winter drought, and annual rainfall varies between 400mm and 2500mm in grasslands and between 200mm and 1350mm in savannas (Rutherford & Westfall 1986, Mucina & Rutherford 2006). Grasslands are cooler than the adjacent savannas and frosts are common in the coolest period between May and August (Schulze 1997). Fog occurs on the upper slopes of the Great Escarpment (Mucina & Rutherford 2006). Summer thunderstorms are common and lightning flash densities are high in these areas (Edwards 1984, Manry & Knight 1986, Schulze 1997). The entire grassland biome in South Africa fits into the Cwb unit in Koppen's classification (Schulze & McGee 1978).

University of Cape Town

Dry and mesic grasslands have been divided along a rainfall boundary of *ca.* 500 – 700mm (Ellery *et al.* 1995). The mesic grasslands, termed "sourveld", made up of "sour" grasses (such as from the tribe Andropogoneae), are generally at higher altitudes (Tainton 1981, Ellery *et al.* 1995). The dry "sweetveld" grasslands are in warmer, lower elevation areas than the sourveld and comprise "sweet" grasses of the Chloridoideae that have a low fibre content and higher nutrient content above ground, making them highly palatable to herbivores (Tainton 1981, Ellery *et al.* 1995). Canopy cover and plant production is higher in sourveld versus sweetveld, resulting in more frequent fires in the sourveld (Ellery *et al.* 1995). Sourveld soils are typically low in nutrient availability as they are leached by the high rainfall, compared to the relatively high nutrient availability soils of the low rainfall sweetveld areas (Ellery *et al.* 1995).

Tree-grass coexistence in savannas

The grasslands and savannas of South Africa are dominated by C_4 grasses and have a distinct dry season that allows the grasses to dry out and fires to occur (d'Antonio & Vitousek 1992). Savannas also have a woody component (Acocks 1953, Scholes & Archer 1997). Much work has explored the coexistence of trees and grasses (Walter

1971, Scholes & Archer 1997, Higgins *et al.* 2000, Sankaran *et al.* 2004, Bond 2008). There are several models which attempt to explain this tree-grass coexistence. For example, the root-niche separation model suggests that tree and grass roots occupy separate rooting spaces and coexist due to use of different resource pools (Walter 1971). However, this hypothesis cannot explain how seedlings survive as their roots must initially occupy the same space as grass roots. The escape hypothesis argues that tree cover in savannas is limited primarily by demographic bottlenecks to recruitment, created by fire and its effects on sapling growth (Bond & van Wilgen 1996, Scholes & Archer 1997). Fire prevents the formation of high densities of juvenile trees and the growth of these juveniles into adults (Bond & van Wilgen 1996). Juveniles may be burnt to the ground many times, and resprout repeatedly from below-ground root stocks, before they become adults (Bond & van Wilgen 1996, Gignoux *et al.* 1997, Scholes & Archer 1997, Higgins *et al.* 2000, Wigley *et al.* 2008).

University of Cape Town

Explanations for the tree-less nature of South African grasslands

Several hypotheses have been proposed to explain the tree-less Highveld grasslands of South Africa (see O'Connor & Bredenkamp (1997)). Acocks (1953) suggested that the grasslands were anthropogenically derived within the last 1000 years and maintained by fire. However, Ellery & Mentis (1992) reviewed palynological and archaeological evidence and concluded that the grasslands were at least 1000 years old and probably much older. There are also a large number of grassland endemics, and palynological evidence that the grasslands have been present since the late Pleistocene (>10 000 BP) (Scott 1989, Meadows & Linder 1993), which discounts this hypothesis.

Feely (1987) proposed that within the Transkei, soils with a shallow, impervious layer or well developed illuvial B horizon limit woody elements. Tinley (1982) proposed a related hypothesis that soil moisture drives the distribution of grasslands, savannas and forests, and grasslands occur in areas where a shallow impermeable layer results in waterlogging during the wet season and excessive drying during the dry season. These hypotheses may be important at local scales, but grasslands are also present on well drained, loose, deep sandy soils (Werger & Coetzee 1978). Tree cover has also been shown to develop on poorly drained soils in the long absence of fire (Westfall *et al.* 1983, Ellery 1992, Titshall *et al.* 2000).

Acocks (1953) also proposed that frost limits trees in cold areas. Some indigenous species are tolerant of frost, such as varieties of *A. karroo*, *Rhus lancea* and *Leucosidea sericea* (Acocks 1953). A number of species grow in specific habitats, towns and plantations in frosty areas, so although frost may decrease the pool of species capable of colonising the grasslands, it does not explain the complete lack of trees across large tracts of grassland.

Fire, driven by wet growing seasons and dry winters, has been suggested as the cause of treeless grasslands (Bond 1997). High rainfall results in high fuel loads which dry out in winter, often assisted by frost, and this together with the high incidence of lightning (Manry & Knight 1986), promotes frequent fires. Fire is also a component of savannas (Trollope 1984) where woody biomass is high. Fire frequencies vary from annual to infrequent in both savannas (Trollope 1984, Balfour & Howison 2001) and grasslands (Tainton & Mentis 1984) and do not differ significantly between the biomes (Coetzee *et al.* 1994), so fire alone does not exclude trees.

University of Cape Town

A more recent hypothesis to explain the tree-less grasslands, proposed by Mills (2003) and Mills *et al.* (2006), involves grass competition. During the growing season, the top 10cm of soil in grasslands experiences rapid, frequent fluctuations between wet and dry states. Conversely, savannas tend to be drier and warmer and the top soil layer is drier for longer periods (Scholes & Walker 1993). Mineralisation is greater in soils that are frequently wetted and dried, rather than permanently wet or dry soils (Birch 1958), and thus there is greater mineralisation in grassland soils. Mills *et al.* (2006) suggest that this continuous mineralisation of organic matter, and release of nutrients, allows grasses to outcompete trees. This hypothesis is yet to be explored.

Structure of this thesis

The aim of this study was to explore the question: What limits the occurrence of fire-tolerant savanna trees in C_4 grasslands? The focus was on higher rainfall grasslands with a climate that could support forest. Three separate hypotheses were tested, outlined as follows:

Chapter 2: Low temperatures and a short growing season in the Highveld grassland areas limit sapling growth to the extent that they cannot grow fast enough to escape the frequent fires and become adults. To explore this, a seedling transplant experiment was set up to measure growth differences between seedlings resulting from differences in temperature in grassland and savanna climates. The extent to which growth differences allow trees to escape the flame zone between fires is explored in Chapter 5.

Chapter 3: Frost prevents trees from growing in the Highveld grasslands. To investigate this, the same experimental set-up and seedlings as for chapter 2 were used. The effect of one particular frost, and the winter as a whole, on the topkill and survival of seedlings was measured.

Chapter 4: The Highveld grassland soils are more leached than soils of the adjacent savannas. The low availability of nutrients in the grasslands causes slow growth of saplings, which would then take too long to escape the frequent fires and fail to become adults. Soils from grassland and savanna areas were collected and analysed to establish nutrient differences between grassland and savanna areas. The effect of savanna and grassland soils on plant growth was then tested using seedlings that were grown in a common garden experiment.

Chapter 5: This chapter compares differences in growth rates obtained, between grasslands and savannas, due to the differences in temperatures and soil nutrient availabilities reported in Chapters 2 and 4. Experimental growth rate differences were extrapolated to growth rates of saplings in natural environments, using reference data for sapling growth in savannas. The likelihood of saplings escaping the flame zone given slower growth in grassland environments is then assessed. This is a final step in exploring the hypotheses of Chapters 2 and 4, which both state that slow growth prevents saplings escaping the frequent fires.

Chapter 6 summarises the results and evaluates how well they answer the central question of 'What limits trees in C4 grasslands?'

University of Cape Town

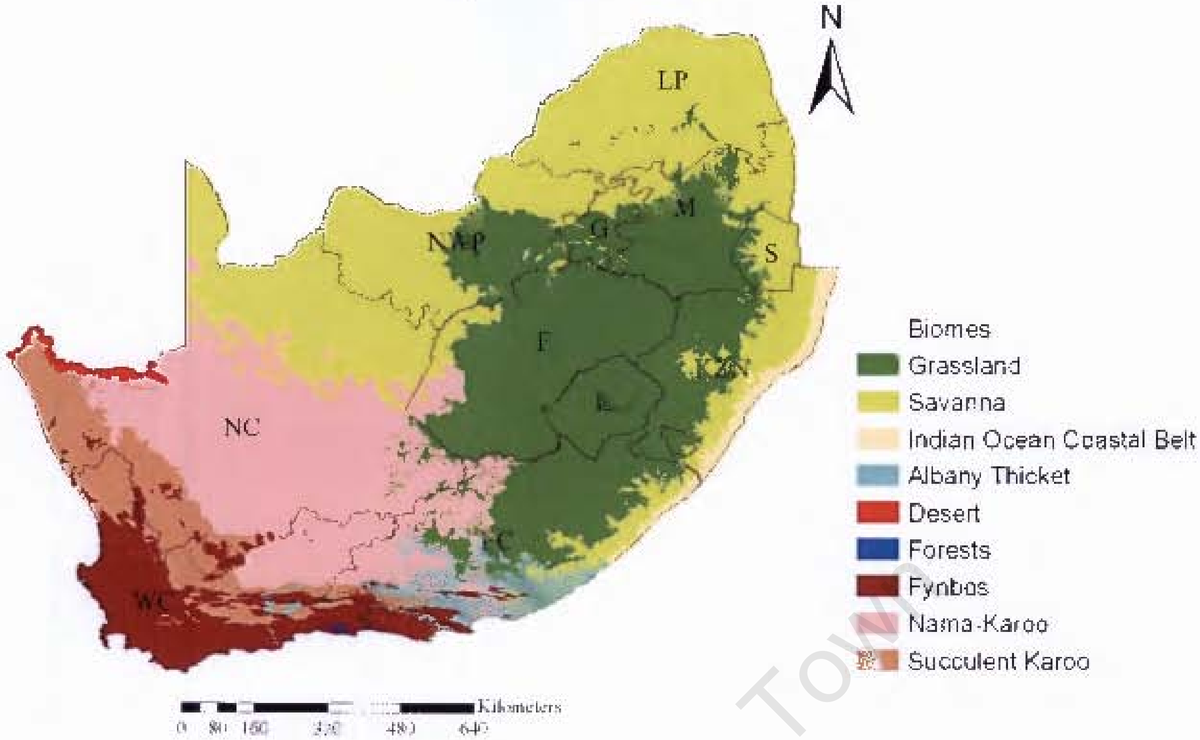


Figure 1.1: A map of the biomes of South Africa showing that grassland and savanna biomes are adjacent in many areas (from Mucina & Rutherford, 2006). EC = Eastern Cape; F = Freestate; G = Gauteng; L = Lesotho; LP = Limpopo Province; KZN = KwaZulu Natal; M = Mpumalanga; NC = Northern Cape; NWP = North West Province; S = Swaziland; WC = Western Cape.

University of Cape Town

Figure 1.2: A transition from wooded savanna to tree-less grasslands, that include grass-less forest patches. The photograph was taken from Seme Hill, Hluhluwe-iMfolozi Game Reserve, at *ca.* 400m, looking east, down to *ca.* 200m above sea level.

Chapter 2: *Acacia* growth across an altitudinal gradient from low savannas to high grasslands

Introduction

Grasslands and savannas cover 11% and 15% of vegetated land surface respectively (Ramankutty & Foley 1999, Asner *et al.* 2004). Both biomes are dominated by C_4 grasses, and have a distinct dry season that allows the grass to dry out and become flammable (d'Antonio & Vitousek 1992). Fire is thus an important factor in both systems. High elevation grasslands in South Africa, commonly known as the Highveld grasslands, are cooler than the adjacent savannas (Schulze 1997, Mucina & Rutherford 2006), yet simulations have shown that their climate can support a woody biomass (Bond *et al.* 2003). Much work has investigated the co-existence of grasses and trees in savannas (Walter 1971, Walker 1987, Scholes & Archer 1997, Higgins *et al.* 2000), yet little experimental work investigates the reason for the lack of trees in grasslands. This is surprising, given the vast expanse and economic value of grasslands.

University of Cape Town

Southern Africa provides an excellent opportunity for studying these two closely related biomes. African savannas are often dominated by members of the *Acacia* genus, and are frequently adjacent to the higher altitude tree-less grasslands (Acocks 1953, White 1983, Mucina & Rutherford 2006). The boundary between the two systems is very distinct in places, analogous to an alpine tree-line (pers. obs.). The crucial difference is that trees cannot survive above a classic altitudinal/alpine tree line (Körner 2003), yet forest patches are common in these grasslands, well away from the biome boundary (Acocks 1953, White 1983, Mucina & Rutherford 2006). The question is then: Why are savanna trees, which can recruit through a grass layer, absent from higher elevation grasslands?

Several hypotheses have been proposed to explain the tree-less grassland in South Africa, including anthropogenic disturbances, frost, fire and aspects of soil (for reviews see O'Connor and Bredenkamp, 1997 and Mills *et al.*, 2006). Grasslands are an end point for the coexistence problem of tree-grass savannas, with grass-less forest at the other extreme. Grasslands and forests provide an interesting challenge for tree-grass coexistence models. The root-niche separation model (Walter 1971) cannot be used to explain why trees do not inhabit their niche in grassland areas. The "escape hypothesis" may assist in explaining the tree-less grasslands. The escape hypothesis argues that tree cover in savannas is limited primarily by demographic bottlenecks to recruitment, especially fire effects on sapling growth (Bond & van Wilgen 1996, Scholes & Archer 1997). Fire prevents the formation of high densities of juvenile trees and the growth of these juveniles into adults (Bond & van Wilgen 1996). Juveniles may be burnt to the ground many times, and resprout repeatedly from below-ground root stocks, before they become adults (Bond & van Wilgen 1996, Gignoux *et al.* 1997, Scholes & Archer 1997, Wigley *et al.* 2008). Both height and stem diameter are important in surviving and escaping the fire trap (Balfour & Midgley 2006, Schutz 2007). Once trees reach a large enough stem size and "escape" height above the flame zone (*ca.* 2 – 4 m) they are relatively immune to stem kill by fire and have "escaped" the fire trap (Trollope 1974, Higgins *et al.* 2000).

University of Cape Town

The grasslands of South Africa are at higher altitudes than the savannas, and therefore experience lower temperatures (Schulze 1997, Mucina & Rutherford 2006). Growth only occurs on days when the temperature exceeds a threshold, below which plant growth slows and/or stops (Fernandez *et al.* 2003, Körner 2003). The cool Highveld grasslands would have fewer days suitable for growth and hence a shorter growing season than the adjacent, warmer savannas. Both lower temperatures and the shorter growth season would lead to decreased growth in the Highveld grasslands.

Temperature, moisture and photoperiod have been demonstrated to be cues for tree and leaf phenology in savannas (Childes 1989, Williams *et al.* 1997, Chidumayo 2001, Jolly & Running 2004, Do *et al.* 2005, Archibald & Scholes 2007) and trees in temperate climates (Greer & Warrington 1982, Greer *et al.* 1989, Bannister *et al.* 1995, Fernandez *et al.* 2003, Körner 2003). Leaf flushing and senescence have been the focus of much of the savanna tree phenology work (Childes 1989, Jolly & Running 2004, Do *et al.* 2005, Archibald & Scholes 2007), rather than the timing of stem growth and its relation to environmental factors (Williams *et al.* 1997, Chidumayo 2001).

Chapter 2: Acacia growth across an altitudinal gradient from low savannas to high grasslands

Based on the escape hypothesis for explaining variation in tree cover in savannas (Bond & van Wilgen 1996, Scholes & Archer 1997, Higgins *et al.* 2000), we propose a new hypothesis regarding the lack of trees in the grasslands of the Highveld. We suggest that due to the cooler and shorter growing season of these grasslands, tree saplings cannot grow fast enough to escape the flame zone in the short intervals between fires. This implies that savanna trees are not limited by growing condition alone, but by the interaction between fire and growth. Savanna trees should be able to grow under the climate of the Highveld grasslands if fire is excluded, as has been shown (Westfall *et al.* 1983, Ellery 1992, Titshall *et al.* 2000), and growth rates should be much lower in grasslands than savannas.

The aims of this chapter were to quantify the differences in growth of seedlings in grassland and savanna climates, and to establish if temperature was driving the growth period of savanna trees. To explore these aims, seedling growth was measured for a year in a seedling transplant experiment across an altitudinal gradient from savannas into grasslands. To confirm results obtained in the altitudinal experiment about the timing of seedling growth in relation to temperature changes, a pot experiment was set up in one location in the following season and more regular measurements taken. Whether differences in growth of seedlings in grasslands and savannas would make a difference to saplings trying to grow above the flame zone, is explored in Chapter 5.

University of Cape Town

Methods

Species selection

Savannas and grasslands are similar in that they have a grass layer that burns; hence fire tolerant savanna species were used in this study. As *Acacia* species are widespread in southern African savannas, and include high and low altitude species that may respond differently to variations in temperature, members of this genus were used for this experiment. Species were selected to represent the full altitudinal range of the genus, from both warm and cool regions. Two varieties of *Acacia karroo* were used as this species is the most widely distributed *Acacia* species in southern Africa and varieties may differ in their growth and survival at different temperatures. The two varieties were, "*A. karroo* (Bloem)" from the Bloemfontein area (*ca.* 1500 m, mean annual temperature (MAT) = *ca.*14°C to 16°C), the other, "*A. karroo* (Hlu)" from eastern KwaZulu Natal, including the Hluhluwe-iMfolozi Game Reserve (*ca.* 100-400 m, MAT = *ca.*18°C to 21°C) (Coates Palgrave (2002) split *A. karroo* into 6 species, naming the Hluhluwe variety *A. natalitia* and the Bloemfontein variety remains *A. karroo* (Swartz 1982)). *Acacia gerrardii* is morphologically similar to *A. karroo* (Hlu), and yet its altitudinal distribution is limited to lower elevations. The use of *A. gerrardii* in this experiment may highlight some of its limitations that restrict its distribution. In the region of the study sites, *A. tortilis* grows at low elevations in hot areas and *A. sieberiana* occurs at mid to high elevations in warm to cool areas. *Acacia mearnsii* naturally occurs between 34°S and 44°S, and altitudes up to 885 m in south east Australia (Sherry 1971). It is an invasive species in the cooler, high elevation regions of South Africa. As it naturally occurs in areas cooler than the range of most southern African *Acacia* species, it is likely to grow better in cool climates and was used as a comparison to indigenous species. This species could not be planted at the Mbuzane site due to nature reserve restrictions on exotic species.

University of Cape Town

Sites

Ten sites were selected across a broad altitudinal gradient (*ca.* 40m to 1700m asl), from savannas to grasslands, and encompassing a wide range of summer heat units (SHUs) (Schulze 1997) (Figure 2.1). Heat units are the sum of degree days above a certain threshold, below which growth does not take place (Schulze 1997). SHUs were used as almost all growth occurs in summer. Sites were chosen in relatively flat areas to control for aspect, avoiding valleys where frost pooling could occur due to katabatic air flow. Ten individuals of each species or subspecies were planted at each of ten sites. Seedlings were planted one metre apart. All sites were fenced to protect the seedlings from mammal herbivory. Seedlings were planted between the 27 October and 9 November 2006.

In this experiment we isolated the thermal effects of the altitudinal gradient on tree seedling establishment by controlling for soil and rainfall differences and grass competition. Soil properties vary across the study area. To control for variation in soil properties, each seedling, across all sites, was planted in the same type of soil. Soil from the Centenary Centre in the Hluhluwe-iMfolozi Game Reserve was used. Seedlings were planted in the ground in 15*l* bags and 70g of slow-release fertilizer (Osmocote exact: see Appendix Box 2.A) was dibbled into the soil of each bag. The ground soil surface and soil in the bag were flush with each other. To control for variation in diversity and biomass of grass between sites, grass was cleared before planting and weeded as necessary, approximately monthly, during the experiment. To control for rainfall variation among sites, the plots were watered during summer. Where possible, a Gardena Water Computer (Basic T 1020) was set up with a sprinkler to water automatically. Where this was not possible, or when they failed, plants were watered by hand. Automatic watering generally occurred every second day, and then twice daily in the extremely hot months. Manual watering generally occurred three times a week. The need to water varied with rainfall, and the rule that plants should never wilt was adhered to.

University of Cape Town

Measurements

Air temperatures were recorded at *ca.* 130cm with DS1921G Thermochron® iButton® data loggers. Height, total stem length and diameter of the stem at about 1cm above the ground were measured in October / November 2006 and again in January 2007, and height and stem diameter were measured in March, June and October / November 2007. Half the plants were cut to ground level, simulating fire, at the end of the growing season in June 2007. Leaves and stems of the cut material were separated, oven dried to constant weight, and weighed. Dry stem weights were used in analyses as some plants at cooler sites had lost leaves to frost, so analysis of total above-ground biomass (leaves and stems) would have been biased against these cooler sites. In October / November 2007 all plants, including sprouts from those plants harvested in June, were harvested. Leaves and stems were separated, oven dried to constant weight, and weighed.

Pot Experiment and Seasonality Experiment

To examine when plants grow during a season, both growth in the transplant experiment, as well as growth of seedlings of two *Acacia* species in a pot experiment, were measured. In the pot experiment, seedlings of *A. karroo* (Hlu) and *A. sieberiana* were planted in 10*l* bags of soil. Plants were watered, and height, total stem length and stem diameter were measured once a month from November 2007 to April 2008 (see also methods section in Chapter 4).

Analyses

Sites were classified into biome according to Mucina and Rutherford (2006). The lowest altitude site, Kirkwood (42m asl), is in the Indian Ocean Coastal Belt Biome, a mosaic of edaphic grasslands, savannas and forest on Holocene sandy soils. It falls within the savanna biome in analyses of tree growth that compare grassland to savanna sites. Two sites failed and are thus excluded from all analyses. The Goss site was shaded and should not have been planted. The Mbuzane site did not receive water for over a month, due to failure of the watering mechanism, during a mid-growing season drought.

Summer heat units are an accumulation of mean temperatures above a certain minimum from October to March (Schulze 1997). The map of summer heat units in Schulze (1997) uses 10°C as a base, as this temperature is applicable to maize, the staple food crop of South Africa. According to Schulze (1997), growth of citrus trees only occurs above an average daily temperature of 13 °C. For lack of other data on growth temperatures of C_3 trees in South Africa, we used 13 °C as a base for calculations of heat units and number of growth days, from data collected during the experiment. Relative height increase was calculated so that comparisons could be made between species that differed in initial sizes. This measure of relative growth was calculated as the change in height per day (Hunt 1982, Hoffmann & Poorter 2002). Natural logarithms of the height per individual were plotted against time in days and the slope was taken as relative height increase. Day length was calculated from sunrise and sunset times, predicted by the NASA/GISS Atmosphere-Ocean Model, as described by Russell *et al.* (1995), and available at http://aom.giss.nasa.gov/srlocat.html.

Statistical analyses were performed using STATISTICA software. Dependent variables were tested for normality where necessary. Correlations were used to test

University of Cape Town

for relationships between site altitude and summer heat units or number of growth days; and between summer heat units and plant height or biomass. Data of height, biomass and relative height increase, between grassland and savanna sites for each species, was not normal or homoscedastic, due to differences in growth between species, and small sample sizes for the biomass data. To analyse this data, Mann-Whitney U Tests were used to compare differences between grassland and savanna sites for all species combined. Differences between species were found using Kruskal-Wallis Tests. Wilcoxon's paired tests were also used to compare between the two biomes, matching species pairs. Repeated T-tests or Mann-Whitney U Tests were not performed for each species between biomes, due to the likelihood of Type I errors. Two-factorial ANOVAs could not be used as the data was significantly heteroscedastic.

University of Cape Town

Results

Temperature differences between grassland and savanna sites

Sites in the higher elevation grasslands had lower average monthly temperatures (Appendix Figure 2.A), and fewer heat units, resulting in shorter growing seasons, than the lower altitude savanna sites (Table 2.1, Figures 2.1 & 2.2). MAT of grassland sites was 15.4°C and 20.0°C for savanna sites. Division between grassland and savanna sites is at *ca.* 1400 SHU degree days ("Expt SHU" in Table 2.1, which are summer heat units calculated from temperature data collected), which is useful to know when looking at Figures 2.3, 2.4 and 2.6.

Seedling height, biomass and relative height elongation

Seedlings were of similar ages and sizes, within each species, for *A. karroo* (Bloem), *A. sieberiana* and *A. mearnsii*, at the start of the experiment (Table 2.2). *Acacia karroo* (Hlu), *A. gerrardii* and *A. tortilis* varied in height and ages within each species at the start of the experiment (Table 2.2). There were no significant correlations between site summer heat units and initial November heights for each species (*A. karroo* (Hlu): r = -0.08; *A. gerrardii*: r = -0.08; *A. tortilis*: r = -0.06; *A. sieberiana*: r = 0.07; *A. mearnsii*: r = 0.14; and p > 0.1 for all) except *A. karroo* (Bloem) (r = 0.43, p

< 0.01) (Figure 2.3). The hottest (Kirkwood) site was measured 2 weeks after it was planted, and when it was removed from the analysis, there was no significant correlation for *A. karroo* (Bloem) ($r = -0.07$; $p > 0.1$).

Height and biomass after one growth season (November to June) was significantly positively correlated with summer heat units for all species (Figures 2.3 and 2.4). Relative height increase was significantly positively correlated with summer heat units for *A. karroo* (Hlu), *A. tortilis*, *A. sieberiana* and *A. mearnsii*, but there was no relationship for *A. karroo* (Bloem) and *A. gerrardii* (Figure 2.3). Overall, *A. mearnsii* had the largest and *A. karroo* (Bloem) the smallest individuals in terms of height and biomass across all sites. The species that were bought from commercial nurseries (*A. karroo* (Bloem), *A. sieberiana* and *A. mearnsii*) had relative height increases that were greater than 0.008cm cm^{-1} day^{-1} across all sites, and those that were grown in the Hluhluwe-iMfolozi research nursery, and were generally older, had relative height increases that were less than 0.008cm cm^{-1} day^{-1}.

University of Cape Town

Growth between savanna and grassland sites

June heights were significantly different between savanna and grassland sites for all species combined (M-W: $U = 17202$, $Z = -6.18$, $p < 0.0001$) (Figure 2.5). There were differences in height between species (K-W: $H_{5,N=473} = 235.61$, $p < 0.001$). Mean height of each species was significantly greater in savanna sites than grassland sites, according to a Wilcoxon's matched pairs test ($N = 6$, $Z = 2.20$, $p < 0.05$). Average heights at savanna sites were between 1.2 and 1.7 times the average heights at grassland sites (Figure 2.5). Total above-ground biomass after one growing season (in June) was significantly greater at savanna than grassland sites for all species combined (M-W: $U = 3990$; $Z = -4.35$, $p < 0.0001$). There were differences in biomass between species (K-W: $H_{5,N=230} = 89.13$, $p < 0.0001$). Mean biomass of each species was significantly greater in savanna sites than grassland sites, according to a Wilcoxon's matched pairs test ($N = 6$, $Z = 2.20$, $p < 0.05$). Average biomass at savanna sites was between 1.4 (*A. mearnsii*) and 5 times (*A. sieberiana*) greater than the average biomass at grassland sites. Relative height increase was significantly greater in savanna than grassland sites for all species combined for the whole growing season, November to June (M-W: $U = 22538$, $Z = -2.61$, $p < 0.01$), and the part of the growing season with the fastest growth, November to January (M-W: U = 21710, Z = -3.28, $p < 0.01$) (Figure 2.5). Species differed significantly in their relative height elongations for the whole season, November to June (K-W: $H_{5,N=475} = 355.01$, $p < 0.001$), and for the November to January period (K-W: $H_{5,N=476} = 332.21$, $p < 0.001$). There was no significant difference between relative height elongations at grassland and savanna sites, according to a Wilcoxon's matched pairs test, for the whole season (N = 6, Z = 1.57, p = 0.12) or for the November to January period (N = 6, Z = 0.31, p = 0.75).

Resprout biomass after simulated fire-loss of above-ground biomass

There was an increase in resprout biomass with an increase in summer heat units, for those seedlings manually topkilled in June and harvested in October (Figure 2.6). *Acacia mearnsii* and *A. karroo* (Bloem) had the smallest resprout biomass. For *A. karroo* (Bloem), *A. tortilis*, *A. gerrardii* and *A. mearnsii*, resprout biomass was poor at the hottest two sites (Malan and Kirkwood). Excluding these two sites, there was a significant positive correlation between summer heat units and biomass for *A. karroo* (Hlu) (r = 0.36, $p < 0.05$), *A. gerrardii* (r = 0.53, $p < 0.01$), *A. karroo* (Bloem) (r = 0.43, $p < 0.05$) and *A. tortilis* (r = 0.72, $p < 0.001$), but not for *A. sieberiana* (r = 0.31, p = 0.07) or *A. mearnsii* (r = 0.36, p = 0.10). If the two hottest sites are included in correlations, there were significant correlations with only *A. sieberiana* (r =0.47, $p < 0.01$) and *A. tortilis* (r = 0.45, $p < 0.05$).

University of Cape Town

Seasonality of growth

Results from the altitudinal gradient experiment showed that the average relative stem elongation of seedlings of all species across all sites decreased through the 2006 to 2007 growth season (Figure 2.7a). Average air temperature across all sites increased from 21.5°C in the November to January period to 22.5°C in the January to March period, and decreased to 17.0°C in the March to June period. Average day length decreased 48 minutes between the November to January and January to March time periods (13.8 hours to 13.0 hours), and a further 1 hour and 48 minutes between the January to March and March to June time periods (13.0 hours to 11.2 hours).

Results from the pot experiment, in the 2007 to 2008 summer growing season, showed that the average relative stem elongation rate of both *Acacia* species (*A. karroo* (Hlu) and *A. sieberiana*) increased from November to January, peaking in January, then steeply decreasing in February with negligible growth after March (Figure 2.7b). Average air temperature increased from November (19.9°C) to February (23.0°C), and only decreased in March (21.9°C) and April (19.4°C). Average day length increased from November to December and then decreased through to April. The decrease in day length from December to January was 12 minutes and from January to February was 39 minutes.

University of Cape Town

Discussion

This experiment compared growth rates across an altitudinal gradient from savannas into grasslands. Specific site factors, such as water availability and partial shading at times, contributed to variation in plant growth from site to site. However, the overall trends along the gradient showed that growth was lower in the cooler grasslands than the warmer savannas, for all species. This translates to a longer time for saplings to grow to a height above the damaging flames and hence a lower probability of escaping to tree height in the interval between fires. This is explored further in Chapter 5.

Along the gradient, averaged grassland sites were significantly smaller, both in height and biomass, than savanna sites, for all species combined. Variations in growth rate during the growing season seem to complicate the relative height increase. Fastest growth occurred in the November to January interval, and the average relative height increase over the whole growing season is reduced due to extremely slow growth between March and June. All species had a greater mean relative height increase at savanna sites than grassland sites, except for *A. karroo* (Bloem). *Acacia karroo* (Bloem) naturally occurs in cool areas, and it may be well adapted to growing in cool conditions. Greater relative height increases were found for species that originated in commercial nurseries (*A. karroo* (Bloem), *A. sieberiana* and *A. mearnsii*), and were transplanted from seedling tray plugs, rather than those species that were moved between bags within the last two weeks before the start of the experiment. Comparisons of height and biomass between species are complicated by differing initial plant sizes. However, across all species there is a general trend for slower growth at cooler grassland sites.

The escape hypothesis focuses on saplings, and both height and stem diameter are important for saplings trying to escape the fire trap (Balfour & Midgley 2006). This experiment involved seedlings, which allocate resources in such a way as to become established in a system. Variation in biomass was greater than variation in stem height across the temperature gradient. Seedlings initially allocate carbon to below ground stores before they begin growing tall (Wigley *et al.* 2008). Therefore, biomass is more relevant than height, as a measure of altitudinal effects on growth in this experiment. It is useful to compare variation in height and biomass among species, as it reveals aspects of a species architecture and strategy. *Acacia karroo* (Bloem), *A. tortilis* and *A. sieberiana* all have a much larger biomass relative to their height, as they have highly branched, cage-like architectures. This suggests that they are adapted to surviving herbivory (Archibald & Bond 2003). *Acacia karroo* (Hlu) and *A. gerrardii* have similar variation in height versus biomass across the gradient, reflecting their tall, unbranched architecture. These "tall" species are from mesic savannas where fire is a more dominant disturbance than herbivory (Archibald & Bond 2003). *Acacia mearnsii* was also a "tall" species, with similar relative changes in biomass and height, but had much greater growth rates than the other species (average *A. mearnsii* was 2.2 times larger in height and 3.8 times larger in biomass than the average of all other species together, across all sites in June). It is interesting to note that this species does not allocate resources to structural defences such as thorns.

University of Cape Town

All species in this study displayed the ability to resprout, although the degree of resprouting varied between species as has been shown elsewhere (Hodgkinson 1998, Neke *et al.* 2006). In general there was an increase in resprout biomass at warmer sites, reflecting larger below-ground storage, due to favourable growing conditions during the previous growing season, as well as favourable conditions at the time of sprouting. The variable but generally poor resprouting at the two hottest sites may for some species be because of the large size of plants before they were cut. Sprouting ability is important for juvenile savanna trees because of the frequent disturbance by fire. Loss of sprouting can be because bark is too thick for buds to grow through or because plants allocate stored root reserve to above-ground growth once they have grown to a threshold height (Bond & Midgley 2001, Bond & Midgley 2003). Maze (2001) and Schutz (2007) found that some large *A. karroo* (Hlu) did not resprout. Neke *et al.* (2006) found that large individuals developed the ability to sprout along stems, and in some species, they also maintained the ability to sprout from the base (see also Hodgkinson (1998)).

Most growth occurred before February in the pot experiment and before the January to March time period in the transplant experiment. Other experiments have also shown savanna tree growth to occur mainly in the early part of the growing season, rapidly declining from February or March (Chidumayo (2001), for *Acacia* species in southern Africa, and Prior *et al.* (1997) and Prior *et al.* (2004) for northern Australian savannas). In temperate regions, both temperature and day length have been demonstrated as cues for cessation of growth at the end of a growing season (Greer & Warrington 1982, Greer *et al.* 1989, Bannister *et al.* 1995, Fernandez *et al.* 2003, Körner 2003). In savannas, phenology and inter-annual variation in phenology, have been related to moisture availability, temperature and photoperiod in different species and in different locations (Childes 1989, Williams *et al.* 1997, Jolly & Running 2004, Do *et al.* 2005, Archibald & Scholes 2007). Here, we have shown experimentally that savanna tree growth decreases as day length shortens in February / March, while plants were being watered, and that this cessation of growth is not linked to temperature.

University of Cape Town

Temperate trees stop growth in order to cold harden before cold temperatures begin (Sakai & Wardle 1978, Bannister *et al.* 1995, Fernandez *et al.* 2003, Körner 2003). Savanna trees grow in areas where they would not need to be cold adapted to survive the winter temperatures, as temperate trees would. Deciduousness and the associated lack of savanna tree growth have been attributed to survival of the seasonal winter drought (Prior *et al.* 1997, Jolly & Running 2004, Do *et al.* 2005). Prior *et al.* (1997) postulated that the lack of above ground growth, despite high carbon assimilation during the latter part of the wet season and early dry season, was because plants were allocating resources below ground. Allocation of resources below ground is important for survival and sprouting after disturbances such as fire (Bond & van Wilgen 1996, Gignoux *et al.* 1997, Wigley *et al.* 2008). Perhaps the early cessation of growth is not simply due to a lack of moisture, but so that plants can allocate reserves below ground before dry season fires. Temperate trees grow in areas where freezing is certain, whereas fires do not necessarily occur every year in savannas. Stopping growth when conditions are still favourable to redistribute resources to below ground stores seems like an expensive strategy when a fire may not actually occur.

Conclusion

This study is the first field experiment in South Africa to compare savanna tree growth across an altitudinal gradient from savanna into grassland habitats. The results show that seedlings established and grew across the entire altitudinal gradient. Growth, measured as height and biomass, was generally greater in savanna than grassland sites, sometimes up to five times greater. To evaluate the ecological importance of these differences, growth needs to be translated into the time it would take for saplings to reach a size above the flame zone. This experiment can be used to assess the escape hypothesis, and vice versa, for why there are no trees in the Highveld grasslands (Chapter 5). This experiment did not explore tree-grass coexistence. An experiment involving both trees and grass would be useful to investigate possible variation in tree-grass competition between savannas and grasslands. Savanna tree phenology research has focussed much on leaf phenology. In this experiment we found growth of savanna trees to decrease with photoperiod rather than temperature, while plants were not water limited. This suggests that photoperiod is the main driver of savanna tree growth in the latter half of the growing season.

University of Cape Town

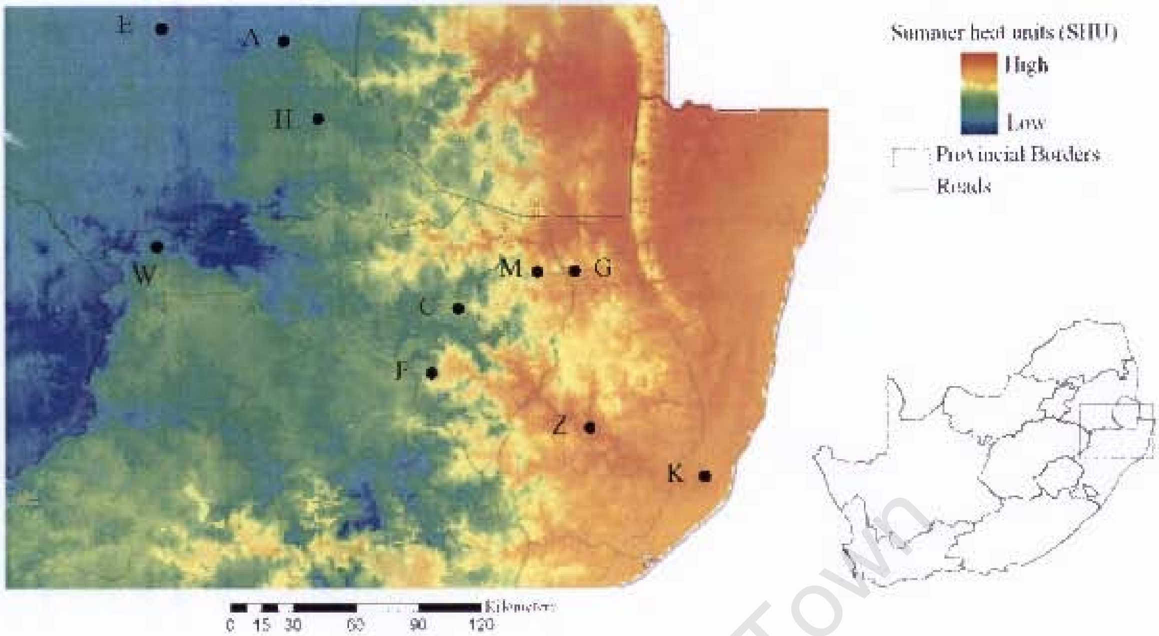


Figure 2.1: A map of summer heat units (from Schulze (1997)) for the region showing site locations. Point labels represent the first letter of each site name (see Table 2.1).

University of Cape Town

Table 2.1: Characteristics of sites in the transplant experiment. Alt = Altitude; Schulze SHU = Summer Heat Units, where summer is October to March, from Schulze (1997); Expt SHU = Summer Heat Units calculated from temperature data collected, for the period 7 November 2006 to 30 April 2007, with a base of 13°C; MAP = Mean Annual Precipitation; MAT = Mean Annual Temperature; # Growth Days = the number of days between 7 November 2006 and 30 April 2007 that had an average temperature of 13°C or more, calculated from temperature data collected; G = grassland; S = savanna; CB = Indian Ocean coastal belt; Lat = latitude; Long = Longitude. Sites were classified into Biome according to Mucina & Rutherford (2006). Weather data was extracted from Schulze (1997). * Site data was not used in analyses as sites failed.

Site	Biome	Alt (m)	Schulze SHU (°days)	Expt SHU (°days)	# Growth Days	MAP (mm)	MAT (°C)	Long (°S)	Lat (°E)
Ermelo	G	1704	1369	807.3	179	699	14	26.490	29.967
Wakkerstroom	G	1648	1472	944.9	187	754	15	27.400	29.917
Athole	G	1570	1539	979.9	193	833	15	26.600	30.500
Hlelo	G	1353	1634	1057.6	191	875	16	26.917	30.550
Comins	G	1078	1871	1294.2	218	720	17	27.717	31.233
Ford	S	808	1963	1460.1	216	841	18	28.000	31.100
Malan	S	554	2289	1772.7	231	623	19	27.567	31.567
Goss *	S	360	2535	1916.8	232	671	21	27.550	31.750
Mbuzane *	S	170	2653	2075.7	233	689	21	28.230	31.799
Kirkwood	CB	42	2500	1887.5	232	1008	21	28.417	32.317

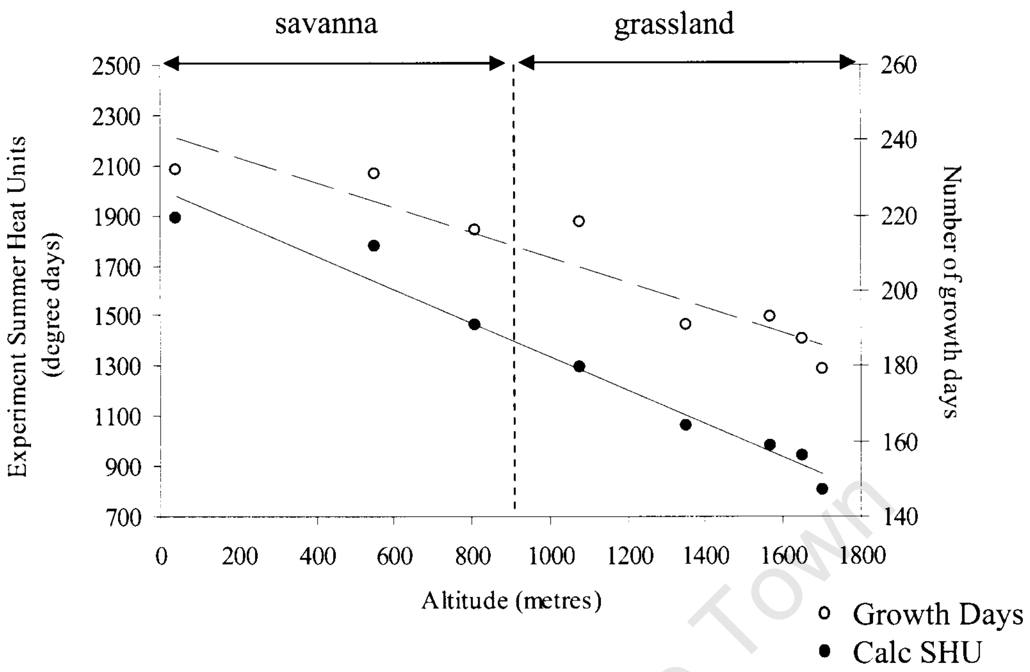


Figure 2.2: The summer heat units (r = 0.98) and number of growth days (r = 0.94) for sites in savanna and grassland biomes along an altitudinal gradient. Sites are classified into biome according to Mucina & Rutherford (2006), and the lowest altitude site from the Indian Ocean Coastal Belt biome is grouped into the savanna biome. Summer heat units (between the start of the experiment, 7 November 2006, and 30 April 2007, the estimated end of the growing season) and the number of growth days (between 7 November 2006 and 30 June 2007, the end of the experiment) are calculated from temperatures recorded at sites and both use 13°C as a base.

Table 2.2: Species used in the transplant experiment, with the age and height of seedlings at the start of the experiment, the origin of the seed and place where the seedlings were grown. (* Approximate at start of experiment. HiP = Hluhluwe-iMfolozi Game Reserve)

Species	**Age***	**Height***	**Origin of seed**	**Origin of seedlings**
A. karroo (Bloemfontein)	6 months	3cm	Bloemfontein	Commerical nursery
A. karroo (Hluhluwe)	8 months	20 – 40cm	HiP	HiP nursery
A. gerrardii	1 – 1.5yrs	20 – 40cm	HiP	HiP nursery
A. tortilis	1 – 1.5yrs	20 – 40cm	HiP	HiP nursery
A. sieberiana	6 months	18cm	Pietermaritzburg area	Commerical nursery
A. mearnsii	6 months	30cm	Originally Australia	Commerical nursery

University of Cape Town

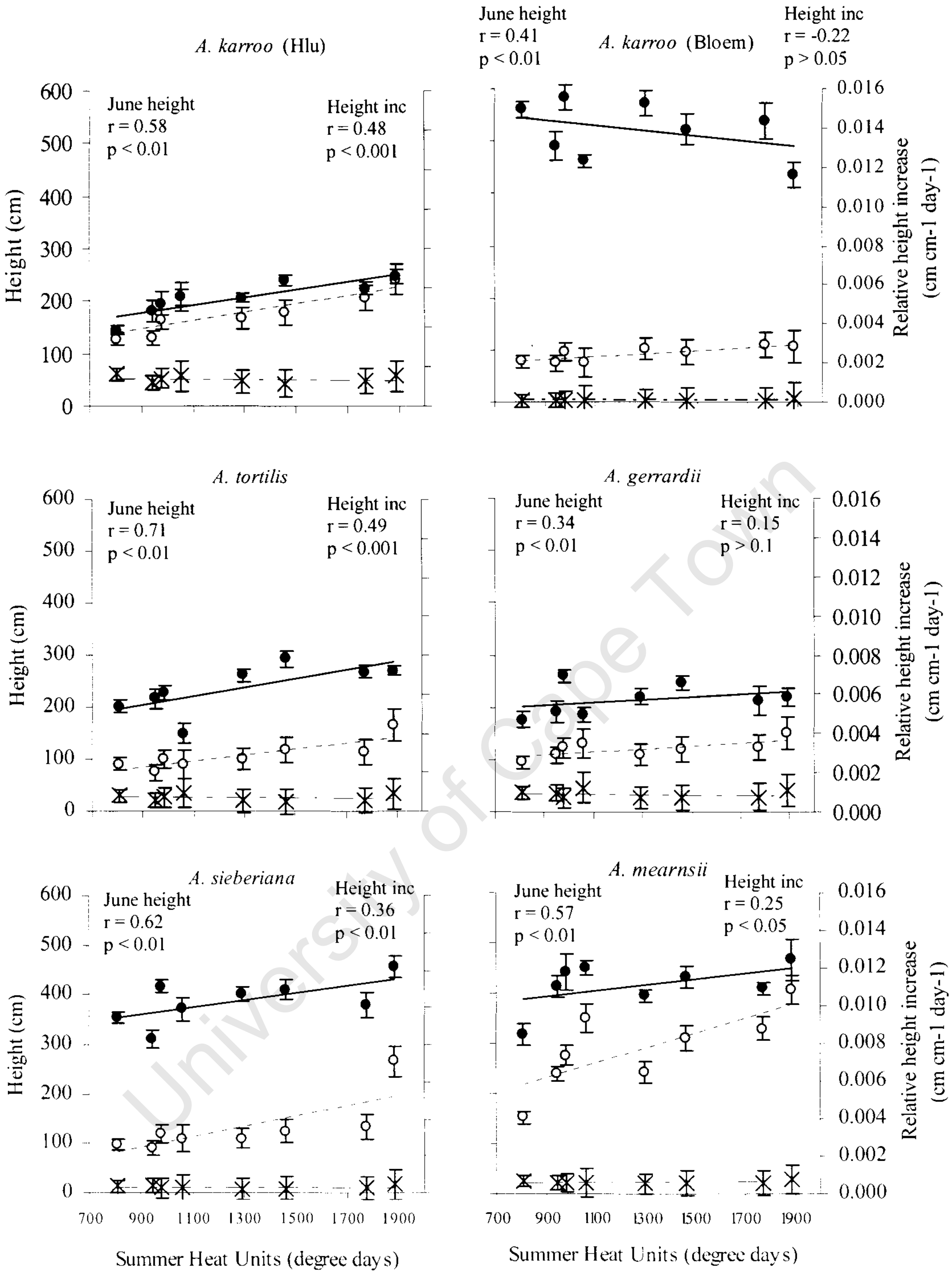
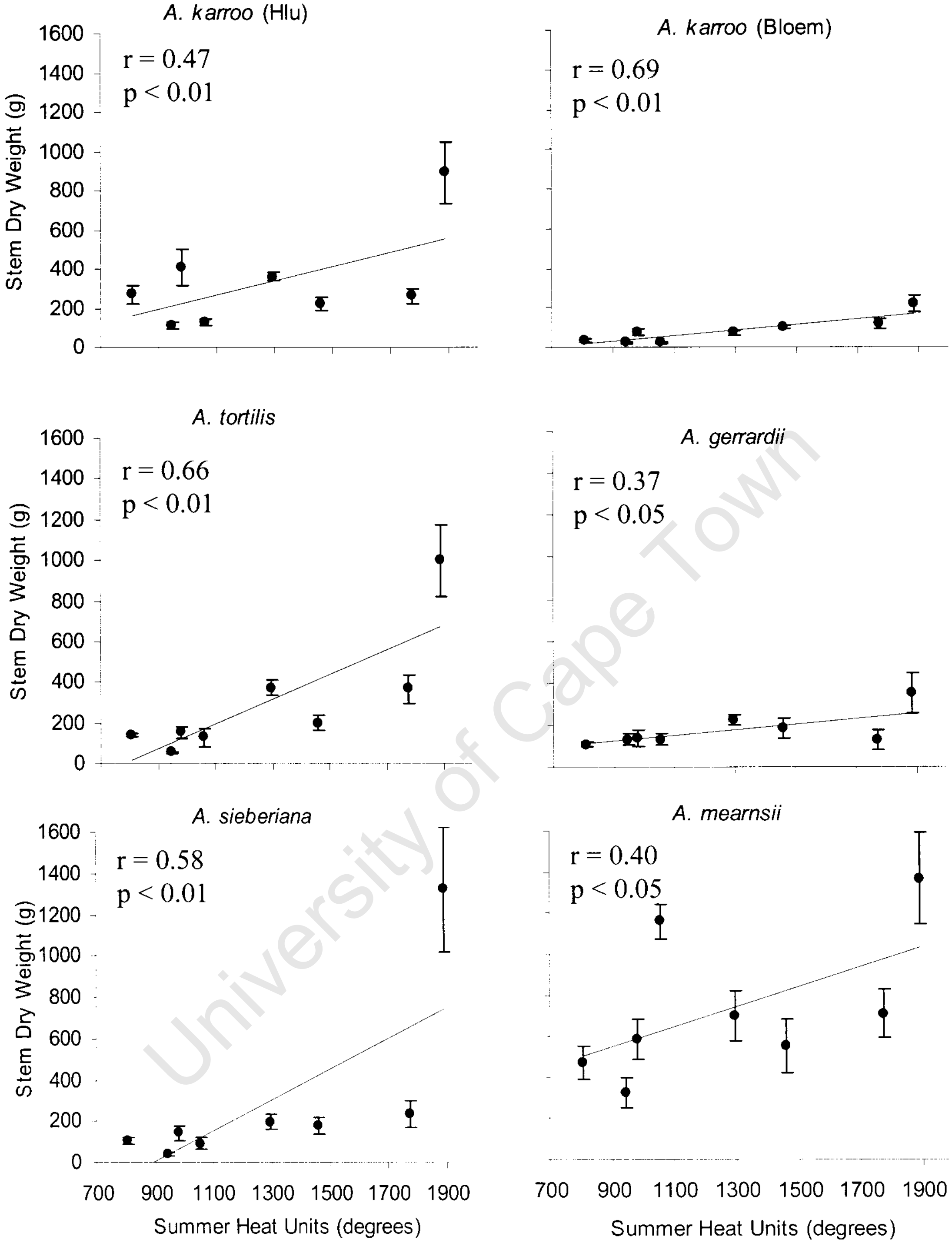


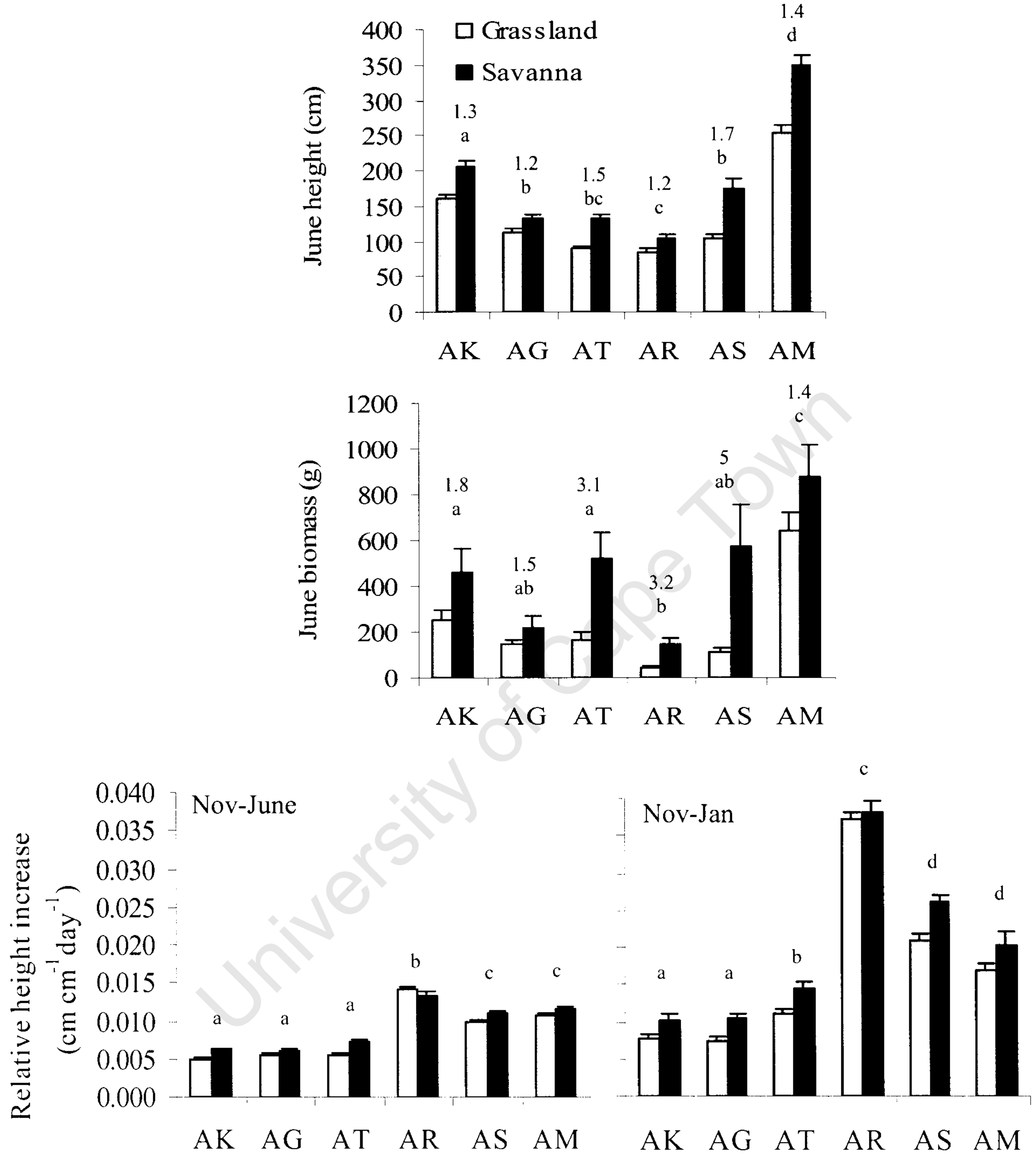
Figure 2.3: The average height of seedlings of various *Acacia* species, at the time of planting in November 2006 (crosses) and after one growing season, in June 2007 (circles); and the average relative height increase (dots), at sites along a gradient of summer heat units (SHU). Bars represent standard errors about the mean. Correlation coefficients and associated p values are shown for June heights and relative height increases (Height inc) with SHU. November heights show no relationship with summer heat units for all species except *A. karroo* (Bloem) (see text). Savanna sites have a SHU of > *ca.* 1400 degree days.

University of Cape Town



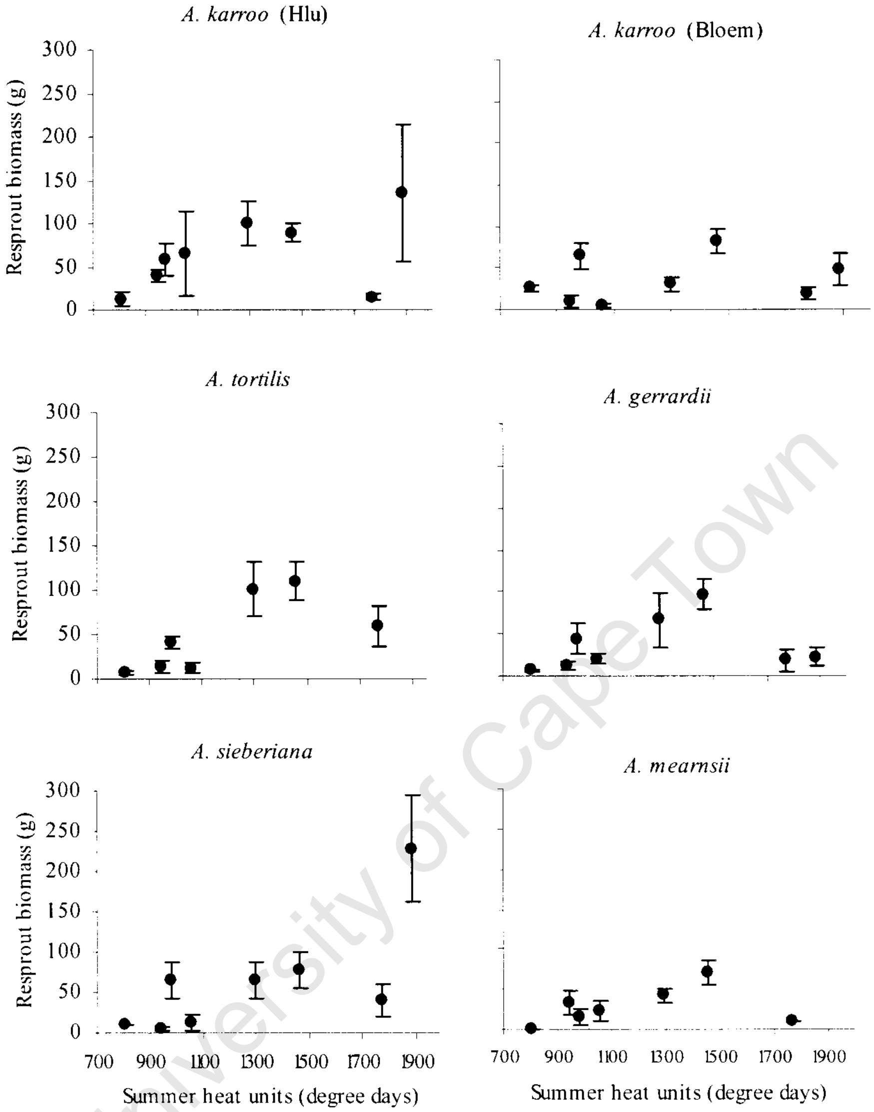
University of Cape Town

Figure 2.4: Dry stem biomass of seedlings that were planted in November 2006 and harvested after one growing season in June 2007 in relation to summer heat units at sites where seedlings were planted. Correlation coefficients and p-values are shown on each graph. Savanna sites have a SHU of > *ca.* 1400 degree days.



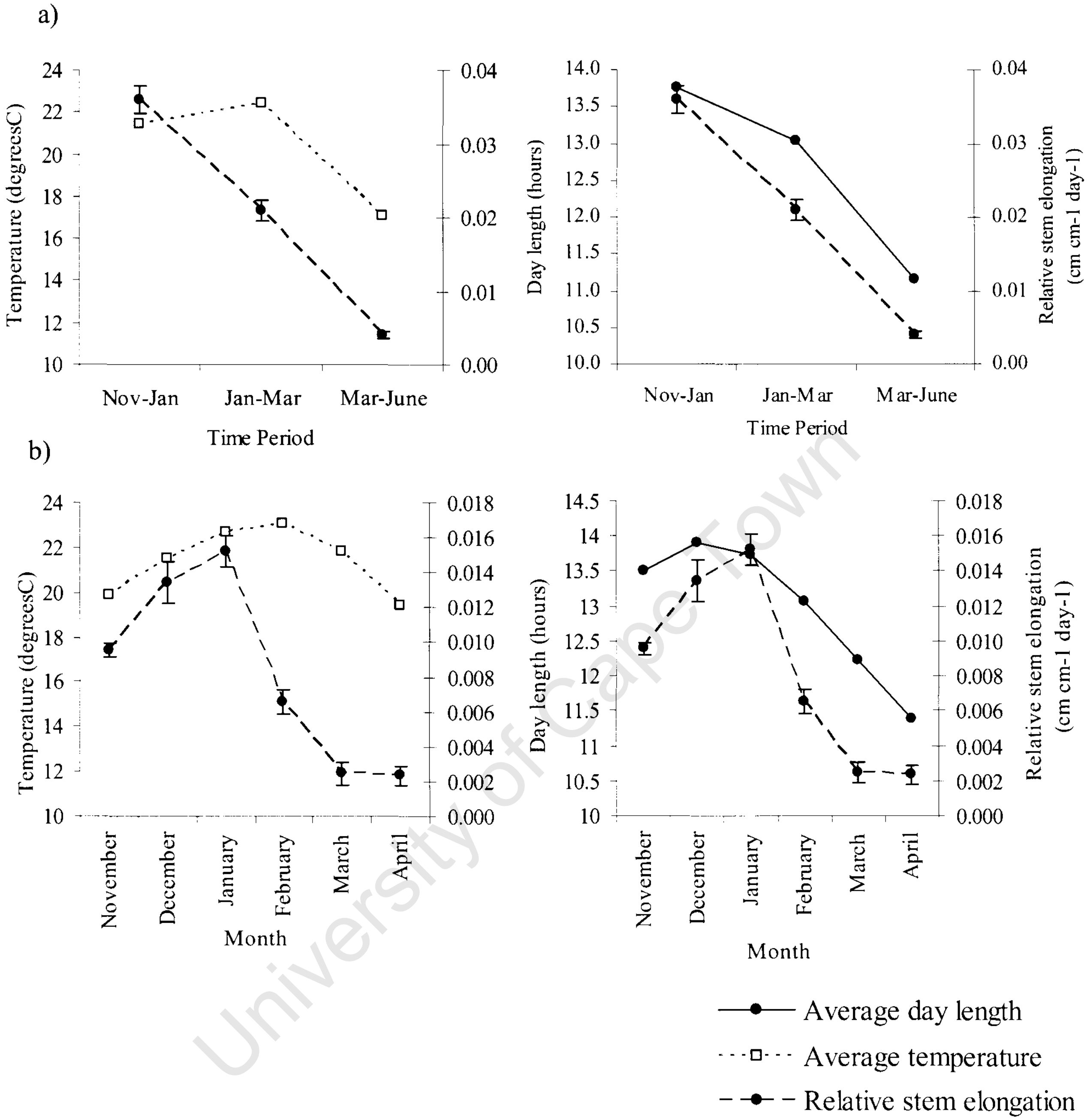
University of Cape Town

Figure 2.5: June height and biomass, and relative height increase (November to June and November to January), between grassland and savanna biomes for *Acacia karroo* (Hlu) (AK), *A. gerrardii* (AG), *A. tortilis*, (AT), *A. karroo* (Bloem) (AR), *A. sieberiana* (AS) and *A. mearnsii* (AM). Bars represent standard errors about the mean. Values above bars are the ratios of averages between savanna and grassland sites for each species. Different letters indicate significant differences between species (both savanna and grassland biomes combined), shown by Kruskal-Wallis Tests (see text).



University of Cape Town

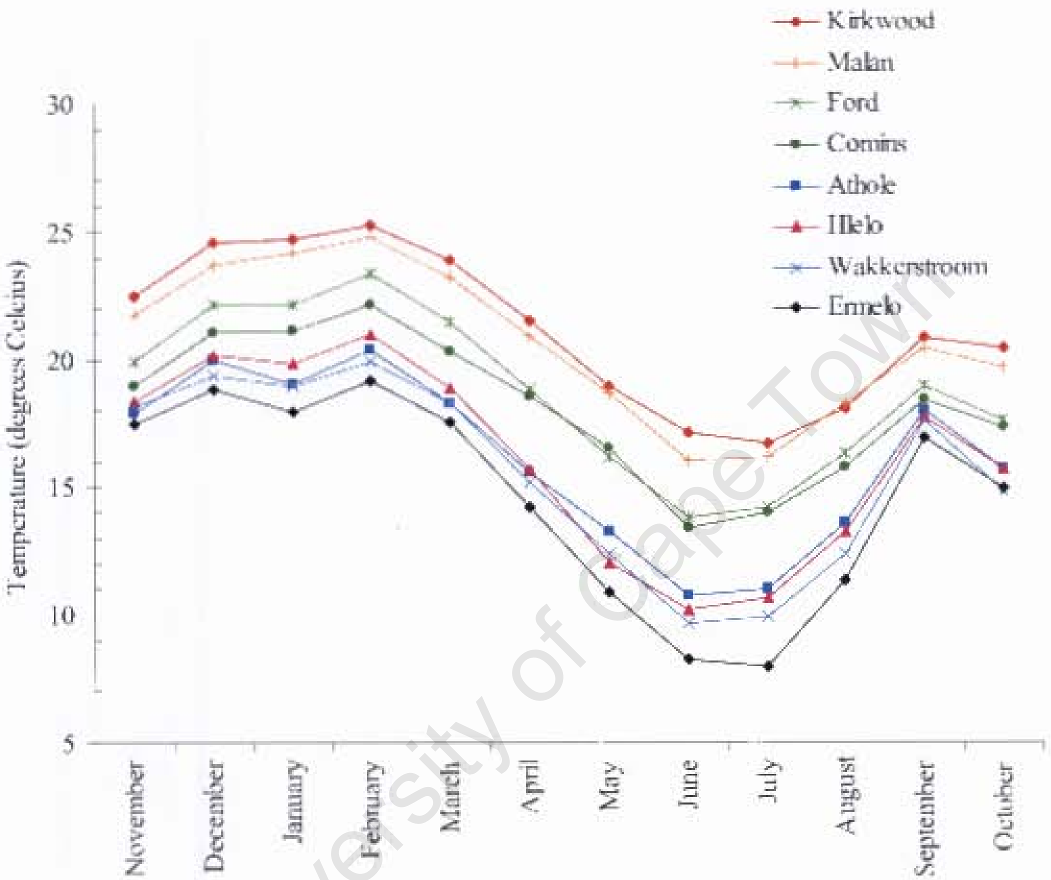
Figure 2.6: Average dry weight of above ground biomass in October 2007 that resprouted from stems that were manually topkilled (cut to 2cm above the ground) in June (n = *ca.*5) at eight sites along a gradient of summer heat units, for different *Acacia* species. Bars indicate standard error about the mean.



University of Cape Town

Figure 2.7: Average day length, temperature and relative stem elongation of *Acacia* species, in different months. a) Relative stem elongation averaged for *A. karroo* (Hlu), *A. karroo* (Bloem), *A. gerrardii*, *A. tortilis*, *A. sieberiana* and *A. mearnsii*, grown in a transplant experiment across an altitudinal gradient. Measurements were averaged for time periods between November 2006 and June 2007 (November to mid-January, mid-January to mid-March and mid-March to mid-June); b) Average relative stem elongation for *Acacia karroo* (Hlu) and *A. sieberiana* grown in a pot experiment, with temperature and day length for each month from November 2007 to April 2008.

Appendix



University of Cape Town

Figure 2.A: Mean monthly temperatures for sites (excluding Goss and iMfolozi), calculated from data collected on site by DS1921G Thermochron® iButton® data loggers. Savanna sites = Kirkwood, Malan and Ford; Grassland sites = Comins, Athole, Hlelo, Wakkerstroom and Ermelo.

Box 2.A: Details of Osmocote slow release fertilizer used in transplant experiment. 70g of fertilizer was dibbled into each 15kg plant bag.

Osmocote Exact 15+9+9+3MgO+Te 12-14M
Standard
NPK Fertilizer containing Magnesium with trace elements 15 + 9 + 9 (+3.0)
Longevity 12-14 months (at 21degC average soil temperature)

15% Total Nitrogen (N): 7.1% nitrate nitrogen; 7.9% ammoniacal nitrogen.
9% Phosphorus Pentoxide (P_2O_5) (=4.0% P) soluble in neutral ammonium citrate and water;
9% Potassium Oxide (K2O) (=7.5% K) water soluble.
3.0% Magnesium Oxide (MgO) (=1.8%Mg)
0.02% Boron (B) water soluble;
0.047%Copper (Cu) 0.035% water soluble;
0.40% Iron (Fe) 0.20% chelated by EDTA;
0.06% Manganese (Mn);
0.020% Molybdenum (Mo) 0.016% water soluble;
0.015% Zinc (Zn) 0.010% water soluble.

Application Rates

	Light feeding	Normal feeding	Heavy feeding
Container nursery stock general	4-5Kg/m^3	5-6Kg/m^3	6-7Kg/m^3
Evergreens	4-5Kg/m^3	5-6Kg/m^3	6-7Kg/m^3
Fast growing conifers		5-6Kg/m^3	6-7Kg/m^3

These rates are based on unfertilized potting substrates or soil. Product can be mixed or dibbled.

Scotts UK Professional Paper Mill Lane, Bramford, Suffolk IP8 4BZ
Scotts International B.V., Nijverheidsweg 5, 6422 PD Heerlen.

University of Cape Town

Chapter 3: Frost as a limitation to *Acacia* tree survival in grasslands

Introduction

Trees can be prevented from growing in grassland areas both due to annual frosts as well as infrequent extreme frost events (Silberbauer-Gottsberger *et al.* 1977, Osmond *et al.* 1987, Fensham & Kirkpatrick 1992, Coop *et al.* 2007). Frost has long been considered a factor limiting trees in the grasslands of the Highveld area of South Africa (Acocks 1953). There appears to be only one study that involves frost in South Africa, and it involves the distribution of the succulent, *Cotyledon orbiculata* (van Coller & Stock 1994). A frost in southern Brazil led Silberbauer-Gottsberger *et al.* (1977) to conclude that the southern limit of the cerrado was likely to be limited by frost, as they found variable survival of different species depending on whether their natural distributions were in warmer or cooler areas. Fensham & Kirkpatrick (1992) concluded that the lack of trees below an inverse tree-line in Tasmania was primarily due to grass competition, but that frost played a role in limiting woody establishment at cooler sites. Coop *et al.* (2007), also working with an inverse tree-line, this time in New Mexico, USA, showed that frost resulted in poor seedling growth and subsequent low seedling survival of fire. They concluded that encroachment of woody species below the inverse tree-line was due to higher temperatures and less frequent fire (Coop *et al.* 2007).

University of Cape Town

Frost leads to loss of biomass by damaging cells, particularly the plasma membranes of cells, and can also affect the structure of a plant (Sakai & Larcher 1987). There are many different types of frost (Sakai & Larcher 1987). Those relevant to the Highveld grasslands include air frosts, where the temperature of the air falls below freezing, and radiation frost. Radiation frost is caused by the loss of long wave radiation to clear night skies (Curtis 1936, Shaw 1954, Swinbank 1963, Jordan & Smith 1995), which can result in plant surfaces being significantly cooler than the surrounding air (Curtis 1936, Shaw 1954). Radiation frost is more intense on long nights with low air humidity (Sakai & Larcher 1987).

Many plants have evolved to avoid or tolerate frost, or replace tissue lost due to frost damage (Sakai & Larcher 1987, Körner 2003). Avoidance includes thermal buffering by thick stems, nyctinastic leaf movements, and insulation, for example by thick bark (Sakai & Larcher 1987), as well as seasonal phenology of tissues sensitive to frost damage (Körner 2003). Plants can avoid freezing by supercooling, where particles that initiate ice formation are moved out of cells (Körner 2003). This prevents ice nucleation inside cells and tissue temperatures can drop well below freezing (Körner 2003). Plants can also tolerate freezing, by controlling ice nucleation, maintaining a fluid plasma membrane and preserving the molecular structure of biomembranes during freezing (Sakai & Larcher 1987, Körner 2003). Seedlings are more susceptible to the effects of frost as they are small with thin stems and do not have the thermal buffering that thicker-stemmed individuals do (Sakai & Larcher 1987). Temperatures are also more extreme closer to the ground (Sakai & Wardle 1978, Bannister 1984, Nobel 1984, Sakai & Larcher 1987, Bannister *et al.* 1995).

University of Cape Town

The aim of this chapter is to test the hypothesis proposed by Acocks (1953) that frost excludes trees from the Drakensberg mountains, and may also exclude woody biomass from the grasslands of the Highveld. To explore this idea, seedlings were planted across an altitudinal gradient from savannas into grasslands and the effects of frost on seedlings qualitatively scored for one particular frost and for a whole winter season.

Methods

Experimental setup, including species selection and site setup, was the same as in Chapter 2.

Measurements

Two methods of assessing damage by frost were recorded for all seedlings across all sites. Firstly, the frost damage of each plant was scored in June, three to four weeks after severe cold temperatures were experienced throughout the region on 22nd – 26th May 2007. In order of increasing damage, plants were scored as: "Whole plant green", "partly green", "partly brittle" or "whole plant brittle". Secondly, the degree of topkill was recorded in October 2007, after the end of the cold season and this reflects damage by frosts over the whole winter. Topkill often describes the death of above-ground plant biomass by fire (for example Hoffmann & Solbrig, (2003)), and here we use the term for death of above ground biomass due to frost. Complete topkill is used here to refer to death of the entire above-ground biomass. Different degrees of topkill may occur, from death of only branch apices, to whole branch death. Plants were scored as: "No topkill", "a few tips killed (*ca.* 25% of above-ground biomass)", "most branches killed (*ca.* 75% of above-ground biomass)" or "complete topkill (100% above-ground biomass)". Survival of individuals was recorded in October 2007.

University of Cape Town

Mapping frost effects

To assist in evaluating the influence of frost in limiting species distributions, the experimental results were used to establish temperature thresholds at which frost damage was observed. Using these temperature thresholds, maps of potential distribution ranges were created, based on isotherms of Schulze's (1997) average May minimum temperatures. Average May minimum temperatures were used as Schulze (1997) does not have a map of average winter temperatures. The average May minimum temperature where 90% of seedlings survived frost (10% mortality) was used as the lower threshold temperature. These experimentally determined potential distributions were compared with actual distributions derived from herbarium records for each species captured in the Precis database (Arnold & Steyn 2005) and the Acocks database (Rutherford *et al.* 2003). Since herbarium records do not have a complete coverage, the actual distribution data was also modelled using climate envelope models, and were developed by Danni Guo at the South African National Biodiversity Institute, SANBI (Guo *et al.* 2008). These climate envelopes created distributions based on probabilities of occurrence. Maps of current species distributions were assumed to be where probabilities of occurrence were greater than 0.3, and these are referred to as "actual distributions" for the purpose of this chapter. Actual distributions could only be modelled for *A. gerrardii* and *A. tortilis*, which had sufficient field data. The degree of overlap of actual distributions on potential distributions was calculated for a section of the distribution range in a broad fragment including the study sites (the study region: 29.448°E to 32.698°E and 26.352°S to 29.051°S), to give an estimate of how well experimentally derived estimates of minimum temperature tolerance predicted actual range limits of the species. The study focussed on the upper altitudinal limits of species where frost is most likely to be limiting. Species absences at low elevations are due to other factors. The analysis assumes that the experimental conditions under which frost response was recorded mimics conditions in natural grasslands.

Results

Sites

University of Cape Town

The sites experienced a range of temperatures and amounts of frost, with grassland sites cooler than savanna sites (Figures 3.1 and 3.2). Average daily minimum temperatures in winter, calculated for the winter months June, July and August, ranged from 1°C to 13°C (Ermelo and iMfolozi sites respectively; Figure 3.2). Measured minimum temperatures over the cold period of 21st – 24th May 2007, ranged from -8°C to 6°C (Ermelo and Malan sites respectively). Both of these measured temperatures for all sites correlated significantly with Schulze's (1997) May average daily minimum temperature (winter average minimum temperature: $r = 0.93$, $p < 0.001$; minimum temperature over 21st – 24th May 2007: $r = 0.90$, $p < 0.001$). Thus the Schulze (1997) average is a good approximation of the temperatures recorded over winter 2007. According to Agricultural Research Council long-term data, the minimum temperature at Ermelo fell to -8°C, or below, 16 times between 1950 and 2000, *ca.* every 3 years (Schulze & Maharaj 2003) (Appendix Figure 3.A).

Frost damage and survival

The frost score shows the response to one particularly severe frost at the start of the cold season, whereas the degree of topkill reveals response over the whole cold season. The number of survivors does not reveal anything about the state of those plants that did survive. For example, both *A. tortilis* and *A. gerrardii* had nine survivors (and one mortality, 10% of 10 individuals) at Athole, but the *A. gerrardii* that survived were completely topkilled, whereas there was very little topkill to *A. tortilis* (Figure 3.3).

Frost only impacted plants at the highest four sites, Ermelo, Wakkerstroom, Athole and Hlelo (Figure 3.3, Appendix Figures 3.B and 3.C). The amount of frost damage and topkill varied between species. At the coldest site, Ermelo, all species had been topkilled by the time sites were visited in June, except for *A. tortilis* and *A. karroo* (Bloem). Some individuals of these, *A. tortilis* and *A. karroo* (Bloem) at Ermelo, still had undamaged shoots in June but by October all species were completely topkilled. *Acacia gerrardii* and *A. sieberiana* were the most frost damaged at the next coldest sites (Wakkerstroom, Athole and Hlelo), followed by *A. karroo* (Hlu), *A. mearnsii* and then *A. tortilis*. *Acacia karroo* (Bloem) was hardly affected by frost at these sites.

At least one individual of each species survived at each site (Figure 3.3). Least survival occurred at the coldest site, Ermelo, where all species had very high mortality (70 – 90%), except *A. karroo* (Bloem), which had only 20% mortality. Survival increased rapidly with increasing temperature and all species showed at least 80% survival (20% mortality) at Hlelo, which has a mean minimum May temperature of 6°C. *Acacia mearnsii* showed 40-50% mortality at three of the warmest sites with deaths occurring over the whole experimental period.

University of Cape Town

Mapping frost effects

Locations of individuals from Precis (Arnold & Steyn 2005) and Acocks (Rutherford *et al.* 2003) data show that the climate envelope derived "actual" distributions are reasonable (Figure 3.4). The actual distributions overlapped the potential distributions by 54% for *A. tortilis*, and 48% for *A. gerrardii*. The frost potential distributions were far broader than the actual distributions. The potential distribution included areas cooler than the actual distribution.

Discussion

In this experiment, we compared temperatures of a frost directly to the effect of this frost on seedlings. We also saw the effect of a whole winter on seedlings, both in terms of the amount of above-ground biomass lost as well as survival. All the species showed at least some survival at all sites, which is surprising given their varied natural distributions (Coates Palgrave 2002). Species showed different amounts of survival and degrees to which they were topkilled. *Acacia gerrardii* was badly affected by frost and many individuals were topkilled at the colder sites. This may reflect a lack of characteristics such as nyctinastic leaf movements or thick insulating bark that limit its distribution and abundance in comparison to *A. karroo* (Hlu). *Acacia sieberiana* and *A. mearnsii* both naturally occur in cool regions, so it is surprising that they did not show better survival in frosted areas. Mortality, mainly of *A. mearnsii*, at warmer sites is not attributed to frost as there is little to no frost in those areas and individuals that died showed no evidence of frost damage; but it may indicate low tolerance to hot growing season temperatures. Freezing plants has a similar physiological effect to heat stress, as water freezes between cells and draws intracellular water out, causing desiccation (Körner 2003). As *A. tortilis* survives in hot areas, its relative cold tolerance may be because it is adapted to desiccation. The two varieties of *A. karroo* showed predictable results given their climatic distributions; the Hluhluwe variety, naturally occurring in warm areas, experienced more topkill and less survival than the Bloemfontein variety, indigenous to colder areas. *Acacia karroo* (Bloem) is evidently well adapted to cold, as it had only 20% mortality at the coldest site, Ermelo, relative to 70% or more for other species.

It is evident that, although frost decreased survival, it did not cause complete mortality of any species at any site. However, it is not known what effect grass may have on the thermal environment both above and below the ground, in the Highveld grasslands. In Australian savannas, temperatures and frost were more severe above grass than bare soil (Ball *et al.* 1997, Ball *et al.* 2002), although these studies did not take heat loss by long wave radiation into account. Seedling growth has been shown to increase within a grass sward (pine trees in C_3 grass) (Maher *et al.* 2005) and decrease above a grass sward (eucalypt trees in C_4 grass) (Ball *et al.* 1997, Ball *et al.*

University of Cape Town

2002). Thus, the relatively good survival in this experiment may not be seen in the presence of grass.

The effects of frost are less when plants are sheltered from an open night sky, for example cactus seedlings sheltered near rocks (Nobel 1984), and tree cover reduced the effects of frost in a Zimbabwean savanna (Childes 1989, Holdo 2006). It would therefore be more difficult for seedlings to establish in open grasslands without shelter of large trees. Seedlings would be relatively well sheltered from the effects of radiation frost while within the grass layer, but not when above the grass layer. Self-protection can also occur, as seen for at least one individual where all upper leaves and branches were killed and one sheltered lower branch remained green and growing (Appendix Figure 3.D).

Frost and fire can interact, as frost results in flammable dead biomass that is highly susceptible to burning. In the study area, after the May frost, severe fires occurred in June, likely due to the large amount of cured biomass, as well as high temperatures, low humidity, and very strong winds (pers. obs.). Severe fires were also recorded after frost events in the 1970s in Zimbabwean savannas (Childes 1989).

University of Cape Town

If frost does exclude trees from grassland areas in South Africa, it is likely to do so because it causes a loss of biomass, which renders a plant less likely to escape the "fire trap". Frost may therefore be an additional contributor to the "fire trap" theory (Bond & van Wilgen 1996, Higgins *et al.* 2000) in cold areas. Larger trees are less likely to be killed by frost, as thick stems cool down more slowly due to thermal buffering (Sakai & Larcher 1987). Temperatures and frosts are also less severe further from the ground, (Curtis 1936, Shaw 1954, Swinbank 1963, Jordan & Smith 1995) particularly above a grass sward (Ball *et al.* 1997, Ball *et al.* 2002), and plant structures are more hardy in older plants and parts of plants rather than seedlings and shoot apices (Nobel 1984, Bannister *et al.* 1995). Seedlings may be caught in the cold temperatures, close to the ground and experience annual loss of above-ground biomass due to frost. Seedlings would then struggle to get tall enough to escape the effects of frost and fire.

The temperatures experienced over the experimental period were not a rare event as temperatures similar to the cold period in May occur approximately every 3 years in the study region. Infrequent severe frosts may exclude trees from grasslands (Osmond *et al.* 1987, Fensham & Kirkpatrick 1992), or create inverse tree-lines by killing trees (Paton 1988), and large infrequent disturbances such as drought, lead to reduced tree biomass in savannas (Fensham *et al.* 2005, Gillson 2006). It is possible that infrequent extreme frost events exclude trees from the grasslands of the Highveld, and longer temperature records would be needed to establish how cold the grasslands can get.

The potential distributions based on frost effects observed in this experiment do not fit the "actual distributions" for either *A.tortilis* or *A. gerrardii*, particularly in the region of the study sites. Thus, frost is not the factor defining the upper altitudinal limit of the species distribution. Rather there are other factors acting, possibly in combination with frost, which limit the natural distribution range. The lower altitudinal limit of the distribution cannot be due to frost as no frost occurs in this area.

University of Cape Town

Conclusion

Mortality was rare at all but the coldest site, Ermelo. If frost limits species distributions, it would do so primarily by causing topkill which would slow or prevent seedlings from growing into taller size classes. Species varied in their response to frost and/or cold temperatures, but survival was in general good, given that areas were high above the limit of their natural distributions. The experiment was conducted in the absence of grass, which is likely to have a negative effect on seedling survival. However, from these results, frost does not account for the upper altitudinal limit of the species distribution.

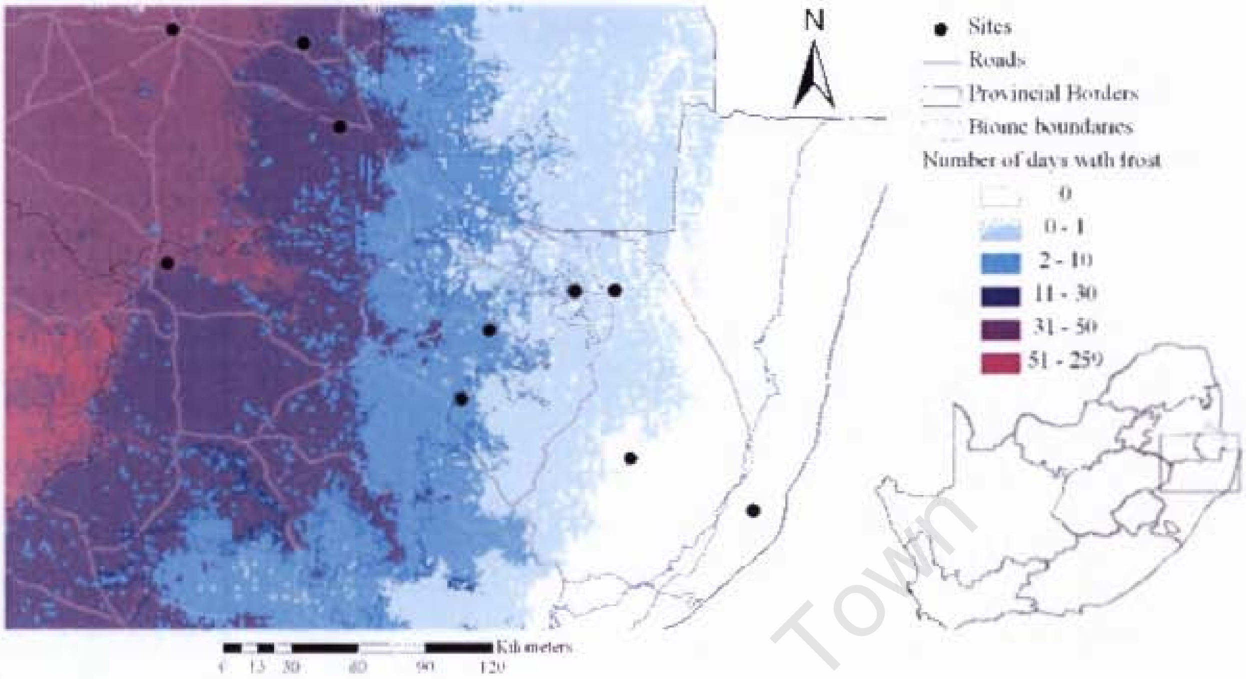


Figure 3.1: A map showing the average number of days with frost in the study region in South Africa (adapted from Schulze (1997)). Study sites are shown as black dots. Biomes include: grasslands, in the western half of the map; savannas in the central region; and the Indian Ocean coastal belt on the eastern coastline (Mucina & Rutherford 2006). Also see Figure 1.1 for a map of the biomes.

University of Cape Town

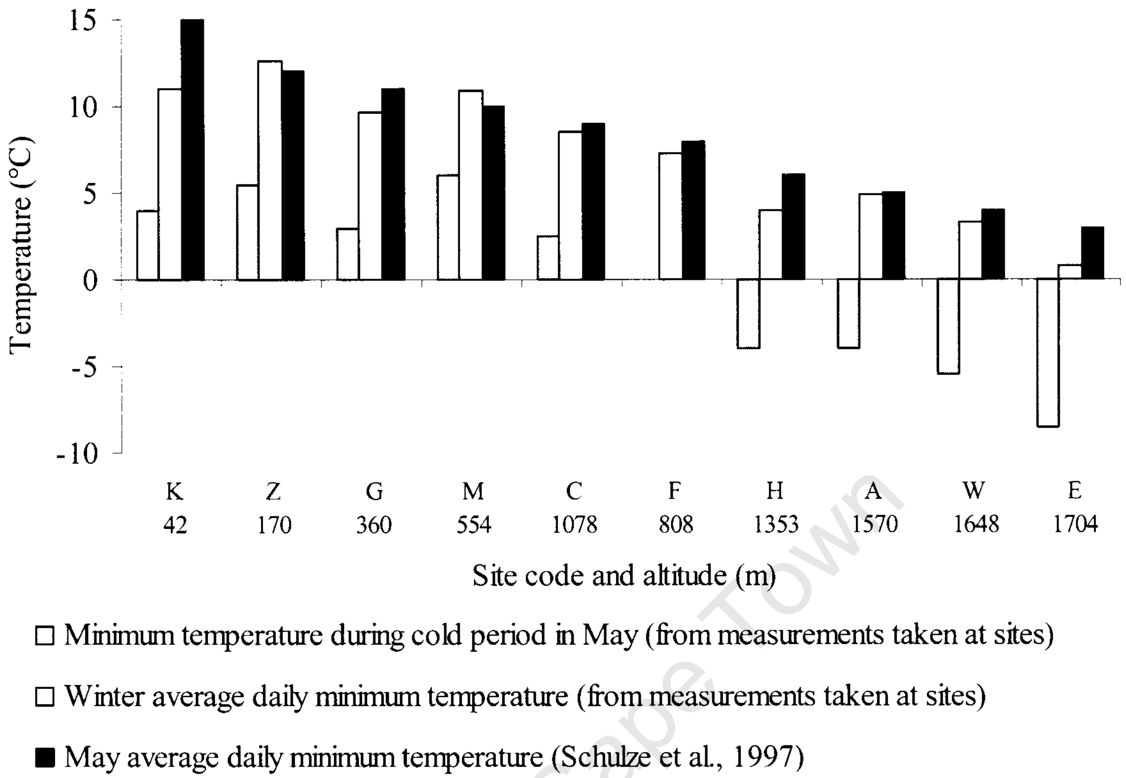
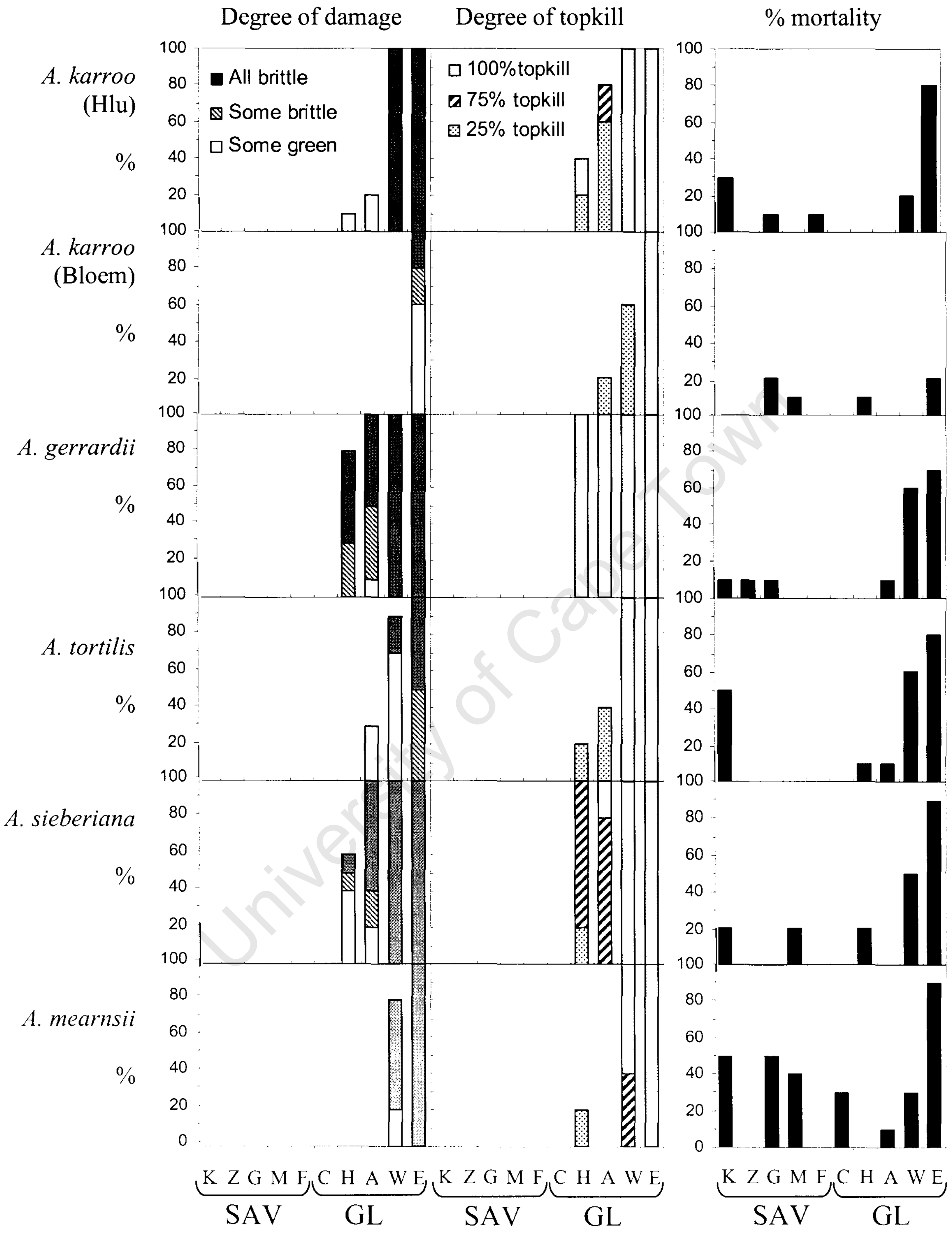


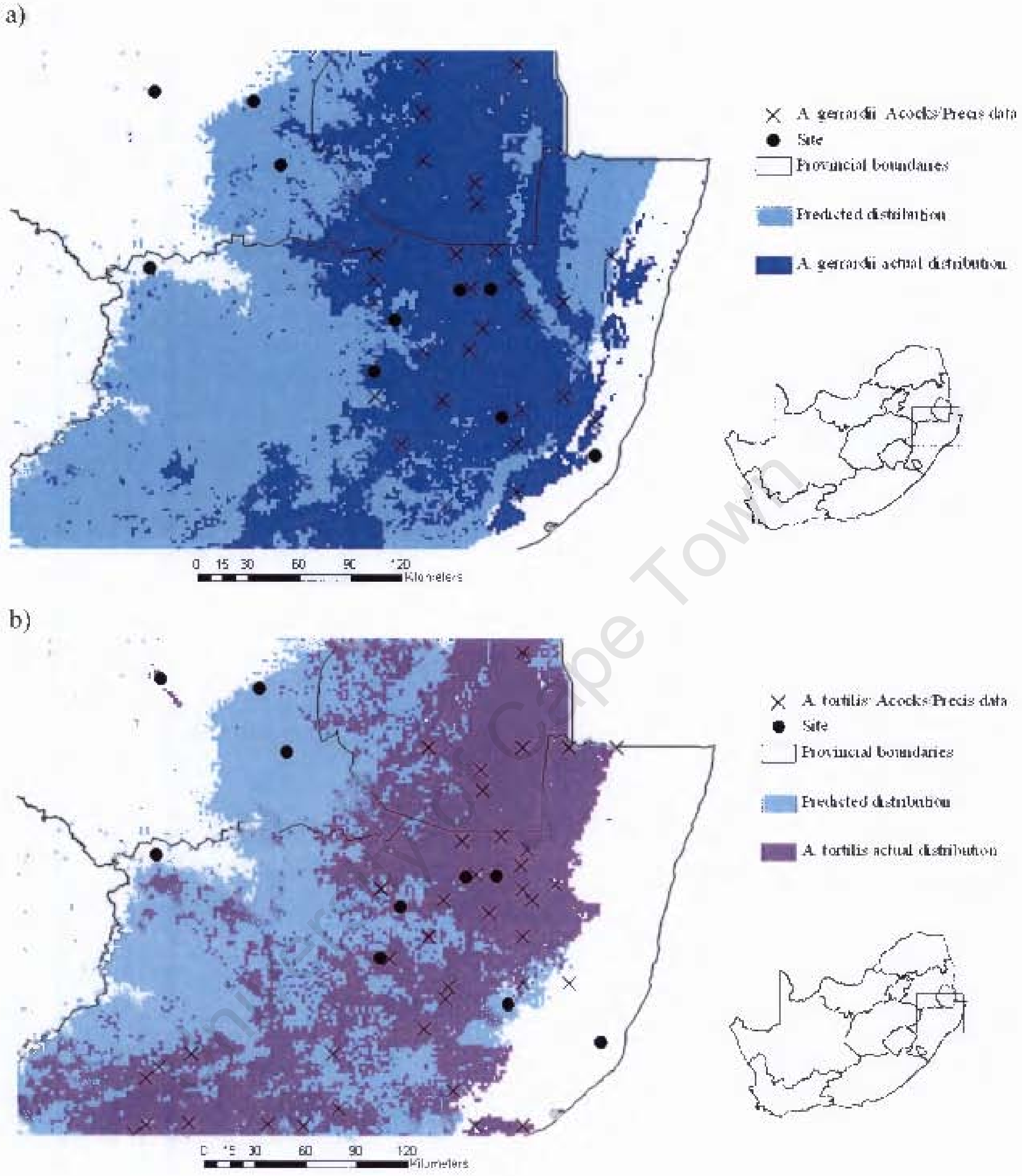
Figure 3.2: Minimum temperatures recorded at each site during the cold period between 22 and 26 May 2007; winter average daily temperatures per site, calculated from recorded data; and May average daily minimum temperatures extracted from Schulze (1997). Site altitudes are shown with site codes (K = Kirkwood, Z = iMfolozi, G = Goss, M = Malan, C = Comins, F = Ford, H = Hlelo, A = Athole, W = Wakkerstroom, E = Ermelo).

University of Cape Town



University of Cape Town

Figure 3.3: Frost effects on seedlings of six *Acacia* species along a gradient of decreasing May minimum temperatures. The degree of frost damage in June after a severe frost, and the degree of topkill after winter in October, for each species at each site. Percentage mortality per species per site were recorded in October. There were 10 individuals per species per site. For site codes, see Figure 3.2. SAV = savanna sites; GL = grassland sites.



University of Cape Town

Figure 3.4: Actual and potential distributions of a) *A. gerrardii* and b) *A. tortilis* for a section of South Africa. Actual distributions were calculated with bioclimatic envelope models using Acocks and PRECIS data, which are also shown (Guo *et al.* 2008). The upper altitudinal limit of predicted distributions is a reclassification of Schulze's (1997) average May minimum temperature map where the number of survivors is 90% or more. The lower limit is not predicted by frost and is cut off at 12°C for *A. tortilis* and 13°C for *A. gerrardii*.

Appendix

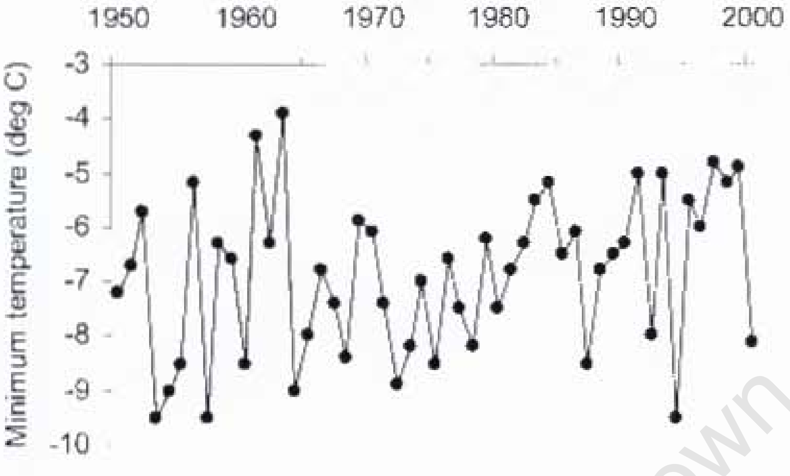


Figure 3.A: Absolute minimum annual temperatures for the Nooitgedacht Agricultural Research Council station near Ermelo between 1950 and 2000 (data from Schulze & Maharaj (2003)).

University of Cape Town

Figure 3.B: The Athole site in June 2007 showing death of some species, and survival of others, particularly *Acacia mearnsii* in the background.

a)

b)

Figure 3.C: The a) Ermelo and b) Wakkerstroom sites in June 2007 shortly after the frost in May 2007. Note the death of almost all above ground biomass in the plot, and large green trees (exotic trees at Ermelo and indigenous trees at Wakkerstroom) in the background of both photographs.

Figure 3.D: An *Acacia sieberiana* individual at the Athole site showing death of upper branches and survival of a lower branch. The survival of the lower branch is likely due to sheltering by the upper branches from loss of longwave radiation to the night sky.

University of Cape Town

mesic grassland areas (King 1978). Arid grasslands do occur at the western end of the grassland biome and are more nutrient rich than the mesic grasslands (Ellery *et al.* 1995). The focus of this study was the mesic Highveld grasslands, in particular in the region of northern KwaZulu Natal, eastern Freestate and southern Mpumalanga (Figure 1.1). In this region, it is expected that, given the age and humid history of the grassland landscapes, the soils would have become leached over time resulting in lower nutrient availability (King 1978). As nutrients are required for plant growth (Marschner 1995, Lambers *et al.* 1998), leaching of nutrients in high rainfall areas or on ancient land surfaces might result in slower growth. Additional effects along the altitudinal gradient include temperature, which influences the rate of mineralisation (Lewis 1986, Miller & Cramer 2004), which may further constrain nutrient availability in the higher altitude, cooler grasslands.

This chapter explores the idea that seedling growth on the leached soils of the Highveld grasslands is reduced due to low nutrients. Slower growth would result in juvenile trees taking too long to escape the frequent fires to become adults. To investigate nutrient effects on growth, seedlings were grown in a common garden experiment to test the effects of savanna and grassland soils on seedling growth.

University of Cape Town

Methods

Plant cultivation

Soils were collected from 10 undisturbed areas, distributed across an altitudinal gradient from lowland savannas into upland grasslands. Soils were collected from within 30 cm of the soil surface in March 2007, and from within 500m of the transplant experiment sites described in Chapter 2.

Fire tolerant savanna species were used as both savannas and grasslands have a grass layer that burns and fire can be frequent in both. Members of the *Acacia* genus were used for this experiment, as they are widespread in southern African savannas and include high and low altitude species that may respond differently to different soil types. *Acacia karroo* ("Hluhluwe variety") occurs in eastern KwaZulu Natal, including the Hluhluwe-iMfolozi Game Reserve (after research by Swartz (1982), Coates Palgrave (2002) called this variety *A. natalitia*). *Acacia sieberiana* has a broader distribution generally in higher altitude areas (Coates Palgrave 2002). Thus, *A. karroo* would be associated with moderate to high fertility soils at lower to mid elevations and *A. sieberiana* with low nutrient soils in high elevation savannas adjacent to the grassland biome.

Sets of six to nine seedlings of *A. sieberiana* (*ca.* 6 months old and *ca.* 18cm tall), and *A. karroo* (Hluhluwe subspecies; *ca.* 1yr old and *ca.* 30-40cm tall) were planted in soil from each of the ten sites. Each seedling was planted in a 10 *l* bag (Appendix Figure 4.A). The experiment took place in an area protected from fire and herbivore disturbance, in the Hluhluwe-iMfolozi Game Reserve. Plants were watered daily or as necessary, depending on rainfall. Plant bags were randomly shuffled monthly to control for variation in localised environmental factors.

University of Cape Town

Air temperatures at *ca.* 130cm were recorded with DS1921G Thermochron® iButton® data loggers. Plant height, total stem length and stem diameter at approximately one centimetre above the soil, were measured monthly from the initiation of the experiment in late October 2007 to late April 2008. Seedlings were harvested on the 30 April and 1 May 2008. Leaf samples were taken for mass-spectrometer analysis. Leaves, stems, roots and nodules were separated, dried to constant weight and weighed.

Soil Analysis

The soil was dried at 70°C for 48 h and sieved (1 mm mesh). Soil pH was determined by shaking 2 g soil in 20 mL 1 M KCl at 180 r.p.m. for 60 min, centrifuging at 10000g_0 for 10 min and measuring the supernatant pH. Total soil nitrogen was determined by digestion with a FP-528 Nitrogen Analyser (Leco Corporation, St Joseph, USA). Soil was prepared for Bray II P analysis by extracting 6.6 g soil in Bray II solution (Bray & Kurtz 1945) before filtering and analysing using ICP-AES (Varian Vista MPX, Melbourne, Australia). To measure the quantity of Total P, soil was digested in an Agua regia solution (2 parts HCl to 1 part HNO_3) in a sand bath for two hours, filtered through Whatman no.1 filter paper and the filtrate analysed against

ICP-AES standards (Varian Vista MPX, Melbourne, Australia). Exchangeable cations were displaced from 10 g soil with 25 mL of 0.2 M ammonium acetate. The samples were filtered through Whatman no. 2, made up to 200 mL and K, Na, Ca and Mg measured using ICP-AES analysis.

Mass Spectrometer Analysis

The oven-dried leaves were milled in a Wiley mill using a 0.5 mm mesh and 2.1-2.2 mg of the leaf sample weighed into a tin capsule (Elemental Microanalysis Ltd, Okehampton, UK). Dried soil samples were sieved (0.5 mm mesh) and *ca.* 40 mg weighed into a tin capsule. The samples were combusted in a Thermo Flash EA 1112 series elemental analyser and the gasses fed into a Delta Plus XP isotope ratio mass spectrometer (Thermo Electron Corporation, Milan, Italy). Two in-house, and one IAEA, standards were used to calibrate the results. The carbon isotopic ratio of a sample was expressed as $\delta^{13}C$ (Ehleringer & Rundel 1989) and the nitrogen isotopic ratios as $\delta^{15}N$ (Evans 2001). Tissue total C and N were expressed as a percentage of dry weight. $\Delta^{15}N$ was calculated as $\delta^{15}N_{soil}$ - $\delta^{15}N_{plant}$ (Robinson 2001) to account for variations in $\delta^{15}N_{soil}$.

University of Cape Town

Data analysis

Sites were classified into grassland and savanna biomes according to Mucina & Rutherford (2006). Final average plant biomass and relative stem elongation were used as the response variables to nutrient availability. As initial plant size, measured as total stem length, differed between treatments, relative stem elongation was also calculated. Measures of relative growth account for variation in starting size and are calculated as the change in the growth variable per day (Hunt 1982, Hoffmann & Poorter 2002). The natural logarithms of total stem length were plotted against time in days, and the slope was taken as relative stem elongation. This was done for growth within the first 122 days of the experiment when growth was exponential, a requirement for the use of relative growth calculations (Hunt 1982). Correlation coefficients were used to describe relationships between growth, altitude and nutrient availability, both as individual nutrients and summarised in a principal components score. Principal components analysis (PCA) using a correlation matrix was performed to group correlated soils attributes, a method that has been proven useful (Brejda *et al.* 2000, Cox *et al.* 2003, Tchienkoua *et al.* 2008).

Results

Soil properties

Soils from grassland sites, all at higher altitudes than the savanna sites, had a lower availability of nutrients. Both pH and T-values were lower in grasslands (Figure 4.1; soil nutrient analyses: Appendix Table 4.A) and were the soil attributes most tightly correlated with altitude. T-value is a measure of the availability of Na, Mg, K and Ca exchangeable cations, combined with H^+ ions. A lower T-value means there are fewer available cations. Other nutrients also varied with altitude and correlations rather than individual graphs are shown (Table 4.1). Total P and Bray II P showed no correlation with altitude. Soil from the lowest altitude site was not included in correlations. This soil is derived from Quaternary sands and is highly leached compared to the geographically close, yet compositionally very different, clayey savanna soils derived from Karoo sediments and doleritic intrusions. There were higher C:N ratios in soils collected from grassland areas (Figure 4.2). Soil $\delta^{13}C$ increased with the altitude from where soils were collected (Figure 4.2; including coastal dune site: $r = 0.75$, $p < 0.05$; excluding coastal dune site: $r = 0.65$, $p > 0.05$).

The results of a principal components analysis are shown in Table 4.2. The first three components explain 86.9% of the variation. Principal component 1 (PC1) accounts for 59.1% of the variation and is interpreted as a leaching gradient from high to low T-values (and associated cations), Mn, total N, pH, total P and B, correlated broadly with altitude (Figure 4.3). PC2 and PC3 are not correlated with altitude and are represented by few nutrients that show little correlation with plant growth in this experiment, such as Bray II P, total C, Zn (PC2), Cu and Na (PC3).

University of Cape Town

Chapter 4: Are the Highveld grasslands tree-less because of nutrient limited growth?

Introduction

The Highveld grasslands are tree-less, yet contain forest patches (O'Connor & Bredenkamp 1997) as well as exotic plantations (Fairbanks *et al.* 2000, O'Connor *et al.* 2003). Dynamic Global Vegetation Models have predicted that if fire was excluded, the climate of the grasslands has the potential to support forests (Bond *et al.* 2003). Given that both the grasslands and savannas are dominated by C_4 grasses and burn regularly (Acocks 1953), it is puzzling that fire-tolerant savanna trees do not grow in the Highveld grasslands. One possibility involves slow tree growth due to nutrient poor soils.

University of Cape Town

The parent material from which soils are derived primarily determines nutrient content in the soil (Vitousek *et al.* 1997). Secondary determinants are climate, vegetation, topography and the age of the soil, mainly through weathering and leaching (Lambers *et al.* 1998). Nutrient availability changes as soils develop and soil properties of old soils on deeply weathered substrates are partially divorced from their parent material. Nutrient availability is generally low in young soils, increasing in middle aged soils, as primary minerals are weathered. As soils age further, nutrients are lost through leaching (Vitousek *et al.* 1997).

The grasslands of South Africa occur on a range of surfaces from the ancient peneplains of the African surface, to recently dissected areas (King 1978, Partridge 1997). The African surface is stable and has undergone gentle lowering rather than large scale dissecting erosion and where it remains is highly leached (King 1978). Savannas occur to a large extent on Post African I surface that is more recent than the African surface (King 1978, Partridge 1997). Both grasslands and savannas occur on recently dissected surfaces. In South Africa, savanna regions have a more arid history which may result in soils that are relatively nutrient rich in comparison to soils in

Acacia seedling growth

Initial total stem lengths of *A. karroo* differed significantly between plants in different soils (K-W: $H_{9,N=74} = 22.0$, $p < 0.01$), whereas those of *A. sieberiana* did not show significant differences ($F_{9,72} = 0.71$, $p > 0.1$) (data not shown). Plant growth, measured as relative stem elongation, varied between soils from the ten sites (*A. karroo*: $F_{9,64} = 9.16$, $p < 0.01$; *A. sieberiana*: $F_{9,71} = 3.58$, $p < 0.01$). Relative stem elongation decreased with an increase in PC1 (the leaching index) (Figure 4.4a; *A. karroo* (not significantly): $r = -0.54$, $p > 0.1$; *A. sieberiana*: $r = -0.76$, $p < 0.05$). Relative stem elongation and final biomass were negatively correlated with the altitude at which soils were collected, for both species, although less significantly for *A. karroo* (*A. karroo*: relative stem elongation: $r = -0.33$, $p > 0.1$, and biomass: $r = -0.60$, $p < 0.1$. *Acacia sieberiana*: relative stem elongation: $r = -0.87$, $p < 0.01$, and biomass: $r = -0.87$, $p < 0.01$; Figure 4.4b and c). In other words, slowest growth occurred in soils with lowest cation content, which were generally from higher altitude grassland sites.

Analysing growth with individual soil nutrients, relative stem elongation and final biomass of *A. sieberiana* were most strongly correlated with pH & K, followed by Mn, Ca, Zn, B, T-value, Mg and Total P (Table 4.3). Relative stem elongation of *A. karroo* was only correlated with Total P; however final biomass of *A. karroo* was significantly correlated with B, T-value, Mg, Mn, N%, C%, Ca, pH, Total P, K and PC1 (Table 4.3). Growth was not correlated with Bray II P and not robustly correlated with total N for both species.

Plants grown in soils with higher leaching indices had lower shoot: root ratios, meaning they produced relatively more root per shoot mass where nutrients were limiting (Figure 4.5; *A. karroo*: $r = -0.70$, $p < 0.05$; and not significantly for *A. sieberiana*: $r = -0.51$, $p > 0.1$). Shoot: root ratios also varied with altitude, although not highly significantly (*A. karroo*: $r = -0.60$, $p < 0.1$; *A. sieberiana*: $r = -0.60$, $p < 0.1$) (data not shown).

When soils were classified into biomes (excluding the soil from the Indian Ocean coastal belt), *A. karroo* seedlings in grassland soils had *ca.* 17% slower stem

University of Cape Town

elongation rates and a third less biomass than those in savanna soils. *Acacia sieberiana* seedlings in grassland soils had *ca.* 25% slower elongation rates and a quarter less biomass than those in savanna soils.

Nitrogen fixation

Nodules were produced by both species in all soil types (data not shown). There were no correlations between $\delta^{15}N$ or $\Delta^{15}N$ with N concentrations in leaves or soils, for either species. $\Delta^{15}N$ was significantly positively correlated with certain soil nutrients (Table 4.4). $\Delta^{15}N$ was significantly positively correlated with nodule dry weight for *A. sieberiana* ($r = 0.55$, $p < 0.001$) and less significantly for *A. karroo* ($r = 0.22$, $p < 0.1$).

University of Cape Town

Discussion

This study set out to test the idea that soils are more nutrient-poor in Highveld grasslands than in savannas; that nutritional differences significantly influence sapling growth; and that the growth rates of seedlings in grassland soils were so much slower that saplings would fail to escape frequent fires and grow into trees, whereas for similar fire frequencies, saplings on savanna soils would escape with a high probability.

The PCA summarised patterns of variation in soil attributes across the 10 soils. The primary axis of variation (PC1) comprised the major cations (T-value), pH and total P. It was correlated with altitude and represented a leaching gradient, from nutrient-poor upland grasslands to nutrient-rich lowland savannas. This is with the exception of the lowland dune sandy soil, which was nutrient-poor. The upland soils are nutrient-poor because the soils are old and highly leached. The low altitude nutrient-poor sandy soil is of relatively recent origin, but its low nutrient status is also due to high rainfall and much leaching. It is interesting that this poor soil does support a woody biomass. The upland sites are all from "sourveld" areas (Acocks 1953, Mucina & Rutherford 2006). The "sweetveld" part of the grassland biome was not sampled, but is higher in nutrients than the sourveld, and yet still supports grassland (Ellery *et al.* 1995).

Soil nutrient availability was a significant determinant of *Acacia* species growth, as seedling growth rates were slower in low nutrient soils. Growth rates (measured as relative stem elongation) of *A. sieberiana* showed strong correlations with numerous soil nutrients, whereas those of *A. karroo* only showed significant correlations with Total P. This may be because the older *A. karroo* seedlings were too large to move between soils at the start of the experiment. *Acacia sieberiana* seedlings were planted as plugs directly from seedling trays, so roots would have experienced very little damage. Unfortunately, plant sizes differed among soil treatments for *A. karroo*, positively influencing treatment differences in final biomass, which is why relative stem elongation rates were also used for comparing treatment effects. When relative stem elongation and final biomass of *A. sieberiana* were analysed, they showed significant correlations with the same soil nutrients. For *A. karroo* final biomass, there were significant correlations with variables similar to those correlated with *A. sieberiana* growth. The nutrients that affected both species were the ones most influencing *Acacia* seedling growth, namely pH, Total P, Mn, B and T-value including K, Ca and Mg cations. Where soils were nutrient poor, plants produced relatively more root mass in relation to shoot mass, indicating that they allocated more resources to nutrient acquisition, as commonly observed in other studies (for example Barger *et al.* (2002)).

University of Cape Town

N and P are often used as indicators of soil fertility, as they frequently limit plant growth (Marschner 1995). N was not well correlated to plant growth, which is not surprising as *Acacia* species fix N, and plant available N is difficult to measure. Plant growth was correlated to Total P, but not Bray II P. Bray II P is an agriculturally derived measure of the amount of P available to crops, and evidently does not show the available P for these *Acacia* species. Mn, Zn, B, T-value and associated cations, and pH were much more robust predictors of plant growth. pH was correlated to all of these nutrients, which is understandable as pH influences soil nutrient availability. In low pH soils there is a high concentration of hydrogen ions, which increases the rate of weathering and hence nutrient input but also the loss of cations by leaching (Lambers *et al.* 1998). pH may thus be a better indicator of soil fertility for *Acacia* species, than the typical N or P. It would be useful to know if grass growth would respond to pH in a similar way to how seedling growth responded, or whether their growth is more strongly correlated with N or P.

Plant $\delta^{15}N$ is affected by many factors, including many instances of N isotope fractionation; $\delta^{15}N$ of the soil; the amount obtained from the atmosphere via N-fixing bacteria; N gains and losses and N pooling (Robinson, 2001). Variations in $\delta^{15}N_{leaf}$ and $\Delta^{15}N$ (which is a measure of $\delta^{15}N_{leaf}$ that accounts for $\delta^{15}N_{soil}$) were not associated with changes in concentration of N in the soil or leaf. One explanation for the higher $\Delta^{15}N$ values is due to N_2 fixation by symbiotic bacteria. $\Delta^{15}N$ values were higher where nodule weights were greater. This makes sense, as more fixation would be expected where more nodulation occurred, as seen in Cramer *et al.* (2007). Higher $\Delta^{15}N$ values in more fertile soils would imply that more fixation occurred where there was more growth. There was no grass in this experiment, but nodulation and fixation still occurred. Cramer *et al.* (2007) showed that for *Acacia* species grown in the presence of grass, acquisition of N from N-fixing bacteria was greater than when they were grown without grass.

The variation in C: N ratios and $\delta^{13}C$ values could be due to many factors including past changes in vegetation, land use practices, as well as variation in decomposition rates (Wedin *et al.* 1995, Garten *et al.* 2000, Wynn *et al.* 2005). During soil organic matter (SOM) breakdown, and subsequent N mineralisation, soil microbes discriminate against ^{13}C during CO_2 respiration of the SOM, resulting in ^{13}C enriched soils (Blair *et al.* 1985, Wynn *et al.* 2005). The greater $\delta^{13}C$ values at higher altitudes found in this study may then provide support for the hypothesis proposed by Mills *et al.* (2006), that faster mineralisation in grassland soils could lead to greater grass competition.

Grass has many effects on seedling and sapling growth, both direct and indirect, including competition for resources such as light, nutrients, space and water (Walter 1971, Walker & Noy-Meir 1982, O'Connor 1995, Scholes & Archer 1997), effects on the thermal environment (Ball *et al.* 2002), the production of fuel for fires (Trollope 1982, d'Antonio & Vitousek 1992) and food for herbivores. Cramer *et al.* (2007) found that although nutrients influenced plant growth, it was competition with grass

University of Cape Town

for nutrients that had a greater impact on seedling growth. It would be intriguing to explore how the grass sward differs between grasslands and savannas, and if these differences are great enough to explain the absence of trees in grasslands.

Results of this experiment support the hypothesis as nutrient availability had a significant influence on tree growth rates. Grassland soils were indeed more leached than savanna soils, and therefore growth in these nutrient-poor soils was slower. The difficulty with this, and other soil hypotheses, is the assumption of homogeneous soil properties in grasslands and savannas. Not all grassland soils are nutrient-poor and not all savanna sites are nutrient-rich (Blackmore *et al.* 1990, Scholes 1990, Ellery *et al.* 1995, Sankaran *et al.* 2005, Mucina & Rutherford 2006). This is highlighted by the nutrient poor coastal belt savanna soils. Growth in the nutrient poor coastal belt soil was slow in this experiment, and in contrast, exceptionally fast growth was seen in the coastal belt region in Chapter 2. The fast growth at this site in the transplant experiment (Chapter 2) may not have been due to nutrients, but high humidity and temperature, as well as the physical ease of growing roots in such loose sand (Bengough 2003). There is also much variation in the soils of the Highveld and yet all are treeless (Ellery *et al.* 1995).

University of Cape Town

Conclusion

The high altitude soils were generally more leached than lower elevation savanna soils and these nutrient differences translated to greater growth in savanna than grassland soils. Whether the "effect size" of the nutrient determined differences in growth rates is large enough to account for failure of saplings to grow into adults in frequently burnt grasslands is discussed in Chapter 5. Soils vary greatly in nutritional states both at low (savanna) and high (grassland) elevations. This is clearly demonstrated by the presence of low nutrient savanna soils on the coastal dune sands in which seedlings of *Acacia* species grew poorly in this study. Ironically, the same soils supported very high growth rates in the seedling transplant experiment. It is interesting to note that there are no consistent differences in tree cover in African savannas linked to nutrients. Indeed, Sankaran *et al.* (2005) found higher tree cover on nutrient poor soils than on nutrient-rich soils in an Africa-wide survey.

Nevertheless, this study does indicate that tree growth does respond to a leaching gradient, and quantifies the magnitude of that response from nutrient-rich to nutrient-poor sites.

University of Cape Town

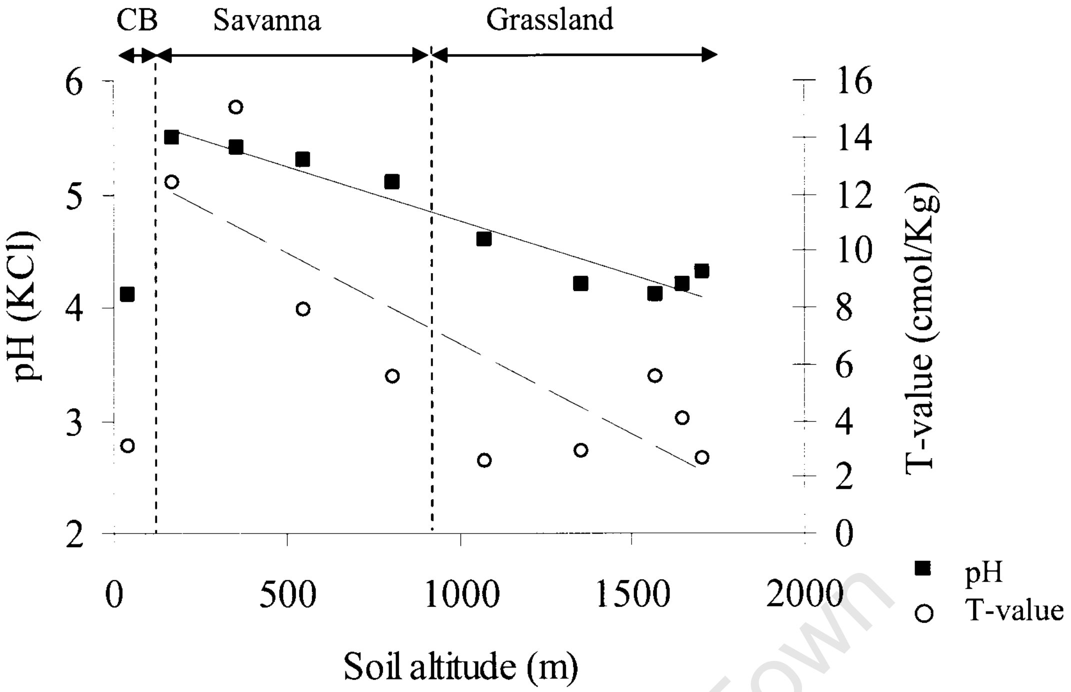


Figure 4.1: Variation of pH ($r = -0.96$, $p < 0.01$) and T-value ($r = -0.83$, $p < 0.05$) with the altitude from where soils were collected. The lowest elevation site was excluded from this correlation analysis. Sites classified into biomes according to Mucina & Rutherford (2006). CB = Indian Ocean Coastal Belt on aeolian sands.

University of Cape Town

Table 4.1: Correlations between soil nutrients and the altitude from which the soil was collected, described by Pearson correlation coefficients and significance levels (*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$). The T-value is a measure of availability of exchangeable cations, K, Mg, Ca and Na, as well as H^+ ions which are not shown. The lowest altitude (coastal belt) site is excluded as a consistent outlier.

	Nutrient		r	
	pH	(KCl)	-0.97	***
	T-value	(cmol/Kg)	-0.83	**
T-value	Mg	(cmol(+)/Kg)	-0.88	**
	K	(cmol(+)/Kg)	-0.67	*
	Ca	(cmol(+)/Kg)	-0.86	**
	Na	(cmol(+)/Kg)	-0.76	*
	C:N ratio		0.72	*
	Mn	(mg/Kg)	-0.65	
	B	(mg/Kg)	-0.60	
	N %		-0.48	
	Cu	(mg/Kg)	0.45	
	Zn	(mg/Kg)	-0.43	
	C %		-0.33	
	Total P	(mg/Kg)	-0.32	
	Bray II P	(mg/Kg)	-0.10	

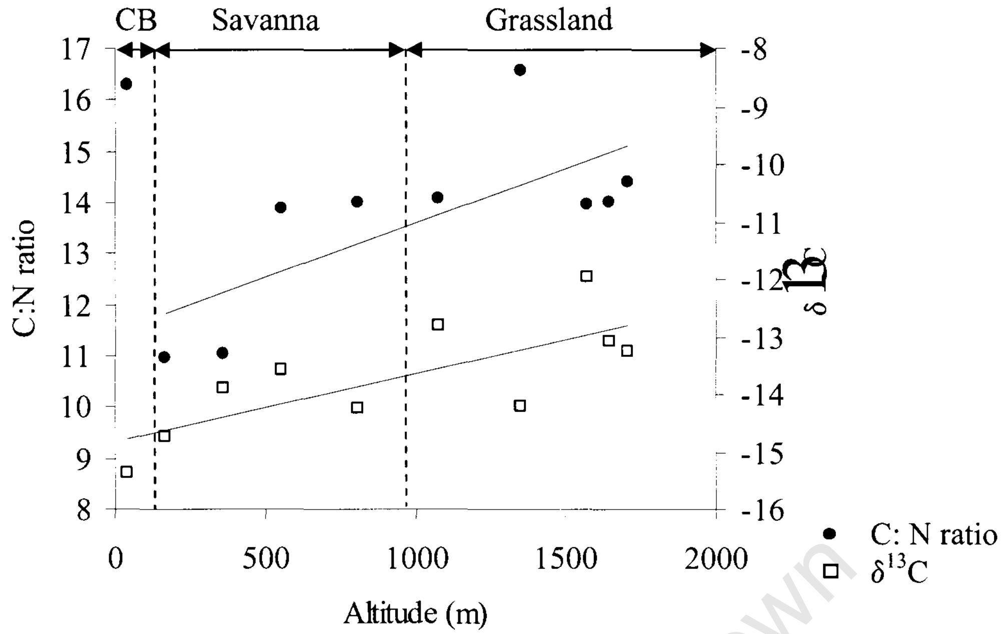


Figure 4.2: The C: N ratios (solid circles, r = 0.72, $p < 0.05$) and $\delta^{13}C$ values (empty squares, r = 0.75, $p < 0.05$) for soils from different altitudes. The lowest altitude (CB) site was excluded from the C:N ratio correlation with altitude. CB = coastal belt sandy soils.

Table 4.2: Results of a principal component analysis (PCA) of soil variables showing factor loadings on the first three components as well as Eigenvalues and the percentage variance explained by these components. Site principal component scores were correlated with altitude and the Pearson correlation coefficients with significance levels (** $p < 0.05$) are shown for each principal component. Factor loadings greater than |0.75| are shown in bold.

	Nutrient		Factor 1	Factor 2	Factor 3
	pH	(KCl)	**-0.84**	0.16	0.33
	Total P	(mg/Kg)	**-0.79**	0.04	-0.46
	Bray II P	(mg/Kg)	-0.42	**0.80**	-0.31
	T-value	(cmol/Kg)	**-0.97**	-0.05	0.19
T-value	Na	(cmol(+)/Kg)	-0.57	-0.26	0.69
	K	(cmol(+)/Kg)	**-0.90**	0.26	-0.09
	Ca	(cmol(+)/Kg)	**-0.90**	0.02	0.39
	Mg	(cmol(+)/Kg)	**-0.95**	0.07	0.11
	Cu	(mg/Kg)	0.01	-0.43	**-0.72**
	Zn	(mg/Kg)	-0.65	0.53	-0.24
	Mn	(mg/Kg)	**-0.92**	0.16	-0.22
	B	(mg/Kg)	**-0.77**	-0.50	-0.02
	N (%)		**-0.84**	-0.43	-0.17
	C (%)		-0.66	-0.54	-0.33
	Eigen value		8.28	2.03	1.86
	% variance explained		59.12	14.48	13.28
	Correlation with altitude				
	r		0.80**	-0.05	-0.60

University of Cape Town

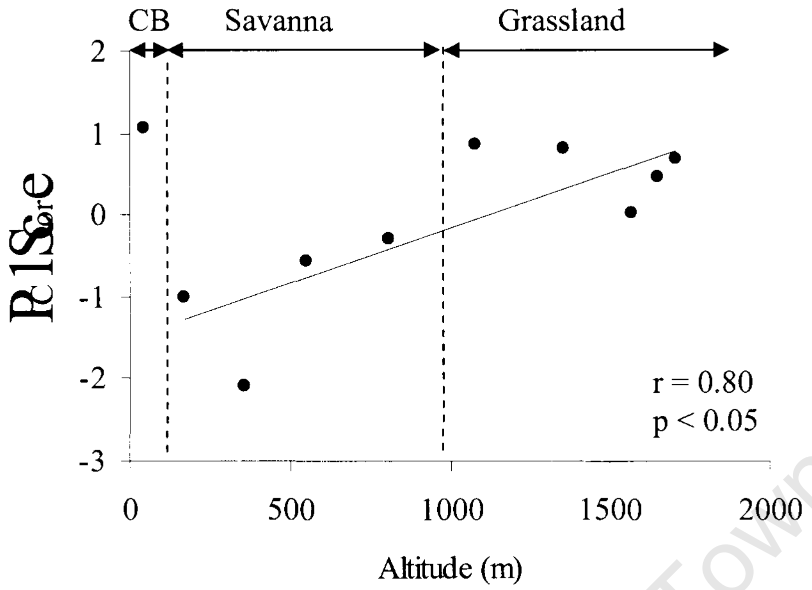
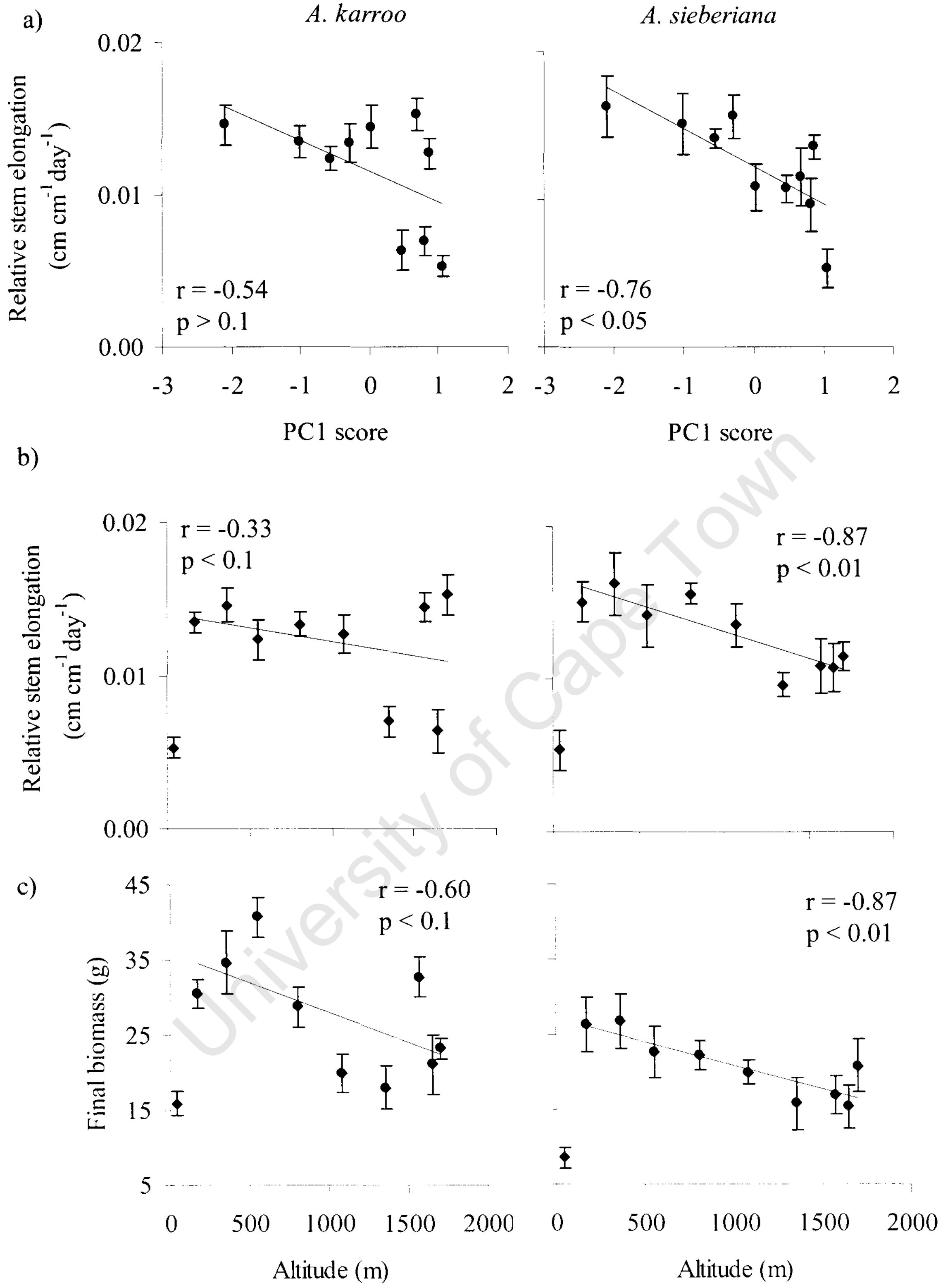


Figure 4.3: Relationship between site scores for PC1 and the altitude from which soils were collected. The lowest elevation site was excluded from the correlation analysis. The scores of sites were calculated according to PC1, a possible leaching index (also see Table 4.2).

University of Cape Town



University of Cape Town

Figure 4.4: The relationship between relative stem elongation and a) PC1, b) altitude, and c) the relationship of final plant biomass with altitude. Relative stem elongation was calculated for acacia seedlings grown in soils of varying nutrients. A principal component analysis was performed on the soil nutrient data, and PC1 was found to represent the major nutrients, be correlated with altitude and thus be a possible leaching index. Altitude refers to the altitude from where soils were collected. The lowest altitude site was excluded from correlation analyses. Pearson correlation coefficients and significance levels were calculated using site means.

Table 4.3: Pearson correlation coefficients and significance levels (** $p < 0.01$, * $p < 0.05$) for correlations between average relative stem elongation (between October and February), average final plant biomass and soil nutrients (n = 10). All soil nutrients were log transformed before the correlation analysis. The lowest altitude (coastal belt) site was included in all correlation analyses except for the last two, as indicated. § = lowest altitude site not included in the correlation analysis.

	Nutrient	Relative stem elongation (cm cm-1 day-1)		Final plant biomass (g)	
		A. karroo	*A. sieberiana*	*A. karroo*	*A. sieberiana*
	pH (KCl)	0.52	0.86 **	0.70 *	0.87 **
	Total P (mg/Kg)	0.65 *	0.67 *	0.68 *	0.64 *
	Bray II P (mg/Kg)	0.45	0.53	0.07	0.55
	Cu (mg/Kg)	0.15	0.10	0.39	-0.03
	Zn (mg/Kg)	0.54	0.79 **	0.55	0.75 *
	Mn (mg/Kg)	0.59	0.84 **	0.79 **	0.83 **
	B (mg/Kg)	0.59	0.71 *	0.85 **	0.75 *
	N (%)	0.43	0.51	0.78 **	0.52
	C (%)	0.30	0.32	0.74 *	0.29
	T-value (cmol/Kg)	0.43	0.67 *	0.80 **	0.71 *
T-value	Na (cmol(+)/Kg)	-0.02	0.24	0.50	0.28
	K (cmol(+)/Kg)	0.53	0.84 **	0.67 *	0.87 **
	Ca (cmol(+)/Kg)	0.45	0.72 *	0.73 *	0.76 *
	Mg (cmol(+)/Kg)	0.41	0.73 *	0.80 **	0.71 *
	Altitude (m)	0.05	-0.16	-0.24	-0.20
	PC1 (leaching index)	-0.54	-0.76 *	-0.79 **	-0.80 **
	Altitude (m) §	-0.33	-0.87 **	-0.60	-0.87 **
	PC1 (leaching index) §	-0.43	-0.77 *	-0.75 *	-0.81 **

University of Cape Town

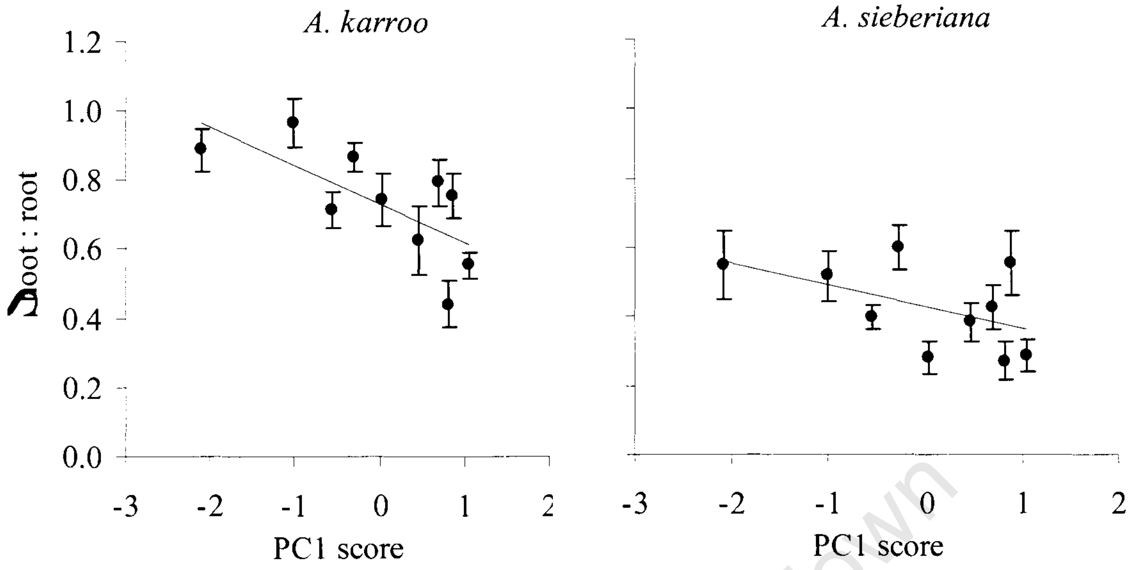


Figure 4.5: The relationship between shoot:root ratios of the two *Acacia* species with site scores according to PC1(*A. karroo*: $r = -0.70$, $p < 0.05$; *A. sieberiana*: $r = -0.51$, $p > 0.1$). Shoot:root ratios were calculated from dry weights of plants grown in different soils for seven months. A PCA was performed on soil nutrient data and PC1 represents a possible leaching index of the major nutrients determining growth.

Table 4.4: Pearson correlation coefficients and significance levels (*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$) for correlations between $\Delta^{15}N$ and soil nutrients, as well as the altitude from where soils were collected. $\Delta^{15}N$ was calculated as $\delta^{15}N_{soil}$ - $\delta^{15}N_{plant}$ (Robinson, 2001). The lowest altitude (coastal belt) site was included in all correlation analyses except for the one with altitude. § = lowest altitude site not included in the correlation analysis.

	Nutrient		r	
	pH	(KCl)	0.45	***
	Total P	(mg/Kg)	0.20	*
	P Bray II	(mg/Kg)	0.42	***
	Cu	(mg/Kg)	-0.10	
	Zn	(mg/Kg)	0.38	***
	Mn	(mg/Kg)	0.36	***
	B	(mg/Kg)	0.18	*
	N %		0.02	
	C %		-0.16	
T-value	T-Value	(cmol/Kg)	0.23	**
	Na	(cmol(+)/Kg)	-0.02	
	K	(cmol(+)/Kg)	0.32	***
	Ca	(cmol(+)/Kg)	0.28	**
	Mg	(cmol(+)/Kg)	0.29	**
	Altitude (§)	m	-0.29	**

University of Cape Town

Appendix

Table 4.A: Results of nutrient analyses for soils, collected from a range of altitudes, used in the soil nutrient pot experiment. Site codes: E = Ermelo, W = Wakkerstroom, A = Athole, H = Hlelo, C = Comins, F = Ford, M = Malan, G = Goss, Z = iMfolozi, K = Kirkwood. There was not enough soil in the Goss sample to calculate Resistivity, and hence Electrical Conductivity (EC). Alt = Altitude. Grassland sites = E, W, A, H, C; savanna sites = F, M, G, Z, K.

Site	Alt	pH	Resistivity	EC	Total P	P Bray II	K	Cu	Zn	Mn	B	N	C	H+	T-Value	Na	K	Ca	Mg
	m	KCl	Ohm		mg/kg							%		cmol/kg		Exchangeable cations (cmol(+)/kg)			
E	1704	4.3	4230	0.59	89.13	9	89	1.38	0.8	10.8	0.27	0.1	0.9	1.26	2.62	0.02	0.23	0.76	0.35
W	1648	4.2	3080	0.81	113.8	4	67	2.22	0.7	15	0.32	0.1	1.2	1.81	4.05	0.04	0.17	1.31	0.72
A	1570	4.1	2260	1.11	194.5	2	62	2.13	0.5	8.8	0.44	0.3	2.5	3.48	5.5	0.05	0.16	1.18	0.63
H	1353	4.2	3960	0.63	45.9	3	145	0.9	0.5	4.5	0.28	0.1	1.3	1.71	2.91	0.04	0.37	0.50	0.29
C	1078	4.6	4880	0.51	73.7	3	59	0.99	0.4	5.9	0.27	0.1	1	0.96	2.59	0.02	0.15	0.97	0.49
F	808	5.1	2490	1	119.4	8	196	1.47	1.5	17	0.29	0.1	1.6	0.76	5.58	0.06	0.50	1.94	2.32
M	554	5.3	1930	1.3	93.05	2	213	2.16	0.7	21.6	0.46	0.2	1.9	0.56	7.92	0.07	0.54	3.30	3.45
G	360	5.4			389.8	9	658	1.03	1.2	33.6	0.43	0.3	2.3	0.91	15.1	0.06	1.68	7.77	4.65
Z	170	5.5	1220	2.05	93.5	4	222	0.59	0.8	16.1	0.47	0.2	1.5	0.61	12.4	0.14	0.57	8.13	2.97
K	42	4.1	3800	0.66	33.29	2	19	0.71	0.3	2.6	0.16	0.1	1.3	1.51	3.07	0.06	0.05	0.89	0.56

University of Cape Town

Figure 4.A: i) *Acacia* seedlings planted in different soils collected from grasslands and savannas at various altitudes. ii) Seedlings of *Acacia karroo* (left-hand two rows) and *A. sieberiana* (right-hand two rows) planted in soils from one site. Photographs were taken in October 2007 at the start of the soil experiment.

University of Cape Town

Chapter 5: Escaping the fire trap

Introduction

The Highveld grasslands of South Africa could climatically support tree growth if fire was excluded (Acocks 1953, Bond *et al.* 2003). It is confusing that savanna trees that are fire tolerant, do not survive in these grasslands. Savanna saplings need to grow above the height of the grass-fuelled ground fires to escape topkill and reach adult sizes (Trollope 1984). Generally, only trees that have done this become reproductively mature. This is the basis of the "escape hypothesis", to explain the coexistence of trees and grasses in savannas (Bond & van Wilgen 1996, Higgins *et al.* 2000). Hypotheses proposed in Chapters 2 and 4 involve the idea that the grasslands have lower temperatures and nutrients respectively, which causes slower growth rates of *Acacia* species, fire-tolerant savanna trees. This prevents trees from ever growing above the height of the frequent fires, to establish themselves as adults (Trollope 1984). The extent to which the slow growth, due to a lack of resources, actually restricts recruitment into adult size classes is not known.

Fire frequencies vary within both grasslands and savannas. In Hluhluwe-iMfolozi Game Reserve, in high rainfall areas (*ca.* 990mm), mean and median fire return intervals were 2.9 and 1.3 years respectively, compared to 3.8 and 1.8 years respectively for low rainfall areas (< 635m) (Balfour & Howison 2001). In both these areas, intervals of up to 10 years between fires may irregularly occur (Balfour & Howison 2001). In the Kruger National Park, overall mean and median fire return intervals were 4.5 years (varying between 2.7 and 7.1 years) and 3.1 years (varying between 1.8 and 4.6 years) repectively (van Wilgen *et al.* 2000). In grasslands, annual and biennial burning is common in higher rainfall areas (> 650 mm), but less frequent in lower rainfall areas (Tainton & Mentis 1984). In burning trials, annual and biennial burning resulted in little difference to biotic and abiotic conditions, which deteriorated under triennial burning regimes (Tainton & Mentis, 1984).

University of Cape Town

Escape opportunities are few in savannas, but savanna trees can resprout numerous times from below-ground root stores, and at some stage, growth rates would be fast enough, and the interval between fires long enough, for recruitment into adult size classes to occur (Bond & van Wilgen 1996, Gignoux *et al.* 1997, Higgins *et al.* 2000). In Chapters 2 and 4 it was proposed that saplings of *Acacia* species would not grow fast enough to escape the flames of fires in the grasslands because of the slow growth caused by low temperatures and a short growing season; or a lack of soil nutrients. Experiments were set up in Chapters 2 and 4 and growth of acacia seedlings, transplanted into grassland and savanna temperatures and soils, was measured. Results showed that, in general, grasslands were cooler and more nutrient poor than savannas, and that growth in these grassland environments was slower than in the savanna environments. The question now is: Are temperature or nutrient effects on sapling growth rate sufficient to prevent adult recruitment?

University of Cape Town

The aim of this chapter is to compare variation in growth rates of seedlings, due to different temperatures and nutrient availabilities in grasslands and savannas. As growth rates were measured for seedlings in controlled pot experiments, they were first calibrated to growth rates of saplings in natural environments. Times to escape height were calculated for both temperature and nutrient derived growth rates and compared to fire frequencies in the region of study.

This analysis therefore allows an evaluation of treatment effects on the probability of tree recruitment under typical fire regimes. It is an attempt to place growth responses in their ecological contexts to evaluate whether they are likely to account for the absence of trees in frequently burnt grasslands.

Methods

Growth rates of seedlings subjected to different temperatures and growing seasons in savannas and grasslands were taken from a transplant experiment in Chapter 2. Growth rates of seedlings grown in soils collected from grasslands and savannas are taken from the pot experiment in Chapter 4.

Mean versus maximum growth rates, ZLTP exclosures

The average (mean or median) shows the centre of a spread of values, and is often calculated to account for natural variation. In the case of the escape hypothesis, we are not interested in average plants. Trees that are going to escape the fire trap are those that grow the fastest. To illustrate this point, growth of saplings in herbivore exclosure plots was used (Hluhluwe-iMfolozi Game Reserve (HiP), Zululand Grass/Tree Project (ZLTP), unpublished data). Sapling heights were measured over five non-consecutive years between 2000 and 2007 when the plots were not burnt (see also, Staver, 2007).

University of Cape Town

Extrapolating measured seedling growth to natural growth

To evaluate the ecological importance of variation between sites and species, growth rates of seedlings from the field experiments were extrapolated to naturally growing saplings. The assumption was that relative differences in growth of seedlings in the experiments would be the same for established saplings grown in the field. Growth of seedlings in the HiP ZLTP exclosures was used to "calibrate" growth rates recorded in the experiments of Chapters 2 and 4. As only the fastest growers would be expected to escape the fire trap, the fastest growing 20% of individuals per species from the HiP ZLTP exclosures were used in analyses. The time it would take individuals to reach an escape height of three metres was used, although flame height varies between fires and hence escape heights can vary between two and four metres (Trollope 1984).

Data sources

The time it would take *Acacia* species to reach escape height was calculated from measurements of both height and biomass for plants grown in different temperatures and those grown in soils of different nutrient availability. In both the experiments that provide data for this chapter, seedlings were used. Seedlings have different growth strategies to saplings, and in the experiment, height was not as good as biomass as an indicator of growth ability, so both height and biomass were used as growth response variables. As the fastest growing individuals are those expected to escape fires, only the fastest two individuals per species at each site were used. The number of individuals per species per site varied between 5 and 10 depending on the data set. In the temperature experiment, the height gain between November and June (10 individuals per species per site); and the total biomass after the November to June growing season (5 individuals per species per site) was used. In the nutrient experiment, variations in height gain between relatively nutrient-poor grassland and relatively nutrient-rich savanna soils are compared using relative stem elongation rates, calculated for data from November 2007 to February 2008 when growth was exponential, a requirement for this calculation (Hunt 1982, Hoffmann & Poorter 2002). Whole plant biomass at the end of the soil nutrient experiment, in April 2008, was used. There were between 5 and 9 individuals per species per site in the nutrient experiment.

University of Cape Town

Sites grouped into biomes

Due to site variations, sites were grouped into biomes, either grassland or savanna (Acocks 1953, Mucina & Rutherford 2006). For the temperature data, two sites (Goss and iMfolozi/Mbuzane) were excluded due to failure of these in the experiment (see methods section in Chapter 2); and the lowest altitude coastal belt site is included as a savanna site. Data from growth in soil from the lowest altitude site is excluded from the nutrient data as a consistent outlier (see Chapter 4), although it showed that all savanna soils are not necessarily rich compared to grassland soils. In excluding this site we are assuming that all grasslands are relatively nutrient poor and all savannas are relatively nutrient rich, which is not true, but is the general trend found in this experiment.

Calculating the time to escape height

The time to escape height for the combined savanna sites was assumed to be equivalent to the fastest growing 20% of individuals measured in ZLTP exclosures in HiP. The time to escape height for each of the two fastest individuals per site was then estimated as:

$$T(esc) = T(esc)HiP \; * \; \frac{\text{mean growth at savanna sites (two fastest per site)}}{\text{growth of individual}}$$

Where: "T(esc)" is the expected time to escape height, and is calculated for each of the two fastest individuals per site. "T(esc)HiP" is the time it takes for the fastest 20% of individuals in the ZLTP HiP exclosure plots to reach an escape height of three metres. T(esc)HiP is 4.24 years for *A. karroo* (Hlu), 4.15 years for *A. gerrardii* and 9.50 years for *A. tortilis* (ZLTP HiP unpublished data). There was no data from HiP for *A. karroo* (Bloem), *A. sieberiana* and *A. mearnsii*, as these species (or subspecies) do not occur, or do not occur in large enough densities in HiP. Thus the *A. karroo* (Hlu) T(esc)HiP was used for these species. It was assumed that the mean of the fastest individuals per species at all the savanna sites (two per site) is equivalent to growth of the fastest 20% of individuals in HiP. Both biomass and height growth were used from both temperature and nutrient experiments.

Height growth

To easily visualise results from temperature and nutrient experiments, graphs of sapling height over time were created using a model from Higgins *et al.* (2000), given the time to grow to an escape height of three metres, as calculated above. This was done for biomass data (means of the two fastest individuals per species per site), from grassland and savanna sites. The model is as follows:

$$h = h_{y-1} + (1 - (h_{y-1})/h_{max})*g_s$$

where g_s is the growth rate of stems (cm year^{-1}), h_{max} is the maximum stem height (m), and h_{y-1} is the stem height in the previous year (Higgins *et al.* 2000).

Results

Mean versus maximum sapling growth rates, ZLTP exclosures

There was considerable intraspecific variation in growth rates within natural populations (Figure 5.1). Expressed as years to grow to escape height, the mean for

University of Cape Town

A. karroo and *A. tortilis* would be greater than 20 years (*ca.* 50 years). The time it would take the fastest individuals of *A. karroo* (Hlu) and *A. gerrardii* to reach an escape height of 3m are similar (2.5 years for the fastest 5% and 4.2 years for the fastest 20%), and *A. tortilis* individuals would take longer (*ca.* 5 years for the fastest 5% and 9.5 years for the fastest 20%).

Mean versus maximum growth rates, temperature transplant experiment

The fastest two individuals per site took less time to reach escape height than the average growers, calculated from both height growth and biomass (*A. karroo* (Hlu) and *A. sieberiana* are used as examples; Figure 5.2). For example for *A. sieberiana* in grassland areas, the time to escape height calculated from mean biomass of all individuals was *ca.* 44 years, but only *ca.* 26 years when calculated from the mean of the fastest two individuals per site (Figure 5.2). The difference in time to escape height between grassland and savanna sites may be less when calculated from the fastest growth rates, than from the mean, as seen for example in biomass data for *A. sieberiana* (Figure 5.2), and thus using the fastest growth rates is a conservative estimate of times to escape height.

University of Cape Town

Extrapolated time to escape height: temperature versus nutrient effects

Between grasslands and savannas, variations in time to escape height were much greater due to temperature differences (up to 33 years difference between grasslands and savannas, calculated from biomass data) than nutrient differences (up to 1.4 years difference between grasslands and savannas, calculated from biomass data) (Figures 5.3 & 5.4). The difference in time to escape height between grassland and savanna sites is greater when calculated from biomass than from height growth, particularly for *A. tortilis*, *A. karroo* (Bloem) and *A. sieberiana* (Figure 5.3).

Discussion

Saplings growing at mean rates would never escape to become adults, given current fire return intervals. Only the fastest growing 20% and 5% of individuals have growth rates that would allow a plant to reach an escape height of three metres in a typical inter-fire period (*ca.* 3 to 5 years). This is our justification for using the fastest 20% of individuals. If seedlings with mean growth rates could become adults, one would expect greater densities of *A. gerrardii* than *A. karroo* or *A. tortilis* in natural environments, as the mean growth rate for *A. gerrardii* is much greater than the others. This is not the case. There are similar numbers of *A. karroo* and *A. gerrardii* found in HiP, and perhaps even more *A. karroo* (pers. obs.), which is reflective of the similar growth rates of the fastest growing 20% and 5% of *A. karroo* and *A. gerrardii* individuals. The difference of *ca.* 4.5 years between the fastest 20% and fastest 5% of *A. tortilis* is dramatic and emphasises this point again – only the exceptional excel. In the case of *A. tortilis*, 5% equated to 24 individuals per hectare, and 20% to 99 individuals per hectare, densities comparable to the number of adults in this area. If all saplings became adults, there would be 428 individuals per hectare, resulting in a closed woodland, which is not what occurs in this area. Saplings may have fast growth rates as they are physiologically exceptional; grow in a place where they have a smaller chance of being eaten or burnt; better access to water and nutrients; or experience less grass competition.

It is expected that naturally occurring individuals would grow slower and thus take longer to reach escape height than those in the transplant and pot experiments because of the effects of competition with grass for above and below-ground biotic and abiotic resources (Scholes & Archer 1997, Ball *et al.* 2002). This is why it is important to extrapolate experimental growth data to those in natural situations.

The results obtained from using biomass data are more likely to be realistic than those from height data as seedlings tend not to grow greatly in height, and biomass is therefore a more useful indicator of growth ability. The variation in time to escape height due to biomass in grassland and savanna sites is larger for *A. karroo* (Bloem), *A. sieberiana* and *A. tortilis*, species that have cage-like architectures (Archibald & Bond 2003) and acquired large biomass at savanna sites. *Acacia karroo* (Hlu), *A. gerrardii* and *A. mearnsii* have tall, pole-like architectures (Archibald & Bond 2003) and their relative biomass differences between grasslands and savannas were not that large.

University of Cape Town

Given the average fire return periods in savannas (van Wilgen *et al.* 2000, Balfour & Howison 2001), and expected times to escape height for saplings in savanna areas, it is evident that recruitment may not occur when fire occurs at an average frequency. Recruitment events are rare (Bond & van Wilgen 1996), and cohorts of saplings tend to recruit when conditions are favourable (Staver 2007), likely when intervals between fires are longer than average. In HiP savannas, fire intervals can be as great as once every 10 years or more, but not often (Balfour & Howison 2001), and these intervals may provide opportunity for sapling escape. In comparison to savannas, there is a lack of fire frequency data for grassland areas. In general, grassland fires occur on an annual or biennial basis, in wetter areas, but may be much less frequent (and even not recommended) in relatively arid grasslands (Tainton & Mentis 1984).

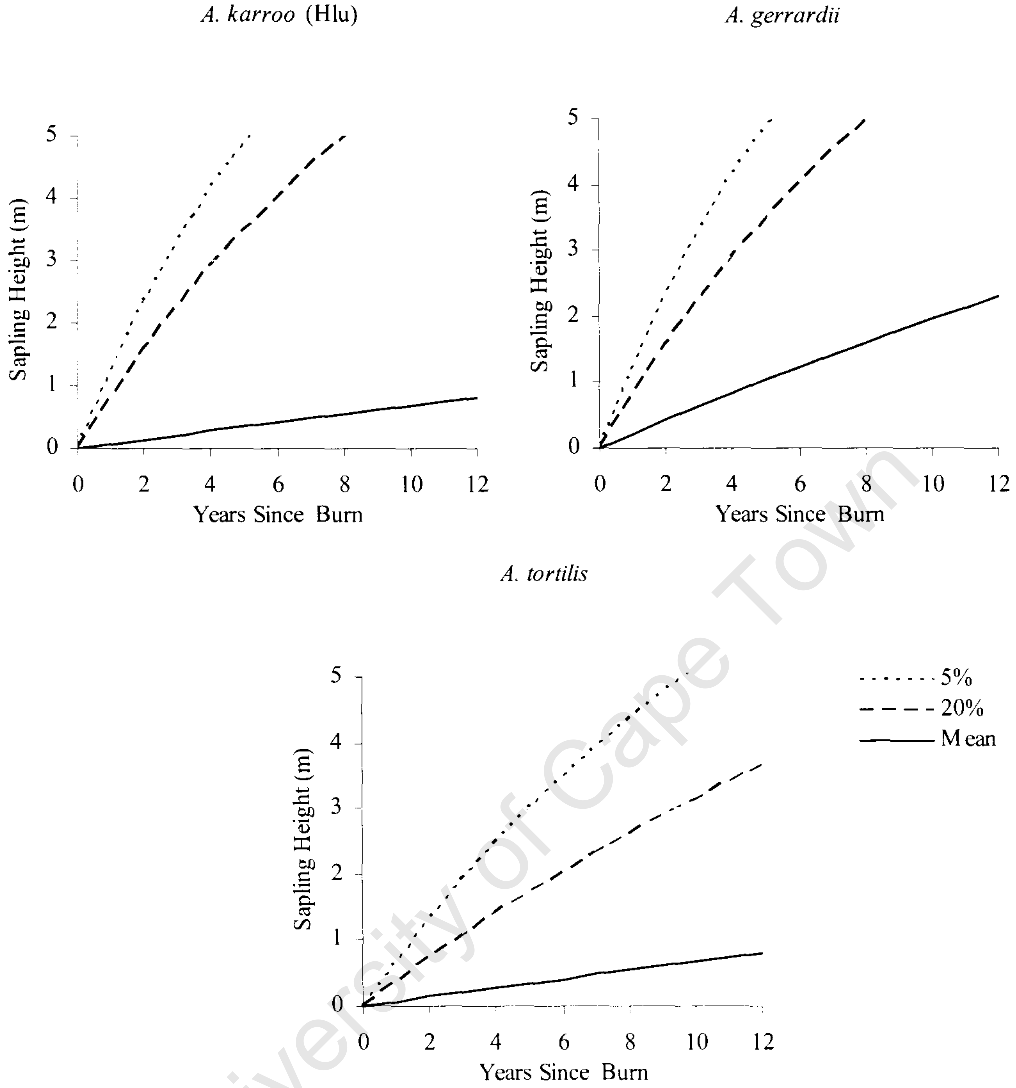
University of Cape Town

Temperature changes result in bigger differences in growth rates between grasslands and savannas than nutrient differences do. Grassland areas burn annually or biennially on average, and intervals of up to six years may occur irregularly, which could provide opportunity for sapling escape. If nutrients alone limited sapling growth in grasslands, saplings would be able to escape as they would grow fast enough to escape frequent fires, and trees would occur on the grasslands. However, if temperature limited sapling growth, escape would be far from possible due to slow growth rates. Therefore nutrients do not have as great an influence on growth rates as temperature does, given the temperature and nutrient changes along the gradient studied. In reality, both temperature and nutrients limit sapling growth, and the time it would take saplings to reach escape height in grasslands would be even longer than predicted in this study. It is then not surprising that the grasslands are tree-less. It is interesting to remember that seedlings grew in both grassland climates and soils, and these alone do not exclude trees from the grasslands. Fire is an essential factor in the maintenance of these tree-less grasslands.

Conclusion

Growth rates, measured as height and biomass were generally greater in savannas than grasslands given temperatures and nutrient availabilities. Interpretation of these results for probability of sapling escape is complicated by enormous intra-population variability in growth rates, and it is likely that only the fastest growers would ever escape fire. Results in this study show that temperature had a greater influence on growth rates than nutrient availability did, within the gradient studied, and low temperatures would have been able to exclude trees from grasslands, but low nutrient availabilities would not have. In reality, low temperatures and low nutrient availabilities act together to result in slow growth rates, hence it is not surprising that the grasslands are tree-less, given the frequent fires.

University of Cape Town



University of Cape Town

Figure 5.1: Growth rates of *A. karroo*, *A. gerrardii* and *A. tortilis* in herbivore-exclosure plots in Hluhluwe-iMfolozi Game Reserve over five non-consecutive fire-free years (Zululand Tree Project, unpublished data). Growth rates are means, fastest growing 20% and fastest growing 5% of individuals in the population. An escape height of 3m was used in calculations and a line is shown at 3m for ease of comparison between graphs.

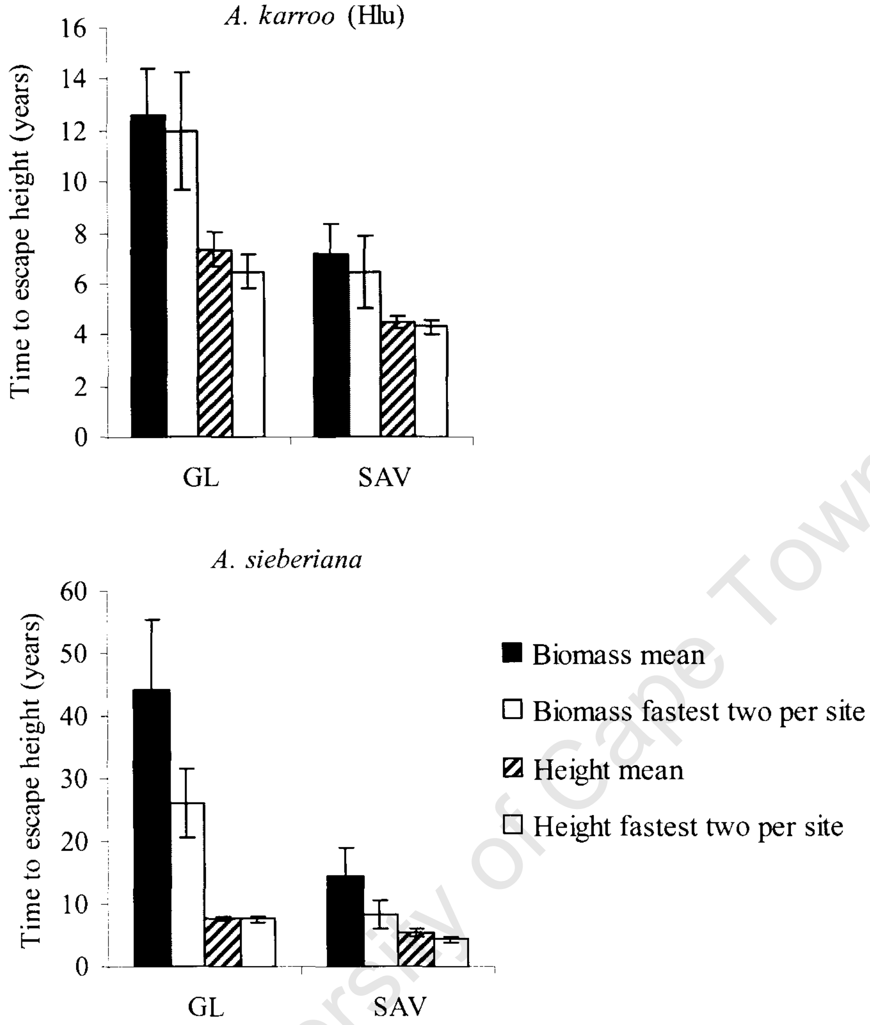
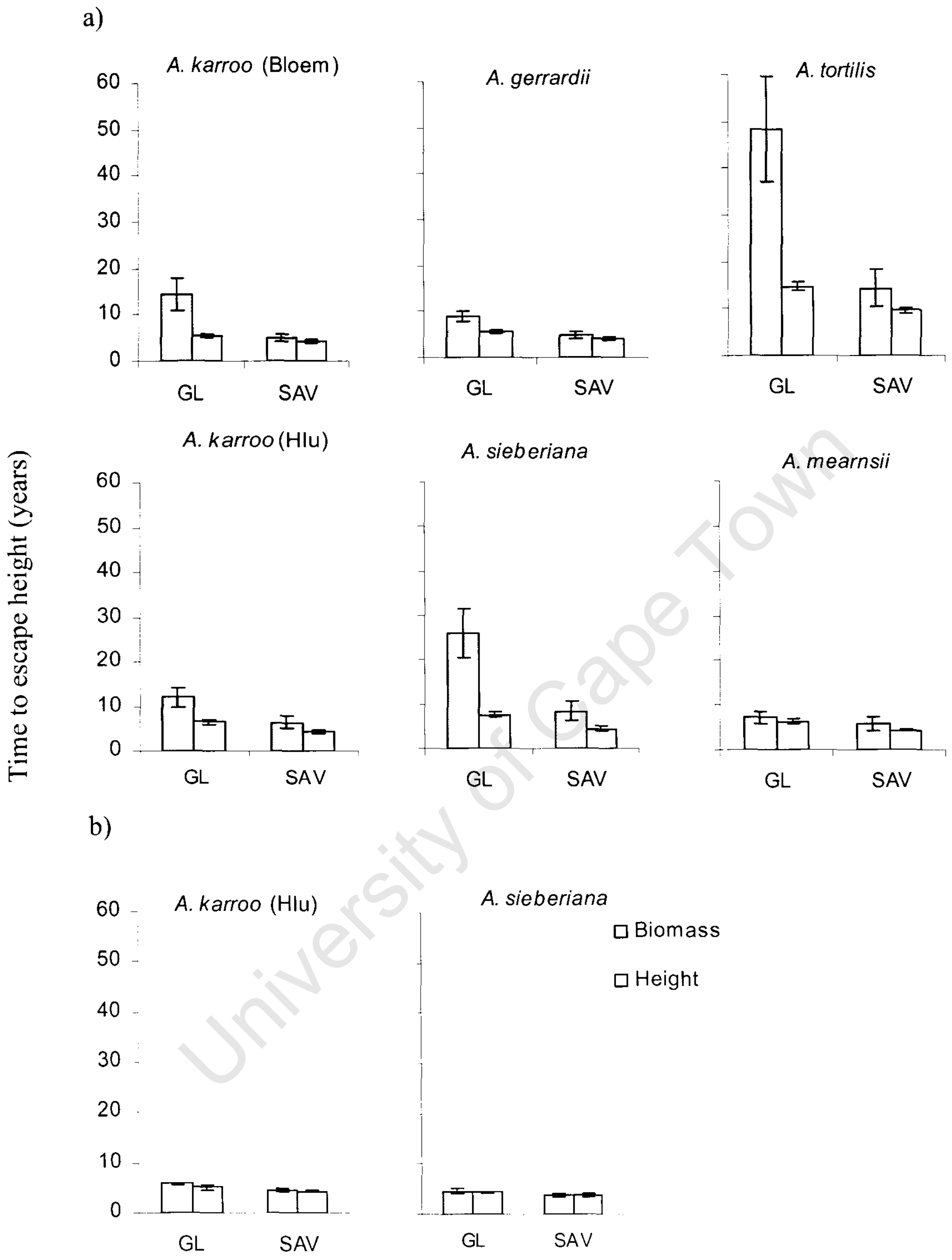


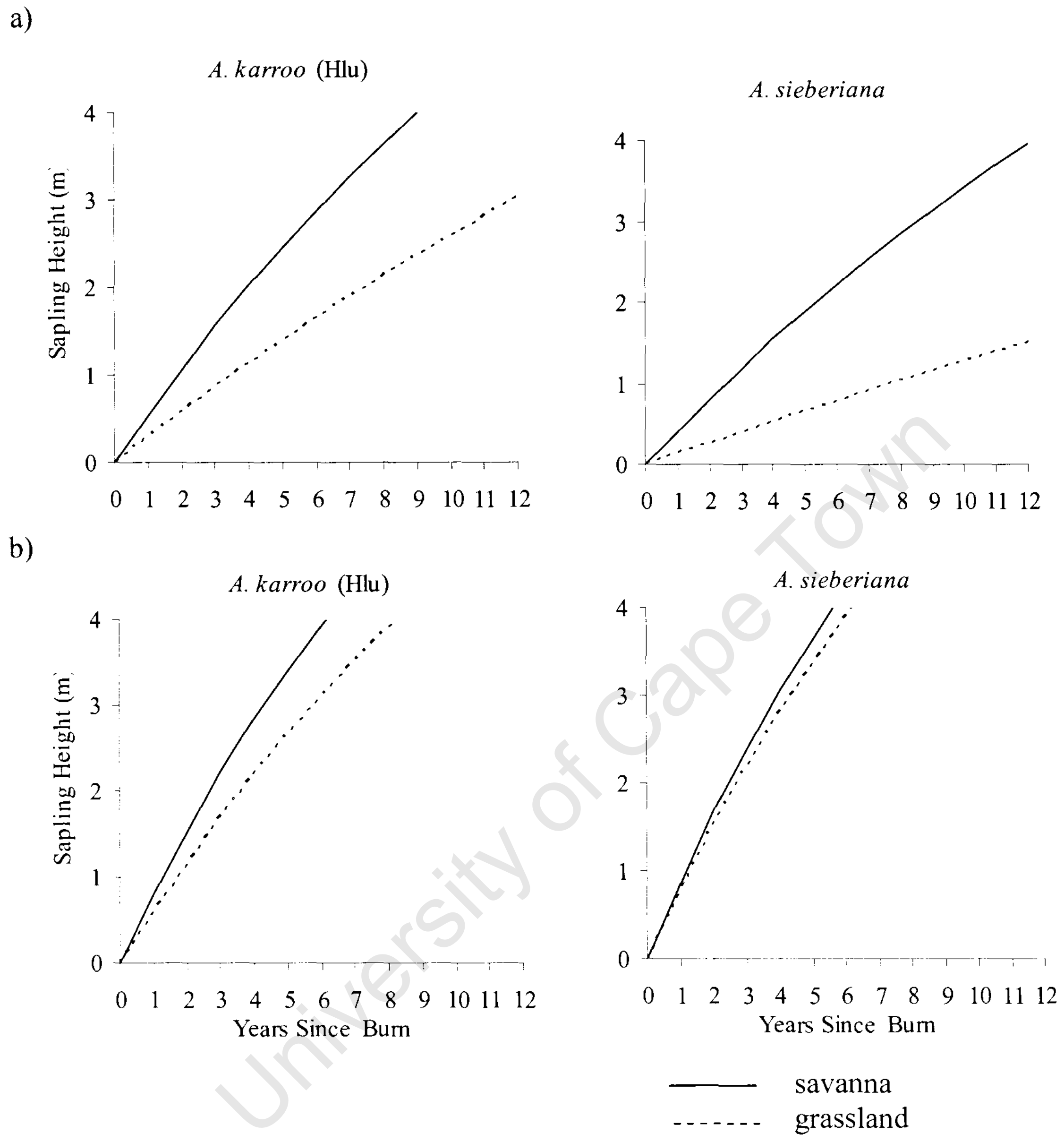
Figure 5.2: Times to escape height calculated from biomass and height data for two *Acacia* species from seedling growth in a transplant experiment in savanna and grassland areas (temperature). Growth of seedlings were extrapolated to natural growth rates by relating them to growth rates of saplings grown within the grass sward in Zululand Tree Project herbivore exclosure plots in Hluhluwe-iMfolozi Game Reserve. GL = grassland; SAV = savanna.

University of Cape Town



University of Cape Town

Figure 5.3: Times to escape height calculated from biomass and height data for various *Acacia* species from a) seedling growth in a transplant experiment in savanna and grassland areas (temperature); and b) seedling growth in soils from grassland and savanna areas (nutrients). Growth of seedlings were extrapolated to natural growth rates by relating them to growth rates of saplings grown within the grass sward in Zululand Tree Project herbivore exclosure plots in Hluhluwe-iMfolozi Game Reserve. GL = grassland; SAV = savanna.



University of Cape Town

Figure 5.4: Changes in sapling height with time in years since a burn (model from Higgins *et al.*, (2000)), for a) seedlings grown in a transplant experiment in grassland and savanna areas (temperature), and b) seedlings grown in a pot experiment with soils from grassland and savanna areas (nutrients). Growth of seedlings in the experiments was extrapolated to natural growth rates by comparison with growth of saplings in a grass sward in Zululand Tree Project herbivore exclosure plots in Hluhluwe-iMfolozi Game Reserve.

Chapter 6: Conclusion

This study was interested in tropical to sub-tropical (not temperate) C_4 dominated ecosystems that occur on freely drained soils in mesic to humid regions. These consist of both tree-less grasslands and wooded savannas.

The grasslands of the Highveld region of South Africa are one of a number of grasslands globally that can support a woody biomass given their climatic conditions, and yet they do not (Bond *et al.* 2003). Other similar grassland areas are in North America (tall grass prairies and Appalachian balds), South America (campos), Australia (balds), and throughout Africa (Bond *et al.* 2005). My thesis addressed the question of what prevents fire-tolerant savanna trees from entering the grasslands. The hypotheses I tested were that slow growth, either due to low temperatures (Chapter 2 and 5) or low nutrient availability (Chapter 4 and 5), prevents trees from escaping the frequent fires; or that frost damage kills trees (Chapter 3). I tested the importance of climate-related effects on growth by establishing a large transplant experiment with ten sites located on an altitudinal gradient from 40m to 1700m. I tested variable soil effects on growth across this gradient by sampling soils from each site and growing seedlings in them in a common garden experiment.

University of Cape Town

Seedlings of six *Acacia* species successfully established and grew across the entire altitudinal gradient, in both grassland and savanna climates. Various factors influenced growth at different sites, but the overall trend was that growth in the cooler grasslands was significantly slower than in the warmer savannas (Figures 2.3, 2.4 & 2.5). Rapid growth only occurred for a short period, in the middle of the growing season, and declined steeply in February and March while temperatures were still high (Figure 2.7). Moisture availability, temperature and photoperiod have been used to explain savanna tree phenology (Childes 1989, Williams *et al.* 1997, Jolly & Running 2004, Do *et al.* 2005, Archibald & Scholes 2007). In the present study plant growth decreased even though plants were not water limited, and the decrease in growth appears to be due to a decrease in day-length (Figure 2.7). Temperate trees have been shown to stop growth in order to cold harden by the time cold temperatures arrive (Sakai & Wardle 1978, Bannister *et al.* 1995, Fernandez *et al.* 2003, Körner 2003). It is a possibility that savanna trees need to stop growing so they have enough time to relocate carbon from shoots to roots before the dry season when the probability of fire is high, as suggested by Prior *et al.* (1997).

Higher altitude soils from my study sites were generally more leached than lower elevation soils (Figure 4.1, Table 4.1). However, nutrient availability varies within grasslands and within savannas (Ellery *et al.* 1995, Sankaran *et al.* 2005), and this intra-biome variation may be greater than the variation between biomes. Evidence for this in my study is shown by the lowest altitude quaternary sandy soil which was relatively nutrient-poor and supported slow seedling growth (Figures 4.1, 4.3 & 4.4), and yet sustains a high tree biomass in situ. There is no doubt that nutrients influence plant growth (Figure 4.4, Table 4.3), but even though there were significant differences between growth in grassland and savanna soils, the effect size (magnitude) of that difference was not large enough to exclude trees from grasslands (Figures 5.3 & 5.4). In contrast, temperature differences in growth were large enough to exclude trees from cool grassland areas (Figures 5.3 & 5.4).

University of Cape Town

Frost caused loss of biomass and reduced survival of seedlings (Figure 3.3), but the altitudinal limit of frost damage did not predict the upper altitudinal limit of the distributions of *A. gerrardii* and *A. tortilis* (Figure 3.4). It is unlikely that frost limits the distributions of the other species since grasslands with no trees occur at far lower elevations than the lower limit of frost damage. *Acacia karroo* (Bloem) was the most resistant to frost damage, which may reflect a physiological adaptation to cold temperatures, as it naturally occurs in cool areas. It is widely acknowledged that some varieties of *A. karroo*, can survive in frosty areas (Acocks 1953, Mucina & Rutherford 2006). Brando & Durigan (2004) also found survival of frost by savanna trees in southern Brazil, and concluded that frost did not define the cerrado boundary. Relocation of resources from shoots to roots in the cold dry season by savanna trees has been explained as an adaptation to fire survival (Bond & Midgley 2001, Bond & Midgley 2003, Wigley *et al.* 2008), but may also assist in resprouting after loss of biomass by frost, as suggested by Trollope (1984). It is interesting to note that traits that are good for surviving fire, such as bark thickness, are also good for surviving frost (Holdo 2006). Given that the temperatures experienced in the major frost in this experiment occurred every *ca.* 3 years in the low temperature records between 1950 and 2000 (Schulze & Maharaj 2003) (Figure 3.A), these temperatures were not exceptional, and there is still the possibility that infrequent extreme frosts may limit the distributions of some savanna trees.

Alpine tree-lines have been explained solely by temperature (Körner & Paulsen 2004). Low temperatures have been used to explain the tree-less nature of grasslands both in South Africa (Bredenkamp *et al.* 2002), and other parts of the world (Webb 1964). However, temperature alone cannot be an explanation for many tree-less grasslands, as trees do survive the climates of these grasslands in fire refugia. Fire alone can also not be used to explain the lack of trees, as savanna trees survive comparable fire regimes. Slow growth due to low temperatures, when combined with frequent fires, has been shown to prevent saplings from becoming adults in the Highveld grasslands in this study. Temperature and fire have also been used to explain a reverse tree-line (Coop *et al.* 2007).

It could be argued that temperature, nutrients and frost, together with frequent fires, all contribute to the lack of trees in the Highveld grasslands. Slow growth due to a low availability of nutrients and cool temperatures, in combination with loss of biomass due to frost and fire, would make it extremely difficult for a sapling to become an adult in this grassland environment. This is assuming that an individual would be able to get to sapling stage. The added effects of grass competition would make sapling escape even less likely. However, grasslands occur in areas with no frost and on relatively nutrient rich and nutrient poor soils. Given that the boundary is so sharp, I do not think it is such a complex ecological question, but rather a slight tipping of the delicate balance that maintains tree-grass coexistence in savannas.

An interesting challenge for tree-grass coexistence models is to explain the tree-less grasslands at one extreme and the grass-less forests at the other. For example, the root-niche separation hypothesis would not be able to explain why no trees occur in grassland areas, given that the deep rooting space is not occupied. The escape hypothesis, on the other hand, has assisted in explaining the lack of trees in grasslands, by incorporating the time that saplings would take to reach escape height, with average fire return intervals.

University of Cape Town

Chapter 6: Conclusion

There have been many hypotheses and much discussion around what determines the tree-less nature of grasslands (O'Connor & Bredenkamp 1997, Bredenkamp *et al.* 2002), but very little experimental work. The enormous magnitude of the experimental work in this study was relatively novel, particularly in South Africa. It is unfortunate that these large-scale experiments are so demanding, as they provide hard evidence for broad scale questions. They also include factors that cannot be mimicked in a laboratory, such as radiation frost and grass competition. It would have been useful to perform a multifactorial experiment, including grass effects, but this was not possible given the time constraints of this project.

Has this study answered the question: Why are the Highveld grasslands tree-less?

The broad experimental design of this study lent itself to comparisons of grasslands and savannas at a large scale. The escape hypothesis provided a context for testing factors that influence growth sufficiently to explain the absence of trees in grasslands versus savannas. Temperature over the growing season was the major influencing factor in this study but is not the only factor influencing growth along grassland-savanna boundaries. The actual boundary was not the focus of this study and the abruptness of the savanna tree-line is puzzling.

University of Cape Town

Locally and globally, there are two different scales of grassland-savanna interface: grassy topped hills and grasslands versus savannas over subcontinents. The grassy topped hills include satellite grasslands in the savannas of South Africa (Acocks 1953, Mucina & Rutherford 2006), the Appalachian balds (Lindsay & Bratton 1979a, b), the south east Australian balds (Webb 1964, Fensham & Fairfax 1996, 2006), and inverted tree-lines (Acocks 1953, Fensham & Kirkpatrick 1992, Coop *et al.* 2007), although these last grasslands are often C_3 dominated. At the broad scale there are interfaces between upland grasslands and lower altitude savannas of South Africa (Rutherford & Westfall 1986, O'Connor & Bredenkamp 1997); the campos and cerrado of South America (Overbeck *et al.* 2007); and the prairies and mesquites of North America (Knapp *et al.* 1999). The different scales do not necessarily need to be explained by different factors. Fire is an integral part of savannas and grasslands and although it cannot be used alone as an explanation for tree-less grasslands, it should not be ignored. This study has shown that the temperature effect on plant growth between savanna and grassland areas is enough to prevent trees growing in the

Highveld grasslands given frequent fire, and this may be the case globally. In the absence of frequent fires, savanna trees would grow in grassland areas. Other factors such as nutrients and frost compound the slow growth of trees in the Highveld grassland soils and also affect other grasslands. Irrespective of the factors influencing growth, for grasslands that burn it is useful to think of growth variations under a blanket of fire.

All the grasslands mentioned have tree invasions at their warmer ends (Webb 1964, Lindsay & Bratton 1980, O'Connor 1995, Jurena & Archer 2003); evidence that temperature plays a major role and that grasslands are being lost through climate change. It is a pity that we do not fully understand these grasslands as we watch them disappear.

University of Cape Town

Future Research

Include grass

The experiments in this study did not incorporate grass. Compared to bare ground, grass alters the thermal environment both above and below ground (Ball *et al.* 1997, Ball *et al.* 2002). Grass may provide shelter from radiation frost for seedlings within the grass sward (Maher *et al.* 2005) but more extreme temperatures above grass may limit seedling survival in cool areas (Ball *et al.* 2002) such as the Highveld grasslands. Trees and grasses co-exist in savannas, but a dense grass sward has been shown to exclude trees from a cool grassland, due to competition for moisture and rooting space (Fensham & Kirkpatrick 1992). Cramer *et al.* (2007) found that although nutrients influenced plant growth, it was the competition with grass for these nutrients that had a greater impact on plant growth. It is possible that a change in environmental factors may create "exceptionally competitive" grasses in the Highveld grasslands (Mills *et al.* 2006), and that a subtle change in environment can disrupt the competitive balance between species (Woodward 1975, Piggott 1984). An investigation of how grass influences seedling or sapling growth and survival in high grassland areas is essential for a fuller understanding of what excludes trees from grasslands.

Other life stages: germination

This study focussed on seedling growth. Germination has been seen to be enhanced by a grass sward in a grassland area in South Africa (O'Connor 1995), but was extremely rare within a dense grass sward in Tasmania (Fensham & Kirkpatrick 1992). It would be interesting to establish the germination ability of savanna trees in a wide variety of grassland areas, particularly in respect of the density of the grass sward.

Global and local savanna tree-lines

The savanna tree-line is hardly recognised. The boundaries between grasslands and savannas exist in vegetation maps, but the patterns have yet to be properly described. It would be interesting to be able to draw savanna tree-lines on individual continents, and just as Körner & Paulsen (2004) have studied the global alpine tree-line temperatures, it would be intriguing to know if savanna tree-lines were at similar temperatures around the world. It would also be useful to take a closer look at the factors influencing the actual biome boundary, through small scale experiments across the savanna tree-line. Factors that maintain tree-lines currently may not have created them initially, and archaeological and palynological data may assist in investigating causal factors, if indeed they are different to those that currently maintain the tree-line.

University of Cape Town

References

Acocks, JPH, 1953. Veld types of South Africa. *Memoirs of the Botanical Society of South Africa* **28**:1-192.

Archibald, S, & WJ Bond, 2003. Growing tall vs growing wide: tree architecture and allometry of *Acacia karroo* in forest, savanna, and arid environments. *Oikos* **102**:3-14.

Archibald, S, & RJ Scholes, 2007. Leaf green-up in a semi-arid African savanna - separating tree and grass responses to environmental cues. *Journal of Vegetation Science* **18**:583-594.

Arnold, TH, & HM Steyn, 2005. PRECIS.pc Specimen Database user guide. 40, SABONET.

Asner, GP, AJ Elmore, LP Olander, RE Martin, & AT Harris, 2004. Grazing systems, ecosystem responses, and global change. *Annual Review of Environment and Resources* **29**:261 - 299.

Balfour, DA, & OE Howison, 2001. Spatial and temporal variation in a mesic savanna fire regime: responses to variation in annual rainfall. *African Journal of Range & Forage Science* **19**:43-51.

Balfour, DA, & JJ Midgley, 2006. Fire induced stem death in an African acacia is not caused by canopy scorching. *Austral Ecology* **31**:892-896.

Ball, MC, JJG Egerton, R Leuning, RB Cunningham, & P Dunne, 1997. Microclimate above grass adversely affects spring growth of seedling snow gum (*Eucalyptus pauciflora*). *Plant, Cell & Environment* **20**:155 - 166.

Ball, MC, JJG Egerton, JL Lutze, VP Gutschick, & RB Cunningham, 2002. Mechanisms of competition: thermal inhibition of tree seedling growth by grass. *Oecologia* **133**:120-130.

Bannister, P, 1984. Winter frost-resistance of leaves of some plants from the Three-Kings-Islands, grown outdoors in Dunedin, New-Zealand. *New Zealand Journal of Botany* **22**:303-306.

Bannister, P, CM Colhoun, & PE Jameson, 1995. The winter hardening and foliar frost-resistance of some New-Zealand species of Pittosporum. *New Zealand Journal of Botany* **33**:409-414.

Barger, NN, CM D'Antonio, T Ghneim, K Brink, & E Cuevas, 2002. Nutrient limitation to primary productivity in a secondary savanna in Venezuela. *Biotropica* **34**:493-501.

Behling, H, VD Pillar, SC Muller, & GE Overbeck, 2007. Late-Holocene fire history in a forest-grassland mosaic in southern Brasil: Implications for conservation. *Applied Vegetation Science* **10**:81-90.

Bengough, AG, 2003. Root growth and function in relation to soil structure, composition and strength. *in* H. de Kroon & E. J. W. Visser, editors. Root Ecology, Ecological Studies 168. Springer Verlag, Berlin.

Birch, HF, 1958. The effect of soil drying on humus decomposition and nitrogen availability. *Plant and Soil* **10**:9-31.

Blackmore, AC, MT Mentis, & RJ Scholes, 1990. The origin and extent of nutrient-enriched patches within a nutrient-poor savanna in South Africa. *Journal of Biogeography* **17**:463-470.

University of Cape Town

References

Blair, N, A Leu, E Munoz, J Olsen, E Kwong, & D Des Marais, 1985. Carbon isotopic fractionation in heterotrophic microbial metabolism. *Appl. Environ. Microbiol.* **50**:996-1001.

Bond, WJ, 1997. Fire. Pages 421-446 *in* R. M. Cowling, D. M. Richardson, & S. M. Pierce, editors. Vegetation of southern Africa. Cambridge University Press, Cambridge.

Bond, WJ, 2008. What limits trees in C_4 grasslands and savannas? *Annual Review of Ecology Evolution and Systematics* **39**:641-659.

Bond, WJ, GF Midgley, & FI Woodward, 2003. What controls South African vegetation - climate or fire? *South African Journal of Botany* **69**:79-91.

Bond, WJ, & JJ Midgley, 2001. Ecology of sprouting in woody plants: the persistence niche. *Trends in Ecology & Evolution* **16**:45-51.

Bond, WJ, & JJ Midgley, 2003. The evolution ecology of sprouting in woody plants. *International Journal of Plant Science* **164**:103-114.

Bond, WJ, JA Silander, J Ranaivonasy, & J Ratsirarson, 2008. The antiquity of Madagascar's grasslands and the rise of C-4 grassy biomes. *Journal of Biogeography* **35**:1743-1758.

Bond, WJ, & BW van Wilgen, 1996. Fire and Plants. Chapman & Hall, London.

Bond, WJ, FI Woodward, & GF Midgley, 2005. The global distribution of ecosystems in a world without fire. *New Phytologist* **165**:525-537.

Bowman, DMJS, 2000. Australian rainforests: islands of green in a land of fire. Cambridge University Press, Cambridge.

Bragg, TB, & LC Hulbert, 1976. Woody plant invasion of unburned Kansas Bluestem Prairie. *Journal of Range Management* **29**:19-24.

Brando, PM, & G Durigan, 2004. Changes in cerrado vegetation after disturbance by frost (São Paulo State, Brazil). *Plant Ecology* **175**:205-215.

Bray, RH, & LT Kurtz, 1945. Determination of total, organic, and available forms of phosphorus in soils. *Soil Science* **59**:39 - 45.

Bredenkamp, GJ, F Spada, & E KazMierczak, 2002. On the origin of northern and southern hemisphere grasslands. *Plant Ecology* **163**:209-229.

Brejda, JJ, TB Moorman, DL Karlen, & TH Dao, 2000. Identification of regional soil quality factors and indicators: I. Central and southern high plains. *Soil Science Society of America Journal* **64**:2115 - 2124.

Chidumayo, EN, 2001. Climate and phenology of savanna vegetation in southern Africa. *Journal of Vegetation Science* **12**:347-354.

Childes, SL, 1989. Phenology of nine common woody sepcies in semi-arid, deciduous Kalahari sand vegetation. *Vegetatio* **79**:151 - 163.

Coates-Palgrave, K, 2002. Trees of southern Africa, 3rd edition. Struik, Cape Town.

Coates Palgrave, K, 2002. Trees of southern Africa, 3rd edition. Struik, Cape Town.

Coetzee, JP, GJ Bredenkamp, N Vanrooyen, & GK Theron, 1994. An Overview of the Physical-Environment and Vegetation Units of the Ba and Ib Land Types of the Pretoria-Witbank-Heidelberg Area. *South African Journal of Botany* **60**:49-61.

Collatz, GJ, JA Berry, & JS Clark, 1998. Effects of climate and atmospheric CO2 partial pressure on the global distribution of C-4 grasses: present, past, and future. *Oecologia* **114**:441-454.

Coop, JD, TJ Givnish, & M Austin, 2007. Gradient analysis of reversed treelines and grasslands of the Valles Caldera, New Mexico. *Journal of Vegetation Science* **18**:43-54.

University of Cape Town

Cox, MS, PD Gerard, MC Wardlaw, & MJ Abshire, 2003. Variability of selected soil properties and their relationships with soybean yield. *Soil Science Society of America Journal* **67**:1296 - 1302.

Cramer, MD, SBM Chimphango, A van Cauter, MS Waldram, & WJ Bond, 2007. Grass competition induces N-2 fixation in some species of African Acacia. *Journal of Ecology* **95**:1123-1133.

Curtis, OF, 1936. Leaf temperatures and the cooling of leaves by radiation. *Plant Physiology* **11**:343-364.

d'Antonio, CM, & PM Vitousek, 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* **23**:63-87 CR - Copyright © 1992 Annual Reviews.

Do, FC, VA Goudiaby, O Gimenez, AL Diagne, M Diouf, A Rocheteau, & LE Akpo, 2005. Environmental influence on canopy phenology in the dry tropics. *Forest Ecology and Management* **215**:319-328.

Edwards, PJ, 1984. Fire regimes in the biomes of South Africa. *in* P. d. V. Booysen & N. M. Tainton, editors. Ecological effects of fire in South African ecosystems. Springer-Verlag, Berlin.

Ehleringer, JR, 2005. The influence of atmospheric CO_2, temperature and water on the abundance of C_3/C_4 taxa. Pages 214-231 *in* J. R. Ehleringer, T. E. Cerling, & M. D. Dearing, editors. A history of atmospheric CO_2 and its effects on plants, animals and ecosystems, Ecological Studies 177. Springer Verlag, New York.

Ehleringer, JR, & PW Rundel, 1989. History, units and instrumentation. Pages 1 - 15 *in* P. W. Rundel, J. R. Ehleringer, & K. A. Nagy, editors. Stable Isotopes in Ecological Research. Ecological Studies 68. Springer-Verlag, Berlin.

Ellery, WN, 1992. Classification of the vegetation of the South African grassland biome. PhD. University of Witwatersrand, Johannesburg.

Ellery, WN, & MT Mentis, 1992. How old are South Africa's grasslands? *in* P. A. Furley, J. Proctor, & J. A. Ratter, editors. Nature and Dynamics of Forest-Savanna Boundaries. Chapman & Hall, London.

Ellery, WN, RJ Scholes, & MC Scholes, 1995. The distribution of sweetveld and sourveld in South Africa's grassland biome in relation to environmental factors. *African Journal of Range & Forage Science* **12**:38-45.

Evans, RD, 2001. Physiological mechanisms influencing plant nitrogen isotope composition. *Trends in Plant Science* **6**:121-126.

Fairbanks, DHK, MW Thompson, DE Vink, TS Newby, HM van den Berg, & DA Everard, 2000. The South African land-cover characteristics database: a synopsis of the landscape. *South African Journal of Science* **96**:69-82.

Feely, JM, 1987. The early farmers of Transkei, southern Africa, before AD 1870. Oxford: British Archaeological Reports, Cambridge Monographs in African Archaeology 24. British Archaeological Reports International Series 378.

Fensham, RJ, & RJ Fairfax, 1996. The disappearing grassy balds of the Bunya mountains, south-eastern Queensland. *Australian Journal of Botany* **44**:543-558.

Fensham, RJ, & RJ Fairfax, 2006. Can burning restrict eucalypt invasion on grassy balds? *Austral Ecology* **31**:317-325.

Fensham, RJ, RJ Fairfax, & SR Archer, 2005. Rainfall, land use and woody vegetation cover change in semi-arid Australian savanna. *Journal of Ecology* **93**:596-606.

University of Cape Town

University of Cape Town

Fensham, RJ, & JB Kirkpatrick, 1992. The eucalypt forest-grassland /grassy woodland boundary in central Tasmania. *Australian Journal of Botany* **40**:123-138.

Fernandez, M, A Royo, L Gil, & JA Pardos, 2003. Effects of temperature on growth and stress hardening development of phytotron-grown seedlings of Aleppo pine (Pinus halepensis Mill.). *Annals of Forest Science* **60**:277-284.

Garten, CT, LW Cooper, WM Post, & PJ Hanson, 2000. Climate controls on forest soil C isotope ratios in the Southern Appalachian Mountains. *Ecology* **81**:1108-1119.

Gignoux, J, J Clobert, & JC Menaut, 1997. Alternative fire resistance strategies in savanna trees. *Oecologia* **110**:576-583.

Gillson, L, 2006. A 'large infrequent disturbance' in an East African savanna. *African Journal of Ecology* **44**:458-467.

Grace, J, 1987. Climatic tolerance and the distribution of plants. *New Phytologist* **106**:113-130.

Greer, DH, P Wardle, & RP Buxton, 1989. Seasonal frost hardiness of *Nothofagus solandri* seedlings from two altitudinally diverse sites in Canterbury, New Zealand. *New Zealand Journal of Botany* **27**:299 - 304.

Greer, DH, & IJ Warrington, 1982. Effect of photoperiod, night temperature, and frost incidence on development of frost hardiness in *Pinus radiata*. *Australian Journal of Plant Physiology* **9**:333 - 342.

Guo, D, R Guo, GF Midgely, JL Wakeling, WJ Bond, & Y Cui, 2008. Future spatial patterns of South African *Acacia* trees. *GRS.*

Herbert, DA, 1938. The upland savannas of the Bunya Mountains south Queensland. *Proceedings of the Royal Society of Queensland* **49**:145-149.

Higgins, SI, WJ Bond, & WSW Trollope, 2000. Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. *Journal of Ecology* **88**:213 - 229.

Hodgkinson, KC, 1998. Sprouting success of shrubs after fire: height dependent relationships for different strategies. *Oecologia* **115**:64-72.

Hoffmann, WA, & H Poorter, 2002. Avoiding bias in calculations of relative growth rate. *Annals of Botany* **80**:37 - 42.

Hoffmann, WA, & OT Solbrig, 2003. The role of topkill in the differential response of savanna woody species to fire. *Forest Ecology and Management* **180**:273-286.

Holdo, RM, 2006. Elephant herbivory, frost damage and topkill in Kalahari sand woodland savanna trees. *Journal of Vegetation Science* **17**:509-518.

Hunt, R, 1982. Plant growth curves : the functional approach to plant growth analysis. Arnold, London.

Jolly, WM, & SW Running, 2004. Effects of precipitation and soil water potential on drought deciduous phenology in the Kalahari. *Global Change Biology* **10**:303-308.

Jordan, DN, & WK Smith, 1995. Radiation frost susceptibility and the association between sky exposure and leaf size. *Oecologia* **103**:43-48.

Jurena, PN, & S Archer, 2003. Woody plant establishment and spatial heterogeneity in grasslands. *Ecology* **84**:907-919.

King, L, 1978. The geomorphology of central and southern Africa. Pages 3-18 *in* M. J. A. Werger, editor. Biogeography and Ecology of Southern Africa. Junk, The Hague.

Knapp, AK, JM Blair, JM Briggs, SL Collins, DC Hartnett, LC Johnson, & EG Towne, 1999. The keystone role of bison in north American tallgrass prairie -

Bison increase habitat heterogeneity and alter a broad array of plant, community, and ecosystem processes. *Bioscience* **49**:39-50.

Körner, C, 2003. Alpine plant life : functional plant ecology of high mountain ecosystems. Springer-Verlag, Berlin.

Körner, C, & J Paulsen, 2004. A world-wide study of high altitude treeline temperatures. *Journal of Biogeography* **31**:713-732.

Lambers, H, FS Chapin, & TL Pons, 1998. Plant Physiological Ecology. Springer-Verlag, New York.

Lewis, OAM, 1986. Plants and nitrogen. Edward Arnold Publishers Ltd., London.

Lindsay, MM, & SP Bratton, 1979a. Grassy balds of the Great-Smoky Mountains - their history and flora in relation to potential management. *Environmental Management* **3**:417-430.

Lindsay, MM, & SP Bratton, 1979b. Vegetation of grassy balds and other high elevation disturbed areas in the Great-Smoky-Mountains-National-Park. *Bulletin of the Torrey Botanical Club* **106**:264-275.

Lindsay, MM, & SP Bratton, 1980. The rate of woody plant invasion on two grassy balds. *Castanea* **45**:75-87.

Maher, EL, MJ Germino, & NJ Hasselquist, 2005. Interactive effects of tree and herb cover on survivorship, physiology, and microclimate of conifer seedlings at the alpine tree-line ecotone. *Canadian Journal of Forest Research* **35**:567-574.

Manry, DE, & RS Knight, 1986. Lightning density and burning frequency in South African vegetation. *Vegetatio* **66**:67-76.

Mark, AF, 1958. The ecology of the southern Appalachian grass balds. *Ecological Monographs* **28**:293-336.

Marschner, H, 1995. Mineral nutrition of higher plants. Academic Press Limited, London.

Maze, KE, 2001. Fire survival and life histories of *Acacia* and *Dichrostachys* species in a South African savanna. MSc. University of Cape Town.

Meadows, ME, & HP Linder, 1993. A paleoecological perspective on the origin of afromontane grasslands. *Journal of Biogeography* **20**:345-355.

Miller, AJ, & MD Cramer, 2004. Root nitrogen acquisition and assimilation. *Plant and Soil* **274**:1-36.

Mills, AJ, 2003. Reciprocal relationships between vegetation structure and soil properties in selected biomes of South Africa. PhD. University of Stellenbosch.

Mills, AJ, KH Rogers, M Stalmans, & ETF Witkowski, 2006. A Framework for exploring the determinants of savanna and grassland distribution. *Bioscience* **56**:579-589.

Mucina, L, & MC Rutherford, 2006. The Vegetation of South Africa, Lesotho and Swaziland. South African National Biodiversity Institute, Pretoria.

Neke, KS, N Owen-Smith, & ETF Witkowski, 2006. Comparative resprouting response of Savanna woody plant species following harvesting: the value of persistence. *Forest Ecology and Management* **232**:114-123.

Nobel, PS, 1984. Extreme temperatures and thermal tolerances for seedlings of desert succulents. *Oecologia* **62**:310-317.

O'Connor, TG, 1995. *Acacia karoo* invasion of grassland: environmental and biotic effects influencing seedling emergence and establishment. *Oecologia* **103**:214 - 223.

University of Cape Town

O'Connor, TG, 2005. Influence of land use on plant community composition and diversity in Highland Sourveld grassland in the southern Drakensberg, South Africa. *Journal of Applied Ecology* **42**:975-988.

O'Connor, TG, & GJ Bredenkamp, 1997. Grassland. Pages 215 - 257 *in* R. M. Cowling, D. M. Richardson, & S. M. Pierce, editors. Vegetation of Southern Africa. Cambridge University Press, Cambridge.

O'Connor, TG, CD Morris, & DJ Marriott, 2003. Change in land use and botanical composition of KwaZulu-Natal's grasslands over the past fifty years: Acocks' sites revisited. *South African Journal of Botany* **69**:105-115.

Osmond, CB, MP Austin, JA Berry, WD Billings, JS Boyer, JWH Dacey, PS Nobel, SD Smith, & WE Winner, 1987. Stress physiology and the distribution of plants. *Bioscience* **37**:38-48.

Overbeck, GE, SC Muller, A Fidelis, J Pfadenhauer, VD Pillar, CC Blanco, II Boldrini, R Both, & ED Forneck, 2007. Brazil's neglected biome: The South Brazilian *Campos. Perspectives in Plant Ecology, Evolution and Systematics* **9**:101-116.

Partridge, TC, 1997. Evolution of landscapes. Pages 5 - 20 *in* R. M. Cowling, D. M. Richardson, & S. M. Pierce, editors. Vegetation of Southern Africa. Cambridge University Press, Cambridge.

Paton, D, 1988. Genesis of an inverted treeline associated with a frost hollow in south-eastern Australia. *Australian Journal of Botany* **36**:655-663.

Piggott, CD, 1984. The flora and vegetation of Britain: ecology and conservation. *New Phytologist* **98**:119-128.

Prior, LD, D Eamus, & D Bowman, 2004. Tree growth rates in north Australian savanna habitats: seasonal patterns and correlations with leaf attributes. *Australian Journal of Botany* **52**:303-314.

Prior, LD, D Eamus, & GA Duff, 1997. Seasonal and diurnal patterns of carbon assimilation, stomatal conductance and leaf water potential in Eucalyptus tetrodonta saplings in a wet-dry savanna in northern Australia. *Australian Journal of Botany* **45**:241-258.

Ramankutty, N, & JA Foley, 1999. Estimating historical changes in global land cover: Croplands from 1700 to 1992. *Global Biogeochemical Cycles* **13**:997-1027.

Robinson, D, 2001. dN_{15} as an integrator of the nitrogen cycle. *Trends in Ecology & Evolution* **16**:153-162.

Russell, GL, JR Miller, & D Rind, 1995. A coupled atmosphere-ocean model for transient climate change studies. *Atmosphere-Ocean* **33**:683 - 730.

Rutherford, MC, LW Powrie, & GF Midgley, 2003. ACKDAT: a digital spatial database of distributions of South African plant species and species assemblages. *South African Journal of Botany* **69**:99 - 104(106).

Rutherford, MC, & RH Westfall, 1986. Biomes of southern Africa - an objective categorization. *Memoirs of the Botanical Society of South Africa* **54**:1-98.

Sakai, A, & W Larcher, 1987. Frost survival of plants: responses and adaptation to freezing stress. Ecological Studies 62. Springer-Verlag, Berling.

Sakai, A, & P Wardle, 1978. Freezing resistance of New Zealand trees and shrubs. *New Zealand Journal of Ecology* **1**:51 - 61.

Sankaran, M, NP Hanan, RJ Scholes, J Ratnam, DJ Augustine, BS Cade, J Gignoux, SI Higgins, X Le Roux, F Ludwig, J Ardo, F Banyikwa, A Bronn, G Bucini, KK Caylor, MB Coughenour, A Diouf, W Ekaya, CJ Feral, EC February, PGH Frost, P Hiernaux, H Hrabar, KL Metzger,

University of Cape Town

HHT Prins, S Ringrose, W Sea, J Tews, J Worden, & N Zambatis, 2005. Determinants of woody cover in African savannas. *Nature* **438**:846-849.

Sankaran, M, J Ratnam, & NP Hanan, 2004. Tree-grass coexistence in savannas revisited - insights from an examination of assumptions and mechanisms invoked in existing models. *Ecology Letters* **7**:480-490.

Scholes, RJ, 1990. The influence of soil fertility on the ecology of southern African dry savannas. *Journal of Biogeography* **17**:415-419.

Scholes, RJ, & SR Archer, 1997. Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics* **28**:517-544.

Scholes, RJ, & BH Walker, 1993. An african savanna: synthesis of the Nylsvley study. Cambridge University Press, Cambridge.

Schulze, RE, 1997. South African atlas of agrohydrology and climatology. Report TT82/96. Water Research Commission, Pretoria.

Schulze, RE, & M Maharaj, 2003. Development of a database of gridded daily temperatures for southern Africa. University of Natal, Pietermaritzburg, RSA, School of Bioresources Engineering and Environmental Hydrology. ACRUcons Report, 41. pp 81.

Schulze, RE, & OS McGee, 1978. Climatic indices and classifications in relation to the biogeography of southern Africa. Pages 19-34 *in* M. J. A. Werger & A. C. van Bruggen, editors. Biogeography and Ecology of Southern Africa. Dr W Junk, The Hague.

Schutz, AEN, 2007. Surviving the fire-trap : resprouting and carbohydrate partitioning of Acacia karroo after topkill. MSc. University of Cape Town.

Scott, L, 1989. Late Quaternary vegetation history and climatic change in the eastern Orange Free State, South Africa. *South African Journal of Botany* **55**:107-116.

Shaw, RH, 1954. Leaf and air temperatures under freezing conditions. *Plant Physiology* **29**:102-104.

Sherry, SP, 1971. The black wattle (*Acacia mearnsii*. De Wild.). University of Natal press, Pietermaritzburg.

Silberbauer-Gottsberger, I, W Morawetz, & G Gottsberger, 1977. Frost damage of cerrado plants in Botucatu, Brazil, as related to the geographical distribution of the species. *Biotropica* **9**:253-261.

Staver, AC, 2007. Spatial and temporal variability in *Acacia* population dynamics. MSc. University of Cape Town.

Swartz, PP, 1982. A numerical-taxonomical evaluation of the taxon *Acacia karroo* Hayne in southern Africa. MSc thesis. University of Pretoria, South Africa.

Swinbank, WC, 1963. Long-wave radiation from clear skies. *Quarterly Journal of the Royal Meteorological Society* **89**:339-348.

Tainton, NM, 1981. Veld and pasture management in South Africa. Shuter & Shooter, Pietermaritzburg.

Tainton, NM, & MT Mentis, 1984. Fire in grassland. *in* P. d. V. Booysen & N. M. Tainton, editors. Ecological effects of fire in South African ecosystems. Springer-Verlag, Berlin.

Tchienkoua, JM, R Njomgang, C Nolte, N Sanginga, & J Takow, 2008. Relationship of soil qualities to maize growth under increasing phosphorus supply in acid soils of southern Cameroon. *Pedosphere* **18**:645-652.

Tinley, KL, 1982. The influence of soil moisture balance of ecosystem patterns in southern Africa. Pages 175 - 192 *in* B. J. Huntley & B. H. Walker, editors. Ecology of Tropical Savannas. Springer-Verlag, Berlin.

University of Cape Town

Titshall, LW, TG O'Connor, & CD Morris, 2000. Effect of long-term exclusion of fire and herbivory on the soils and vegetation of sour grassland. *African Journal of Range and Forage Science* **17**:70-80.

Trollope, WSW, 1974. The role of fire in preventing bush encroachment in the Eastern Cape. *Proceedings of the Grassland Society of South Africa* **9**:67 - 72.

Trollope, WSW, 1982. Ecological effects of fire in South African savannas. *Ecological Studies* **42**:292-306.

Trollope, WSW, 1984. Fire in Savanna. Pages 149 - 176 *in* P. d. V. Booysen & N. M. Tainton, editors. Ecological Effects of Fire in South African Ecosystems. Springer-Verlag, Berlin.

van Auken, OW, 2000. Shrub invasions of North American semiarid grasslands. *Annual Review of Ecology and Systematics* **31**:197-215.

van Coller, A, & WD Stock, 1994. Cold tolerance of the southern African succulent, *Cotyledon orbiculata* L. across its geographical range. *Flora* **189**:84-89.

van Wilgen, BW, HC Biggs, SP O'Regan, & N Mare, 2000. A fire history of the savanna ecosystems in the Kruger National Park, South Africa, between 1941 and 1996. *South African Journal of Science* **96**:167-178.

Vitousek, PM, OA Chadwick, TE Crews, JH Fownes, DM Hendricks, & DA Herbert, 1997. Soil and ecosystem development across the Hawaiian islands. *GSA Today* **7**:1 - 8.

Walker, BH, 1987. Determinants of tropical savannas. UK:IRL, Oxford.

Walker, BH, & I Noy-Meir, 1982. Aspects of the stability and resilience of savanna ecosystems. Pages 556 - 590 *in* B. J. Huntley & B. H. Walker, editors. Ecology of Tropical Savannas. Springer-Verlag, Berlin.

Walter, H, 1971. Ecology of Tropical and Subtropical Vegetation. Oliver &Boyd, Edinburgh.

Walter, H, 1979. Vegetation of the earth and ecological systems of the geo-biosphere. Springer-Verlag, New York.

Weaver, JE, 1954. North American Prairie. Lincoln Press, New York.

Webb, LJ, 1964. Historical Interpretation of Grass Balds of Bunya Mountains South Queensland. *Ecology* **45**:159-&.

Wedin, DA, LL Tieszen, B Dewey, & J Pastor, 1995. Carbon-Isotope Dynamics During Grass Decomposition and Soil Organic-Matter Formation. *Ecology* **76**:1383-1392.

Werger, MJA, & BJ Coetzee, 1978. The Sudano-Zambezian region. Pages 301 - 462 *in* M. J. A. Werger, editor. Biogeography and Ecology of Southern Africa. Junk, The Hague.

Westfall, RH, CS Everson, & TM Everson, 1983. The Vegetation of the Protected Plots at Thabamhlope-Research-Station. *South African Journal of Botany* **2**:15-25.

White, F, 1983. The vegetation of Africa. UNESCO, Paris.

Wigley, BJ, MD Cramer, & WJ Bond, 2008. Sapling survival in a frequently burnt savanna: mobilisation of carbon reserves in *Acacia karroo*. *Plant Ecology*.

Williams, RJ, BA Myers, WJ Muller, GA Duff, & D Eamus, 1997. Leaf phenology of woody species in a North Australian tropical savanna. *Ecology* **78**:2542-2558.

Woodward, FI, 1975. The climate control of the altitudinal distribution of *Sedium rosea* (L.) Scop. and *S. telephium* L. II. The analysis of plant growth in controlled environments. *New Phytologist* **74**:335-348.

University of Cape Town

References

Wynn, JG, MI Bird, & VNL Wong, 2005. Rayleigh distillation and the depth profile of C-13/C-12 ratios of soil organic carbon from soils of disparate texture in Iron Range National Park, Far North Queensland, Australia. *Geochimica Et Cosmochimica Acta* **69**:1961-1973.

University of Cape Town