

**Local versus landscape effects of bush encroachment on
plant available light, soil moisture, frost occurrence and
herbaceous productivity and composition**

Thesis submitted in fulfilment of the requirements for the degree of
MASTER OF SCIENCE of RHODES UNIVERSITY

By

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March 2015

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Abstract

Bush encroachment is a global phenomenon and a pressing concern for South African rangelands. The expansion and increase in density of *Vachellia karroo* (hereafter referred to as *Acacia karroo*) has been documented in the Eastern Cape and KwaZulu Natal in South Africa. This increase in woody species in savannas is often at the expense of grass cover and thus is causing concern about how this will impact agriculture due to possible loss of grazing capacity. To understand the impacts of bush encroachment the effect of trees on their micro-climate and abiotic factors and in turn on the herbaceous layer needs to be examined. The objective of this study was to quantify the effect of *Acacia karroo* encroachment on the light environment, soil moisture and frost occurrence in the sub-canopy and inter-canopy micro-habitats, and how these changes affected herbaceous plant productivity and composition. Another question that is being addressed here is whether, and how, the local tree effects scale up in the landscape and whether prediction can be made based on the effects of individual trees. The study was undertaken on a farm, Endwell, in the Smaldeel, Eastern Cape. At the study site, a semi-arid savanna, *Acacia karroo* has been encroaching since the 1980's. The study was conducted at three scales: landscape, stand-wide and local scale. The landscape scale was represented by four areas with 0, 21, 45 and 72% tree canopy cover, the stand-wide scale consisted of transects with varying percentages of tree canopy cover within each of the four levels of encroachment. The local scale was represented by the sub-canopy and inter-canopy environment to test the effect of trees.

At the local scale plant available light and soil moisture were lower in the sub-canopy than inter-canopy regions, with leaf area index being higher in the sub-canopy. This local negative effect of the tree canopy on light and soil moisture in the sub-canopy did not scale up predictably in the landscape. At the stand-wide scale light in the inter-canopy was reduced as shading increased. Frost was excluded from under the canopies and frost incidence decreased at higher tree cover. Grass productivity was reduced in the sub-canopy, possibly due to lower light and soil moisture. Overall biomass increased from the low to medium level of encroachment but lowest at the high level of encroachment. Grass composition and cover was only slightly affected by tree canopy cover and C₄ grass species were still present in the sub-canopy and at lower light environments. At the levels of *Acacia karroo* encroachment encountered at this study site, it seems unlikely that palatable or desirable C₄ would be excluded from the system and that a shift from C₄ to shade-tolerant species would occur. This is due to tree canopies at the site not reducing light to such an extent that they would outcompete grasses, and likely the very low grazing pressure at these

sites. Herbaceous biomass at these sites were still sufficient to carry a fire in the inter-canopy region and sufficient grazing for herbivores. In the sub-canopy region fires will be excluded thus with higher the portion of sub-canopy areas increasing at the high levels of encroachment they may interrupt fire spread. Thus it was concluded that *Acacia karroo* encroachment up to 45% tree cover is currently not creating negative feedback on herbivory, but low stocking rates appear to be key to maintain this.

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Acknowledgements

Thank you to Dr. Susanne Vetter and Prof. Brad Ripley for giving me the opportunity to do a postgraduate degree and their guidance and as support throughout the duration of this study.

Thanks to Rhodes University for funding of the Masters Degree (Sandiswa Imbewu).

Thank you to Derek, Anne and Tony Painter for granting me access to their farm and their warm hospitality and assistance. Also a warm thanks to Alwyn Davies for assistance on the farm.

Thanks to all the people who assisted with field work and for their company during field trips (Sattar Sacranie, Nelene, Theuns and Geraldine Klopper, Ruan Scheepers, Kyle Snow and Matt Janks).

Thanks to Mardi Nolands and Riaan Strauss for all the assistance with organising field trips and field equipment.

Thank you to Andrew Skowno for help with the site map and providing aerial photographs.

Declaration

This dissertation, submitted for the degree of Master of Science in the Department of Botany, Rhodes University, represents original work by the author and has not been submitted in any form to any other institution. Where mention has been made of the work of others, it has been duly acknowledged in the text.

A handwritten signature in black ink that reads "Ckloppe". The signature is written in a cursive style and is positioned above a solid horizontal line.

CHRISNA KLOPPER

I certify that the above statement is correct.

A handwritten signature in black ink that reads "S. Vetter.". The signature is written in a cursive style.

Dr. S. VETTER

Supervisor

Chapter 1: Introduction

1.1. Background

Savannas are one of the world's major biomes, covering approximately one fifth of the global surface (Sankaran *et al.* 2004) and is important from both a socio-economic and conservation point of view (Scholes & Archer, 1997; Sankaran *et al.* 2005). Savannas are mixed plant communities consisting of a continuous grass layer and discontinuous woody layer (Scholes & Archer, 1997; Scholes, 2003). In tropical and sub-tropical savannas the herbaceous layer is generally dominated by C₄ grasses and the woody layer by C₃ trees and shrubs (Ratnam *et al.* 2011). The presence of C₄ grasses distinguishes these savannas from forests or thickets which are dominated by C₃ grasses, shrubs and trees (Ratnam *et al.* 2011). C₄ grasses have two key features: they are generally fire tolerant and shade intolerant, whereas C₃ grasses are more shade tolerant and fire intolerant (Ratnam *et al.* 2011). C₄ grasses are highly productive during the growing season and dry out quickly during the dry season, decomposing slowly to provide fuel which drive fires in savanna systems (Lehmann *et al.* 2011). The characteristics of the herbaceous layer, and in particular its continuity and flammability, are key to maintaining savanna structure and function, and are sensitive to increased woody cover (Bond 2008, Ratnam *et al.* 2011).

The relative abundance of trees and grasses in savannas is determined by climate, soil properties, and disturbance such as fire and herbivory (Vetaas, 1992; Sankaran *et al.* 2004; Archibald *et al.* 2005; Kraaij & Ward, 2006). In arid and semi-arid environments, climate plays an important role in regulating tree densities, whereas in mesic savannas, disturbances are more important in shaping and maintaining the tree-grass relationship. In arid and semi-arid savannas woody production is constrained by water availability and is thus strongly influenced by mean annual rainfall, allowing tree-grass coexistence (Sankaran *et al.* 2005). In mesic savannas, water is less of a limiting factor to tree establishment, and disturbances such as fire and herbivory interact to control woody cover (Staver *et al.* 2011). High browsing pressure in mesic savannas can suppress seedling establishment and even growth, which extends the period during which they are more prone to fire damage, suppressing the transition to mature adults (Roques *et al.* 2001; Balfour & Midgley, 2008). Long term fire exclusion in wet savannas can lead to greatly increased woody cover; this in turn leads to shifts in herbaceous species composition from fire tolerant to more shade tolerant grass and forb species. Ultimately, increased woody cover can result in a biome shift from fire tolerant

and flammable savanna vegetation to fire-free and shade tolerant forest or thicket. Bush encroachment is a global phenomenon (O'Connor *et al.* 2014) that is predicted to result in widespread loss of C₄ dominated grasslands and savannas, with important conservation and economic consequences (Bond 2008, Bond & Parr 2010). A better understanding of how increased woody cover affects the grass layer, and in particular at what densities functional switches to a less flammable grass layer occurs, thus has important management consequences.

1.1.1. Tree influence on abiotic environment and herbaceous layer

Trees play a vital role in savannas. Their presence can alter vegetation composition and production, resource availability and the micro-climate in the sub-canopy and inter-canopy environments (Scholes & Archer, 1997; Treydte *et al.* 2007). Historically, trees occurring in savannas have been viewed as competitors for grasses, but trees can have positive, neutral or negative effects on their immediate environment. Trees positively affect their immediate environment through facilitation and negatively through competition; generally the effect of trees on grasses is a combination of these two processes (Holmgren *et al.* 1997). The net outcome will depend on the climate, resource availability and frequency and intensity of disturbances such as fire and herbivory, as well as the species-specific characteristics of the tree and the grasses in its vicinity (Vetaas, 1992; Ludwig *et al.* 2004; Treydte *et al.* 2007). The interaction and strength of the effect that a tree has on its surrounding environment decreases with distance from the tree and also depends on the characteristics of the tree in question, for example whether or not it is a nitrogen-fixer (Stuart-Hill & Tainton, 1989a; Soliveres & Eldridge, 2014). In savannas, the presence of trees creates three spatially distinct habitats: 1) the sub-canopy area, 2) the rooting zone beyond the canopy, and 3) the open savanna area outside of the rooting zone (Scholes, 2003). At high tree densities, the open area beyond the rooting zone decreases as the rooting zones overlap with increased tree density (Breshears, 2006). In the sub-canopy area there is competition between tree and grasses for resources such as light, water and nutrients. The amount of plant available light is decreased in the sub-canopy environment. Closer to the trees there can be a minor shade effect but the main factor is competition for soil resources (Scholes, 2003). In some cases, increases in soil moisture and nutrients (Hagos & Smit, 2005; Augustine & McNaughton, 2006) have been found under tree canopies, although decreases in soil moisture have also been documented. Only small areas in savannas completely escape the effect of trees, and this area decreases as tree cover increases (Scholes, 2003). Within their rooting zones, trees affect resource availability and

microclimate in both positive and negative ways. These changes in abiotic environment affect the grass layer, resulting in changes in composition, cover and productivity (Abule *et al.* 2005).

Light and rainfall is intercepted by the canopy reducing the photosynthetically active radiation (PAR) and rainfall that reaches the understory environment (Skarpe, 1992; Scholes & Archer, 1997). Shading in the sub-canopy area can reduce the ambient temperature and decrease the evaporative demand of plants (Amundson & Belsky, 1995). Rainfall is intercepted by the canopy and is redistributed reaching the sub-canopy environment through stem-flow, fall through or along the drip line. The interception and loss of water via the tree canopy and increased root competition can potentially create drier sub-canopy compared to the inter-canopy region. In contrast some studies have found the soil moisture in the sub-canopy to be higher than the inter-canopy zone. The amount of soil moisture in the sub-canopy environment depends on the amount of rainfall reaching the understory. This is determined by how heavy the rainfall event was, as well as the tree species and specific characteristics (Belsky *et.al.* 1989). The effects that trees have on their environment may vary with season. In arid and semi-arid savannas trees may have a net positive effect on the understory during the dry season as shading increases soil moisture (Ludwig *et al.* 2001) and can prolong the growing season compared to the inter-canopy environment. During the wet season, trees can improve the nutrients status of grasses and enhance growth (Treydte *et al.* 2007). Tree species can increase available soil nutrients under their canopies, but the extent of this varies between species and also with tree age and size. Soil organic matter and soil N, P and Ca have been found to be significantly higher under tree canopies than in the area outside the canopy (Belsky *et al.* 1993). Trees in savannas are referred to as ‘islands of fertility’ due to the increased soil nutrients status under the canopy (Belsky *et al.* 1989; Treydte *et al.* 2010). Three mechanisms have been proposed by which trees can better the nutrient status of the soil: 1.) acting as a nutrient pump, 2) trapping atmospheric dust and 3.) herbivore deposits under the canopy (Scholes & Archer, 1997; Augustine & McNaughton, 2006). In Southern African savannas increased soil nutrients and higher soil fertility under tree canopies have been documented as a result of the tree acting as a nutrient pump and bringing nutrients from deeper soils up to the surface and dung from animals gathering under trees enriching the soil (Ludwig *et al.* 2004; Ludwig *et al.* 2001; Treydte *et al.* 2007).

In cases where the presence of the tree suppresses grass productivity the percent bare ground increases, which makes the area more prone to water loss through surface runoff (Scholes &

Archer, 1997). The effects on the abiotic condition under tree canopies at different densities will directly affect the vegetation. With increased tree cover, the C₄ grass species dominating in the more open areas will become scarcer and replaced by more shade tolerant C₃ grass and forb species that thrive under tree canopies (Ratnam *et al.* 2011). Herbaceous biomass has been shown to decrease with increased tree cover and density (Riginos *et al.* 2009; Smit, 2004).

1.1.2. The effects of tree age, size and density

Tree size and age can determine the extent to which the presence of a tree affects the surrounding environment. Smaller trees may facilitate by shading and reducing evapotranspiration (Amundson & Belsky, 1995), whereas larger trees may have a stronger competitive effect (Vetaas, 1992). Tree size and architecture, as well as the tree species, will influence the amount of light that is intercepted and how much of a shading effect the tree has on its surrounding environment (Ludwig *et al.* 2004; Soliveres & Eldridge, 2014). The amount of rainfall intercepted by the canopies is positively correlated to canopy size, thus larger canopies will result in less water reaching the sub-canopy and thus drier soils (Vetaas, 1992). The water that is intercepted by the canopy will either be re-distributed into the atmosphere through evapotranspiration or dripping off at the edges of the tree canopy (Vetaas, 1992). Large individual *A. karroo* trees can influence the vertical water distribution in the soil layer as far as 2.5m away from the stem (Stuart-Hill & Tainton, 1989a). The amount of soil moisture available also depends on the trees species in question as well as the intensity of the rainfall event. Large individual trees contribute to the availability of soil nutrients this becomes more pronounced with older trees where soil nutrient content is significantly higher under the canopies (Ludwig *et al.* 2004; Grellier *et al.* 2103). The increase in soil nutrients benefits the grass species found in the sub-canopy and as a result, these grasses have higher nutrient content and are more favourable for grazing (Ludwig *et al.* 2001; Treydte *et al.* 2009).

Compared to individual trees bush clumps or high tree densities have a net negative effect on the herbaceous layer, but trees at intermediate to low cover generally have a net positive effect depending on the tree species and the environmental conditions (Angassa *et al.* 2012). Increased tree density and canopy cover amplifies the individual tree effect, but can also alter the net effect of trees on the herbaceous layer, for example from a positive effect on soil moisture due to shading to a negative one through greatly increased root competition (Smit,

2005). With increased tree density, the overall shading effect increases, as does the effect of root competition. With increased tree density, grass productivity thus decreases at high tree density. This reduces the grazing capacity of an area, and if grazer densities are not reduced in response, this leads to increased grazing pressure on the remaining grass species (Angassa, 2005). This cycle results in the loss of palatable grass species and can create the opportunity for more trees to establish, leading to even higher trees densities (Scholes & Archer 1997; Simioni *et al.* 2000; Ludwig *et al.* 2004).

1.1.3. Bush encroachment

Bush encroachment is a global phenomenon which has been documented in North and South America (Staver *et al.* 2011; Ratajczak *et al.* 2012), Australia (Burrows *et al.* 1990) and Africa (Roques *et al.* 2001; O'Connor *et al.* 2014). It is seen as one of the most pressing concerns in South African rangelands (O'Connor *et al.* 2014) and is likely to have serious negative impacts on the agriculture and conservation sectors (Scholes & Archer, 1997; O'Connor *et al.* 2014). Bush encroachment is defined as the expansion and increase in density of an indigenous woody species in its original domain at the expense of grass cover (O'Connor, 1995; Hudak & Wessman, 1998; Richter *et al.* 2001). In the last 50 years woody cover in South Africa has significantly increased across a variety of land uses (Wigley *et al.* 2010; Buitenwerf *et al.* 2012). An estimated 10 – 20 million ha⁻¹ of land has been encroached by woody species, and the area affected is increasing at a rate of 0.041% y⁻¹ to 1.275% y⁻¹ throughout South Africa (Ward, 2005; O'Connor *et al.* 2014). Bush encroachment is driven by both local factors, including changes in land management (farming practices, exclusion of large herbivores), altered fire regimes and variation in rainfall, and global factors such as long-term climate change and increased CO₂ concentrations (O'Connor *et al.* 2014). In arid and semi-arid savannas, the increase in bush density has been attributed to changes in mean annual rainfall interacting with other factors such as overgrazing (Angassa, 2005; Kraaij & Ward, 2006). In mesic savanna, changes in fire regimes have been cited as one of the major contributors to woody cover change (Bond *et al.* 2003; Bond & Midgley, 2012). Current theories suggest the increase in CO₂ concentrations has led to global changes in woody cover, with this factor interacting with local drivers resulting in increased tree cover (Wigley *et al.* 2010; Buitenwerf *et al.* 2012). The increase in CO₂ concentrations increases the growth and carbon storage of woody plants and allows them to increase in abundance, especially when other factors such as overgrazing or years with above or below average rainfall come into play (Bond & Midgley, 2000; Bond, 2008; O'Connor & Chamane, 2012).

As woody cover increases, changes in microclimate, soil resources and herbaceous layer characteristics can be expected. This will become more prominent at higher tree densities. Since bush encroachment results in the suppression of grass species grazing capacity of encroached areas is generally reduced, which has a negative impact on livestock farming and conservation (Britz & Ward, 2007; Riginos & Grace, 2008). The feedback effects between fire, herbivory and tree establishment and growth that help to contain tree densities in savannas are altered by bush encroachment (Bond & Keeley, 2005; Gillson & Ekblom, 2009; Riginos, 2015). The increased cover and abundance of less flammable C₃ plant species under dense tree cover can also lead to savanna systems becoming less fire prone (Ratnam *et al.* 2011). Once a critical threshold of tree density has been reached, an irreversible switch to closed woody vegetation thus becomes increasingly probable.

1.1.4. Scale: Local vs. landscape

The effect of trees on the microclimate, soil resources and the herbaceous layer has generally been studied at two different scales (Scholes & Archer, 1997). At the local tree scale, the focus has been on the effect of individual trees on the sub-canopy environment, while at the landscape scale, the effect of tree density has been studied on herbaceous composition and productivity at the scale of the entire stand or grazing camp (Scholes & Archer, 1997; Riginos *et al.* 2009). Studies at these two scales have led to different conclusions about the effect of trees on their environments. Scattered individual trees were generally found to have a net positive effect on the abiotic environment and herbaceous layer directly beneath their canopy and/ or surrounding environment (Belsky, 1989; Stuart-Hill & Tainton, 1989b; Ludwig *et al.* 2001; Treydte *et al.* 2007), while negative effects of tree density have been recorded at the landscape scale (Mordelet & Menaut, 1995; Riginos *et al.* 2009).

Many studies undertaken at an individual tree level have documented the positive effects of single trees on the sub-canopy environment and grass production (Riginos *et al.* 2009). At the local tree scale, the microclimate in the sub-canopy is affected by the individual tree, and the specific characteristics of that tree determine the magnitude of these effects (Stuart-Hill & Tainton, 1989b; Scholes & Archer, 1997). Some studies have looked at the effect of higher tree densities or bush encroachment on sub-canopy environment and grass production and have generally found contradictory results as they documented both positive and negative effects depending on tree species and the climate and environment in which the study took place (Scholes & Archer, 1997; Smit, 2005). The positive or negative effects of individual

trees at local scale may change when tree density increases, and the effects of individual trees thus do not necessarily scale up directly to the landscape level. The net effect at the landscape level will be influenced by tree density, with increased tree density usually resulting in a net negative landscape effect on the herbaceous layer (Scholes & Archer, 1997; Riginos *et al.* 2009). Whether the effect of tree density at landscape scale is the reason for the changes in grass cover and productivity is not clear. Factors such as rainfall (Sankaran *et al.* 2005), increased competition between tree and grasses as well as overlapping in the roots and canopies of trees (Breshears, 2006) or other factors such as herbivory or fire could be driving changes at the landscape level (Riginos & Grace, 2008).

Considering these different results it is surprising that only a few studies have attempted to integrate these two approaches to determine how, and by what mechanisms, the local tree effects on the sub-canopy and inter-canopy scale up to the landscape scale under different tree densities (Teague & Smit, 1992; Breshears, 2006; Riginos *et al.* 2009). The way the effects of individual trees scale up to landscape level is affected by the level of tree encroachment (Riginos *et al.* 2009). Trees alter their environment, and by intercepting light and soil moisture they create a heterogeneous mosaic of inter-canopy and sub-canopy patches. Because tree density affects the characteristics of these patches it can potentially alter feedback effects, thus it is important to understand how these individual effects change from the local tree scale to the landscape scale (Breshears, 2006). From a management point of view, it is important to understand how changes in the relative proportion of woody plants in a savanna influence ecological processes, especially feedbacks on fire and herbivory that further affects the likelihood of further encroachment (Riginos *et al.* 2009). A key question which arises from this is how the effects of trees on the characteristics of the herbaceous layer scale up, and whether it is possible to make prediction about how different tree densities might influence their environment.

1.2. Research aims and objective

The objective of this study was to quantify the effects of varying degrees of *Vachellia karroo* (henceforth referred to as *Acacia karroo*) encroachment on the light environment, soil moisture and frost occurrence in the sub- and inter-canopy microhabitats, and how the resulting changes in each microhabitat affected the composition and productivity of the herbaceous layer. This study examined whether, and how, the effects of individual trees on

the sub-canopy microhabitat scaled up to stand-wide and landscape light availability, soil moisture and herbaceous composition and productivity.

Three different scales were used in this study to answer the question of how the effects of individual trees scaled up from local to landscape scale. The *local scale* or ‘local tree effect’ examines the influence of the presence of a tree canopy on the sub-canopy environment compared to the inter-canopy environment. The *stand-wide scale* represented various tree canopy covers along 12 transects (50 m long), with each individual transect having a different tree canopy cover. This will be used to determine how local effect of tree canopies (sub-canopy vs. inter-canopy micro-habitats) compare at each tree canopy cover and if these effects scale up along a gradient of increasing cover. Lastly the landscape scale, this will compare these effects (at the local tree scale) at four different degrees of bush encroachment. The landscape scale takes into consideration a much larger area (100 m x 50 m) and the tree cover across the landscape will be considered. The landscape, stand-wide and local scales represent areas of several 0.5 hectares, < 500 m² and a few m², respectively

Predictions based on the local tree effect and how this scales up at the stand-wide cover were based on a study by Riginos et al. (2009). This study compared how the tree affects plant available light (% transmittance and photosynthetically active radiation) and the herbaceous basal cover the sub-canopy and inter-canopy micro-habitats and whether this local effect changes with increased tree canopy cover. The hypothetical outcomes of this are represented in Figure 1.1. Thus the presence of the tree and the stand-wide tree cover can either have positive, negative or no effects on the herbaceous layer. By looking at the relationship between the local tree effect and tree canopy cover the prediction about how these effects scale up can be made.

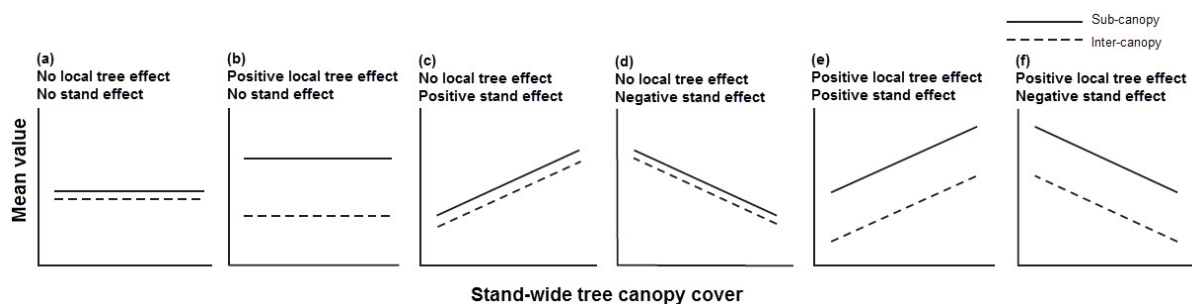


Figure 1.1: Diagrams showing the theoretical effects of the sub-canopy and inter-canopy on the mean values of the abiotic factors (light transmittance, photosynthetically active radiation and leaf area index – Chapter 3) and herbaceous basal cover (Chapter 4) across the stand-wide tree canopy cover gradient (Source: Riginos et al. 2009).

Riginos et al. (2009) also used the herbaceous productivity in the sub-canopy and inter-canopy to make calculation to determine the expected values for herbaceous biomass as a function of percent tree canopy cover. This was then compared to the stand-wide herbaceous productivity (across both micro-habitats) for each tree canopy cover point. This gave some insight into how predictions made based on data collected from one tree density would scale up at different tree densities and whether the assumption can be made that the effect will scale up linearly. The hypothetical outcomes are represented in Figure 1.2. I will be applying this to leaf area index, % light transmittance, PAR and herbaceous basal cover at various percentages of tree canopy cover. This will be used to determine whether these factors scale up with increased tree cover and whether predictions can be made based on the findings at a given percent tree cover.

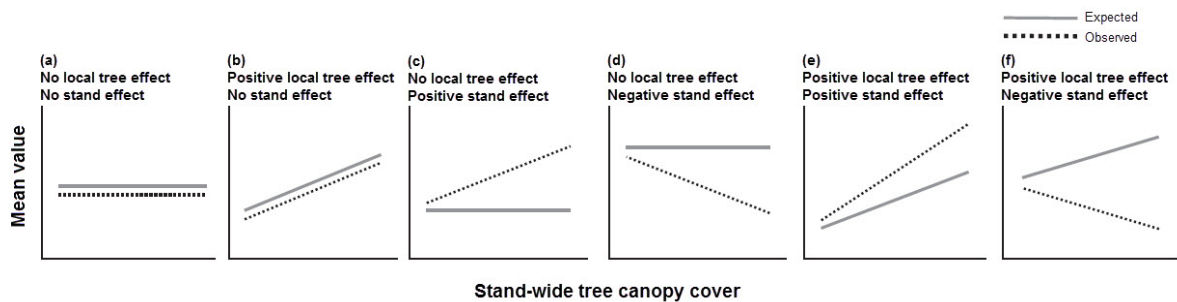


Figure 1. 2: Diagram showing how the theoretical mean observed values for the abiotic factors (light transmittance, PAR and LAI) can change with tree canopy cover and how the patterns can agree or vary from the mean expected abiotic values (Source: Riginos *et al.* 2009).

1.3. Thesis overview

Bush encroachment is a pressing concern in South Africa. Understanding the effects of varying degrees of encroachment at different scales on the abiotic environment and herbaceous layer is important for informing management plans and conservation of the savanna biome. In view of this, the study aims to answer the following questions:

- 1.) How do tree canopies affect leaf area index, light transmittance and photosynthetically active radiation at the local and landscape scale at different stages of bush encroachment and do the local tree effects scale up in the landscape? This topic will be addressed in Chapter 3

2.) How do tree canopies affect the herbaceous productivity and composition at the local and landscape scales and do the local tree effects scale up in the landscape? This topic will be addressed in Chapter 4

The focus in Chapter 2 will be on the study site and to quantify bush encroachment at the selected sampling sites. Tree canopy cover at the landscape and stand-wide scale will be examined as well as quantifying the tree layer in terms of size and density. In Chapter 3 the effect of trees at the three scales on the leaf area index (LAI), plant available light (percent transmittance and PAR) and soil moisture. Here prediction about how these factors scale up from the local tree scale to the stand-wide tree scale will be made. How these abiotic factors respond to tree cover is important as the changes in plant available light and soil moisture as these changes are likely to influence the herbaceous layer. Thus understanding how trees influence these factors will also help understand the responses of the herbaceous layer at different scales. It likely that it will be a combination of the changes in plant available light and soil moisture and not just tree density that will results in changes in the herbaceous layer productivity and composition. In Chapter 4 herbaceous cover and composition and productivity will be examined at three scales. The effects of local tree scale and stand-wide tree scale on individual grasses will also be addressed and how these effects scale up at stand-wide cover. The impact of plant available light on the occurrence of grasses and the shifts in dominance will also be determined. In Chapter 5 the key findings in this study and their implications for the savanna ecosystem feedbacks and agriculture and conservation will be discussed.

Chapter 2: Overview of study sites and quantification of *Acacia karroo* encroachment

2.1. Introduction

When looking at the effects of bush encroachment on the herbaceous layer and abiotic conditions it is important to consider the density of the trees at the encroached areas as well as the size of the individual trees and tree biomass across the landscape. The density as well as tree size will determine the degree to which trees may affect their environment through shading and root competition. Tree density (number of tree.ha⁻¹), tree size and above ground tree biomass was expected to be higher at the more encroached sites. Tree basal area of savanna trees have been found to correlate with above ground tree biomass (Shackleton, 1998; Shackleton & Scholes, 2011) and is thus a “key metric of above ground woody biomass” (Lehmann *et.al.*2014). Basal area was used to describe tree size and as a proxy to compare above ground tree biomass between sites.

The mean and range of tree sizes at each of the sites also gives an indication of the length of time for which the sites have been encroached. If bush encroachment were an ongoing process resulting in increased tree density over time (as opposed to a single cohort of trees “escaping” once-off), the more densely encroached sites would be expected to reflect a longer history of encroachment. If this is the case, tree size would be expected to be highest at the highest level of encroachment. I expected the low and medium levels of encroachment to reflect more recently encroached sites and predicted them to have smaller trees. Alternatively, if bush encroachment occurred primarily via a single cohort of trees establishing in a particularly favourable year, I would expect tree size to be relatively uniform across sites. The process through which the area has become encroached can be determined by studying aerial photographs taken over several years.

The aim of this chapter is to introduce the study area and explain how the sites where sampling took place were selected. Tree encroachment on the farm was examined and the tree size at the sites was determined. This was done to establish when these sites became encroached and to give an indication of the age of the trees.

2.2. Study Area

This study will focus on various degrees of canopy cover at four stages of encroachment by *Acacia karroo*. *Acacia karroo* has been one of the major encroaching species in the Eastern Cape and KwaZulu Natal, expanding its distribution and increasing in density (Balfour & Midgley, 2008). It is one of the main species encroaching in the Amathole Montane grassland, Bisho Thornveld and Eastern Cape Thicket vegetation (Dube *et.al.*, 2011). Documentation of the encroachment by *Acacia karroo* in the Eastern Cape dates back to 1890's and has been recorded since the 1950's (Acocks 1953, O'Connor *et al.* 2014).

2.2.1 Location

The study site is located in the Smaldeel region in the Eastern Cape, South Africa. The Smaldeel region spans approximately 130km in a west/east direction from Somerset East to Fort Beaufort. The boundary in the north lies along the Bosberg, Winterberg, Elandsberg and Amatola mountains and in the south along the Fish River (Martens *et al.* 1996). The area spans approximately 0.63Mha (Danckwerts & Marais, 1989) and the predominant land use is commercial livestock farming (Martens *et al.* 1996).

The study was done on the farm "Endwell" situated 30km west of Fort Beaufort (Figure 2.1). The farm is predominantly used for cattle farming and has low stocking rates (4 ha.LSU⁻¹). The farm has had a 40 to 60% increase in *Acacia karroo* cover between 1985 and 2009 (Figure 2.3). Fire and other methods of bush control have been excluded from farming practice in the known history of the farm. The only exception to this took place in 1966, when the entire farm was manually cleared of all unwanted tree species including *Acacia karroo*. In recent years, trees in small selected areas on the farm have been poisoned (in 2006). Small livestock such as goats were removed from the farm 20 years ago. The farm has low numbers of game including greater kudu (*Tragelaphus strepsiceros*), impala (*Aepyceros melampus*), waterbuck (*Kobus ellipsiprymnus*) and common duiker (*Sylvicapra grimmia*).

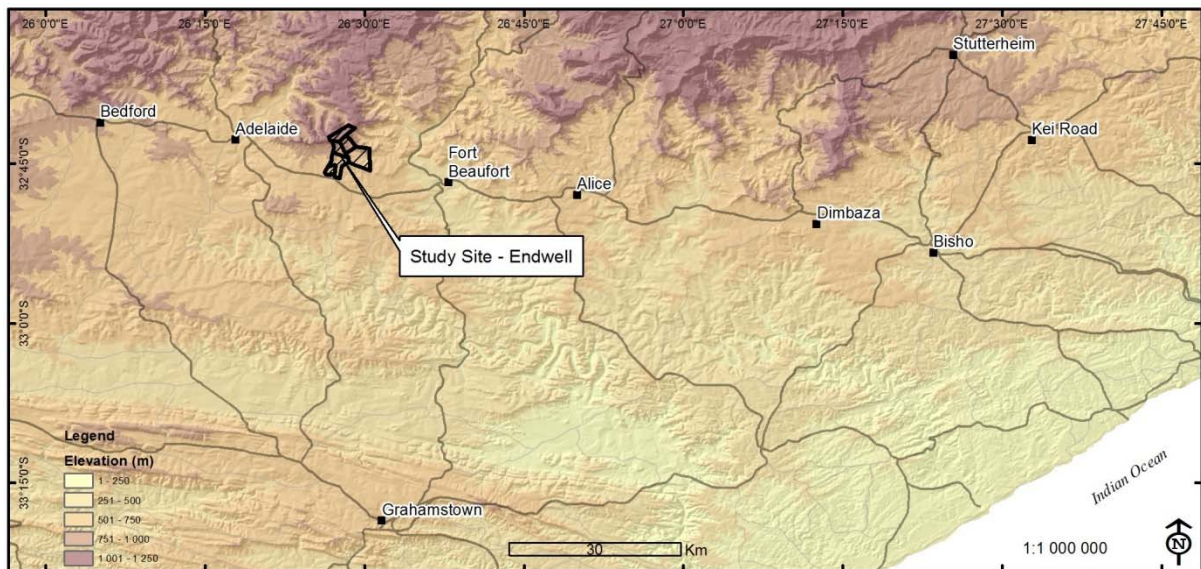


Figure 2.1: The location of the study site (Endwell farm), in the Eastern Cape, South Africa (Supplied by Andrew Skowno).

2.2.2 Vegetation

The vegetation in the area was classified by Acocks (1953) as False Thornveld of the Eastern Cape, and was more recently reclassified by Mucina and Rutherford (2006) as a mixture of Bedford Dry Grassland and Bisho Thornveld. The area is typical semi-arid savanna with a mixture of tree and grass species. The dominant tree species in this area is *Acacia karroo* (Acocks, 1953). *A. karroo* has always occurred in this area mostly as isolated individuals, with a recent increase in density. This is evident from the aerial photographs in Figure 2.3. Other large woody species such as *Olea europaea* and shrubs such as *Scutia myrtina* also occur in the area, but at very low numbers in the sites selected for sampling. These shrub species are usually associated with clumps of *Acacia karroo* and grow at the base of the tree. The most abundant grass species occurring in this area are *Themeda triandra*, *Sporobolus africanus*, *Cymbopogon caesius*, *Digitaria eriantha* and *Eragrostis curvula* (Mucina & Rutherford, 2006). Forage in this veld type has high protein content sufficient to sustain cattle farming throughout the dry season and is characteristic of warm savannas with fertile soils (Scholes, 1990).

2.2.3 Climate and soils

The Smaldeel has a mean annual rainfall fall of 450mm – 650 mm, with distinct wet and dry seasons. Most rain falls during the summer months, with bimodal peaks in March and October (Martens *et.al.*, 1996). The farm on which the study took place has a higher average rainfall than that of the area. Rainfall was measured using a standard rain gauge approximately 500m from the nearest experimental plot. Rainfall records span the period from 1952 until 2014; the mean annual rainfall for the farm is 764 mm, with March being the wettest month (Figure 2.2). The farm experiences one or two severe frost events most winters (Martens *et.al.*, 1996). The predominant soil forms in the area are Glendora Trevanian and Mispah (Martens & Morris, 1994). These soils contain a mixture of clay, sandy and loam soils with a slow drainage rate (Schulze, 2008).

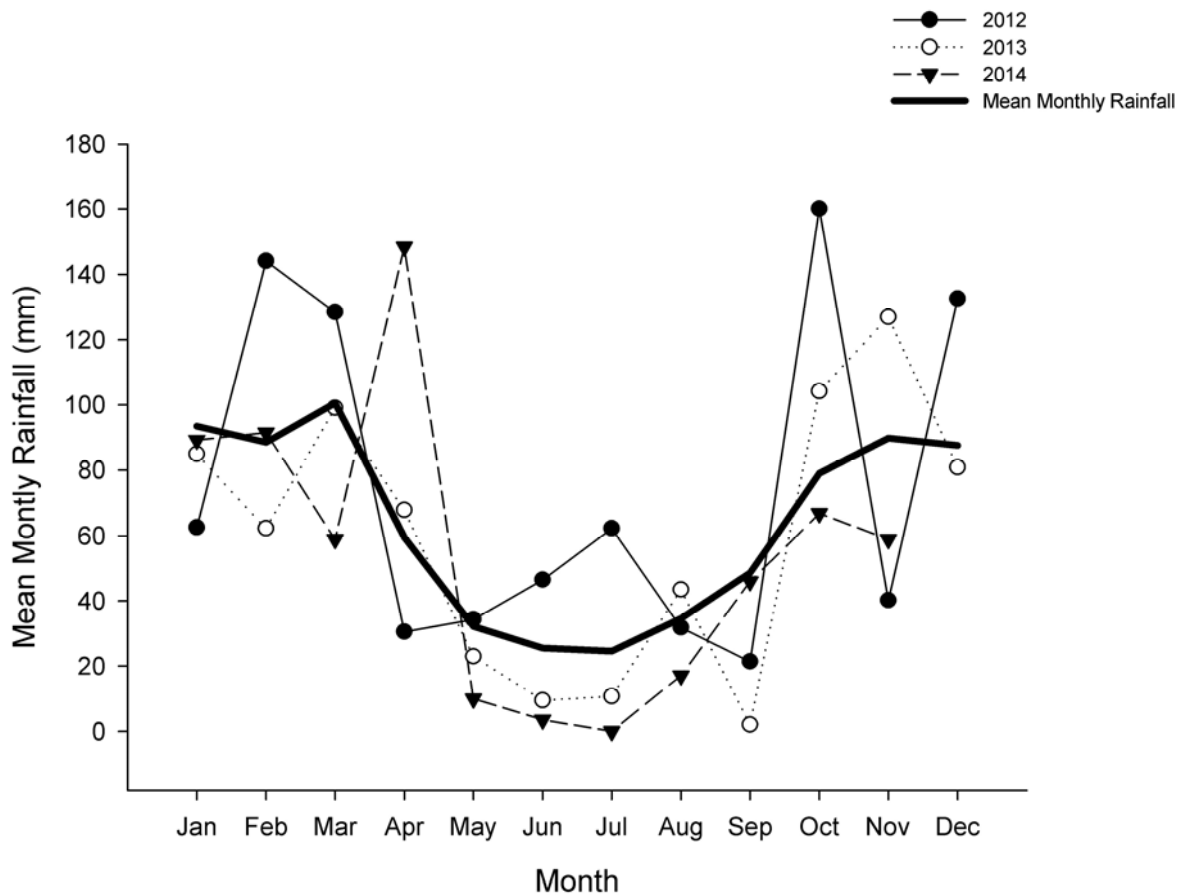


Figure 2.2: The mean monthly rainfall for the study period (2012 – 2014), with mean annual rainfall measuring 864 mm (2012), 714 mm (2013) and 589 mm (2014 – excluding the rainfall data from December). The mean monthly rainfall recorded for every rainfall event on the farm from 1923 to 2014 is shown with the solid thick black line. Even though the December rainfall data was not included in the 2014 data set, this year was considered as having below average rainfall. Source: Derek Painter, Endwell.

2.3. Selection of sampling sites and quantification of canopy cover at the landscape scale

Digital aerial photographs dating back to 1949 were used to determine whether bush encroachment had occurred on the farm, i.e. to ascertain that there was a switch from sparse to dense tree cover from 1949 to 2009. The 2009 photographs are satellite images as a digital sensor system replaced the analogue photography method in 2008 (National Geospatial Information, 2011). These aerial photographs were georeferenced using the most recent satellite photographs from 2009. I imported the aerial photographs into ArcGIS 10 (ARC/INFO software by Environmental Systems Research Institute, Redlands, CA, 2010) and projected them using Transverse Mercator WGS 27 to match the 2009 satellite images. The scale of the satellite images was 1:10 000 with a resolution of 0.5m. The scale of the aerial photographs was 1:30 000 with resolutions ranging from 2.5m to 5m (National Geo-spatial Information, 2011). I selected 10 reference points on the aerial photographs and matched these with the 2009 satellite images to rectify the aerial photographs.

The aerial photographs and satellite images were used to identify four areas that had become encroached since 1949. These areas would represent an unencroached site with no tree cover visible on the satellite image and three encroached sites with approximately 25%, 50% and 75% canopy cover (Figure 2.3). The areas that represent each of these levels of encroachment were selected using orthorectified SPOT 5 satellite images of the farm taken in 2009 (National Geo-spatial Information 2011). I selected these areas based on two criteria: 1.) they were dominated by *Acacia karroo* at the time of the study, and 2.) they were open savanna (< 5 % tree cover) prior to 1949 and were encroached after this date (Figure 2.3). I excluded any areas where trees were had been poisoned in the past (personal communication with the farm owner).

I quantified the percent tree cover for the final sites selected using the 2009 orthorectified images in ArcGIS 10 (Esri, 2010). I used the aerial photographs from 1949 to 2009 to determine whether the selected sites had become encroached over this period of time and when, if they had become encroached, had this occurred. I used the 2009 SPOT 5 satellite images to determine the current percent tree cover. This was done by placing 100 m x 50 m grids, which consisted of 1m x 1m cells, on the satellite photographs over each of the selected areas. Within these grids, each cell was classified manually as 'tree' or 'grass' based on the vegetation form that covered more than 50% of the cell. I then calculated the percent tree

cover at each site as the percentage of total cells dominated by tree cover. The three selected areas of 100 m by 50 m were found to have 21%, 45% and 72% canopy cover, and are hereafter referred to as the open, low, intermediate and high levels of encroachment respectively. The open site was selected on the basis that there were no tree present.

The four sites are located along the same slope of increasing altitude. (Figure 2.3). Moving from the high level of encroachment to the open site, there is a slight increase in elevation, from 755 m.a.s.l. at the high level of encroachment to 761, 773 and 787 m.a.s.l. at the medium, low and open sites respectively.

2.4. Stem density and basal area at the stand-wide and landscape scales

At the sites with low, medium and high levels of encroachment, I used the line intercept method to sample tree basal area and density. The open site had no trees and was therefore not included in the sampling. Four 50 m long and 4 m wide fixed belt transects were set up within the same 100 m x 50 m block used to calculate the tree cover in each area. This gave a total sampling area of 800 m² at each level of encroachment. The transects were placed parallel to one another, at least 10 m apart and as far from farm roads or fences as possible. The GPS coordinates of the starting and end points of each transect were recorded and markers (poles with flags) were also placed at as the ends and several points along all transects to facilitate re-sampling of points long the transects. Transects were then divided up into quadrats (1 m x 4 m) at 1m intervals along all transects. In each of the quadrats, I recorded the number of stems and the basal circumference (cm) of each tree trunk immediately above the basal swelling. Trees with a basal circumference < 10 cm or height < 50 cm were excluded. Tree density per hectare was determined for each of the three levels of encroachment. The basal circumference was used to calculate the basal area of each tree and was then used to calculate the total basal area per hectare for each transect. The formula used to calculate the basal area was as follows:

$$A = C^2 / (4 * \pi), \text{ where } A = \text{Area}, C = \text{circumference}$$

I used a one way ANOVA to compare mean stem density and stem basal area between the three encroached sites. A post-hoc test (Tukey HSD) was used to detect pairwise differences between the four sites. The four belt transects used at each of the levels of encroachment are

pseudo replicates as I was unable to replicate the tree densities at different sites. This was unavoidable and has to be kept in mind when reading the results. Statistical analyses were carried out in STATISTICA V10.0 (StatSoft. Inc., Tulsa, USA, 2010).

Tree density differed significantly between the low level of encroachment (625 trees.ha⁻¹) and the two more encroached areas (medium and high with 963 and 900 trees.ha⁻¹ respectively). The high level of encroachment had a slightly lower tree density than the medium encroached site, but had larger trees. There was no significant difference between the tree basal area .ha⁻¹ of the low and medium levels of encroachment. Tree basal area .ha⁻¹ was significantly lower in both the low (p = 0.0004) and medium (p=0.025) levels of encroachment compared to the high level of encroachment (Figure 2.4).

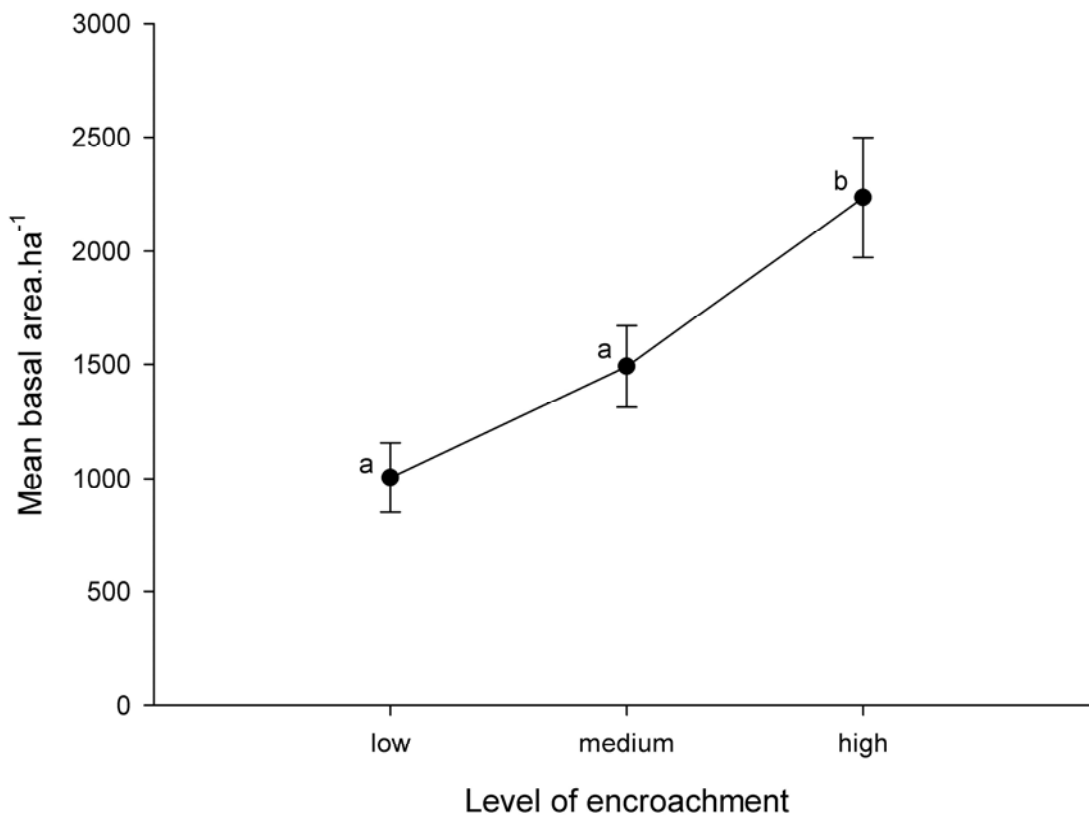
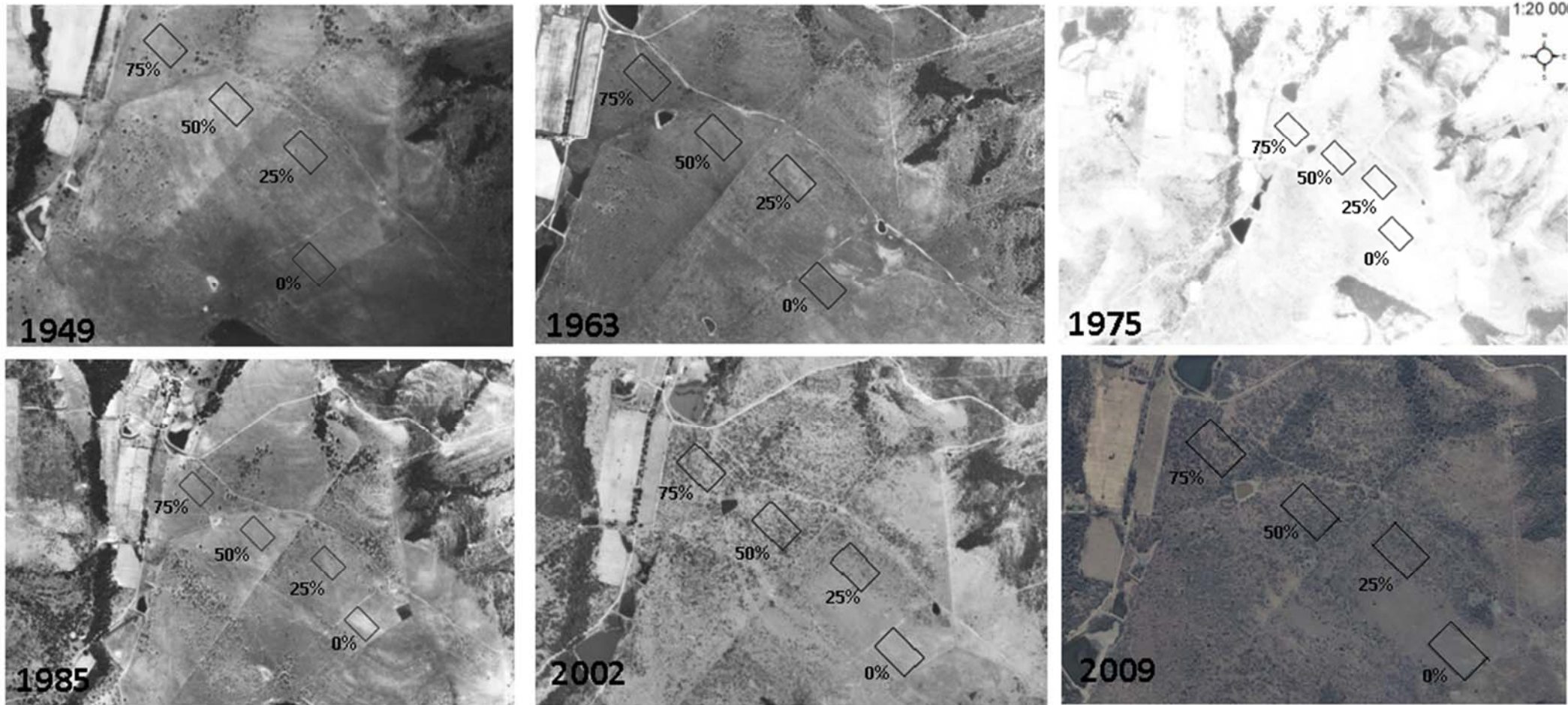


Figure 2.4: Mean basal area (cm² .ha⁻¹) and standard error for each of the three levels of encroachment with tree cover (low: 21%, medium: 45% and high: 72%). Means labelled with the same letter are not significantly different.



1

2 **Figure 2.3: Aerial photographs dating back to 1949 of the study area on the farm (Endwell). The four areas that were selected for data collection are shown on the**
3 **photos.**

4

2.5. Do more densely encroached areas reflect a longer history of encroachment?

The farmer reported that the site with 72% cover became encroached first, followed by the site with 45% cover, and most recently the site with 21% cover (which became encroached during the 1990s). Exact dates could not be determined, however, as there is a gap in the aerial photographs between 1985 and 2002, which was the period during which woody cover in the area, increased sharply. According to the farmer, the area had become encroached during the 1990's, possibly following a severe drought in the region during 1991 and 1992. The time period following droughts would be ideal for the *A. karroo* seedlings to establish as a result of grass mortality and increased grazing pressure on grasses, reducing competition with the seedlings (Roques *et al.*, 2001; Vetter, 2009)

Mean tree size increased with increased level of encroachment (Figure 2.4), indicating a progressive increase in bush encroachment over time rather than a single cohort at the scale of the farm. At the low level of encroachment all trees, with one exception, fell into the categories with basal diameters smaller than 150cm² (Figure 2.5). If one assumes that age is weakly correlated with size, all these trees may be of similar age and this could be an indication of a cohort at this site (Wiegand *et al.* 2005). From observations made from studying the aerial photographs, this area was the last to be encroached by *Acacia karroo*, after 2002 (Figure 2.3). At the medium level of encroachment, the majority of the trees have a basal area smaller than 200cm² (Figure 2.5). While this is not much larger than the low level of encroachment, the distribution between the size classes is much more even, suggesting a number of recruitment events. This area also has a few larger and older trees that would have established before the encroachment of the small trees. The high level of encroachment has a much more even distribution between the size classes with more large trees, but still 33% of the trees in the smallest size class. In the area there were already a few large trees that had established in the 1980's (Figure 2.3). The pattern of encroachment by *A. karroo* shows that the trees are encroaching up the hill slope. The crest of the hill is still largely unencroached. This could be a progressive encroachment from where it seems to have started (high level of encroachment) at the foot of the slope moving upwards. This has been documented in other studies, where the hill slope had much higher woody cover than the crest (Hottman & O' Connor, 1999). Other underlying differences in the topography and soil structure could also have caused this pattern of encroachment. As this is a gentle slope it

could possibly form a catena formation where rainfall infiltrates the soil and leaches the crest, resulting in nutrients and water collecting along the slope and drainage line (Ben-Shahar, 1990; Colgan *et al.*, 2012). This means the soil lower down the slope will be more nutrient rich than closer to the crest. This could also have influenced and facilitated the recruitment of trees along the bottom and side of the slope and exclude them from the crest. The stem density at each of the three levels of encroachment exceeded the maximum number of 300 trees.ha⁻¹ considered optimal for grass production by Aucamp *et al.* (1983). This, however, refers to large trees and at all the encroached areas at the site there was a mixture of small and large trees. Thus, the impact of the trees density will reflect not only the number of trees alone, but also their size. The changes in the tree density as well as tree cover and size will have an effect on the environmental conditions. Tree canopies intercept light and rainfall, the size of the tree will determine the amount of rainfall (Vetaas, 1992) and light (Ludwig *et al.* 2004) that will be intercepted by the canopy.

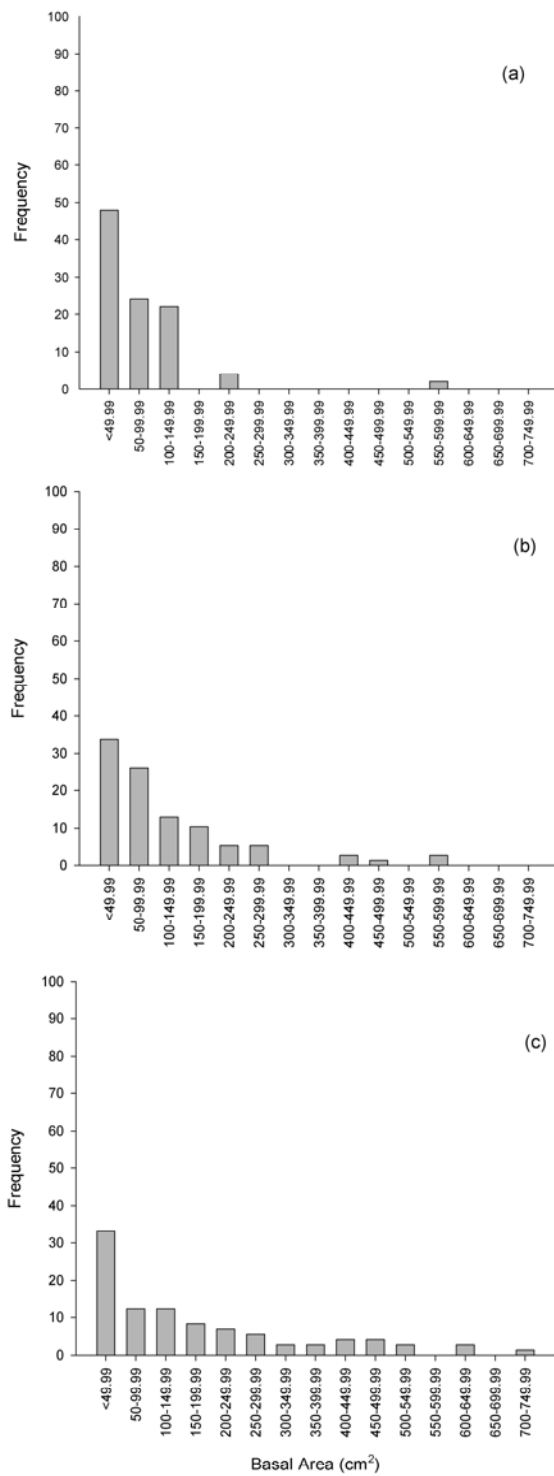


Figure 2.5: Frequency distribution of Acacia karroo tree basal area at (a) low (21%), (b) medium (45%) and (c) high (72%) canopy cover. Tree stem densities at the sites were 625, 963 and 900 trees.ha⁻¹ respectively.

Chapter 3: The effect of tree density on plant available light, soil moisture and frost occurrence

3.1. Introduction

Tree canopies intercept light and rainfall, thus reducing the amount of photosynthetically active radiation and soil moisture available under the canopy (Skarpe, 1992). Tree species can increase the nutrients under the canopies, though the extent of this varies between species (Smit & Swart, 1994; Moyo *et al.* 1998). Soil organic matter and soil nitrogen and phosphorus have been found to be significantly higher under tree canopies than in the area outside the canopy (Belsky *et al.* 1993; Holdo *et al.* 2012). The effects on the abiotic condition under the tree canopies at the various encroached sites directly affect the herbaceous vegetation. The herbaceous layer responds to increased tree cover, with a shift from C₄ grass species in the more open area to C₃ or more shade tolerant C₄ species under tree canopies and increasing abundance of these species at the more encroached areas (Ratnam *et al.* 2011). Grass biomass generally decreases with increased tree cover and density (Smit, 2005; Rigninos *et al.* 2009). In this chapter, the focus is on the effect that tree presence has on the light environment and soil moisture availability in the sub-canopy environment compared to the inter-canopy, and how tree canopies affects frost occurrence. These factors will be examined across a tree canopy cover gradient at various levels of encroachment to determine how local tree effects scale up at the stand-wide and landscape scale.

3.1.1 Effect of trees on abiotic factors

Light availability plays a major part in vegetation patterns in areas influenced by tree canopies. It is a limiting resource in the sub-canopy environment and a resource with a large amount of spatial variation (Martens *et al.* 2000; Simioni *et al.* 2004). Tree canopies intercept light, reducing the amount of photosynthetically active radiation (PAR) that reaches the sub-canopy environment (Sage & Kubien, 2003). The extent to which tree canopies affect light availability and microclimate depends on the leaf area index (LAI) and canopy architecture of the tree in question (Vetaas, 1992; Scholes & Archer, 1997). The leaf area index of savanna tree species is much lower than that of forest species, but savanna trees still decrease direct and indirect solar irradiance by 25 – 90% under the canopy depending on the tree size, age and species (Belsky *et al.* 1989; Georgiadis, 1989; Sage & Kubien, 2003). Leaf area index is

used as a measure to quantify tree canopies and is a function of tree size (Breda, 2003). Leaf area index is an important variable when considering the impact of canopies on their sub-canopy environment. Leaf area index influences the sub-canopy and inter-canopy microclimate and determines how much light and rainfall is intercepted and is related to CO₂ assimilation (Breda, 2003; Ryu *et al.* 2010). Thus with increased tree cover the leaf area index (LAI) increases, reducing the amount of light that penetrates the canopy. The irradiation in the sub-canopy environment during the darker hours of the day can be reduced by as much as 65% and during the brighter hours by 45% (Belsky *et al.* 1989). Under individual trees, solar irradiance can be reduced by as much as 45 – 65% under tree canopies (Belsky *et al.* 1993). Light availability decreases with increased tree canopy cover (Martens *et al.* 2000). Tree density also influences how much light is intercepted by the tree canopies. At intermediate tree cover (10-20%), irradiance under canopies can be reduced by up to 50% of that in the open (Ludwig *et al.* 2004). Bush clumps (high tree density) reduce irradiance directly under the tree to 11% of PAR in the open and at the edge of the canopy by 25% of that in the open (Jarvel & O'Connor, 1999).

The annual productivity of the herbaceous layer in savannas is directly related to the annual rainfall in arid and semi arid savannas and increases with increased rainfall (Scholes, 1990; Amundson & Belsky, 1995). This is largely due to the fact that herbaceous productivity is limited by water in arid and semi-arid savannas (Scholes, 1990). Savannas have distinct wet and dry seasons resulting in strong competition for water between tree and grasses in arid and semi-arid savannas (Scholes & Archer 1997; Wiegand, 2005). The presence of the tree canopy can decrease or increase soil moisture in the sub-canopy compared to inter-canopy or open areas. Reduced irradiance under tree canopies results in decreased temperature under the canopy in savannas (Belsky *et al.* 1989, Belsky *et al.* 1993; Vetaas, 1992) as well as reducing evapotranspiration (Ludwig *et al.* 2004). This can result in increased soil moisture in the sub-canopy area (Scholes & Archer, 1997; Jarvel & O'Connor, 1999; Treydte *et al.* 2007). The effect of shading on water availability is more pronounced in dry season or in water-limited savannas (Ludwig *et al.* 2001). When the understory is not water limited, shading has a net negative effect on the understory as growth becomes light-limited (Ludwig *et al.* 2001). Some studies have documented no changes in soil in the sub-canopy compared to the inter-canopy, or that the soil moisture content varied with season (Belsky *et al.* 1993; Moustakas *et al.* 2009).

Trees can also affect soil moisture via a suite of other processes, the net effect of which may be positive or negative (Scholes & Archer, 1997). Trees can increase soil moisture through hydraulic lift, where water is taken up from the deep soil by tree roots and lost in the top soil layers, making water available for grasses to use (Caldwell & Richards, 1989; Ludwig *et al.* 2004). Soil in the sub-canopy may be drier than that of the inter-canopy due to rainfall interception and root competition under the tree (Belsky *et al.* 1989). During rainfall events, tree canopies intercept rainfall and the rainfall that does not evaporate into the atmosphere is distributed to the ground through stem flow and dripping of the drip line (Vetaas, 1992). The extent to which tree canopies intercept rainfall depends on the canopy size and structure as well as the intensity of the rainfall event (Scholes & Archer, 1997). The amount of rain that is redistributed to the soil depends on the tree species. Tree size shows a positive correlation with rainfall interception, stem flow and fall through (Vetaas, 1992). The amount of rain that reaches that understorey also depends on how heavy the rainfall event was (Vetaas, 1992). Tree roots compete for soil moisture in savannas that are water limited. As the mean annual rainfall increases, the increased available soil moisture results in reduced root competition (Kambatuku *et al.* 2011; Dohn *et al.* 2013). The soil moisture at the start of the growing season may be higher under the tree canopies, but with increased root competition the soil moisture decreases faster than in the inter-canopy zone, resulting in higher soil moisture content outside the canopy (Belsky *et al.* 1989; Belsky *et al.* 1993).

Frost occurs rarely in savannas, and most tropical and sub-tropical savannas are frost free. The effect of frost on the herbaceous production and survival is thus not well documented (Holdo, 2005; Holdo, 2006). Vegetation structure and topography influence air temperature profiles which in turn determine the occurrence and extent of frost (Holdo, 2006). If the leaf temperature of a plant drops far enough below freezing and enough heat is lost into the atmosphere at the correct atmospheric conditions, the plant can suffer from frost even if the air temperature does not fall below freezing (Inouye, 2000). At plant cellular level, crystals can form within or between plants cells during severe frost events; this can cause physical damage to plants, possibly resulting in physiological problems in the plant (Inouye, 2000). Plants in early life stages (seedlings and saplings) and new growth in plants are most susceptible to frost damage. Many of the grass species that characterise southern African savannas are adapted to frost, dying back and resprouting, although little is known about the relative susceptibility of shade- vs. sun-adapted grasses to frost. Savanna trees are generally intolerant of frost, and although *Acacia karroo* can tolerate frost to a degree (Wakeling *et al.*

2012) its seedlings die back during frost events (Barnes *et al.*, 1996; L. Perumal, unpublished data). Winter minimum temperatures are higher under tree canopies than outside the canopies (Iponga *et.al.* 2009) and the difference between maximum and minimum temperatures is smaller (Belsky *et.al.*, 1989). The more constant evening temperatures under the canopy compared to the significant decrease in the inter-canopy environment could prevent frost formation under the canopy. In South Africa, two types of radiative frost, hoar- and blackfrost, are most common. Black frost occurs in very cold conditions and results in cell sap freezing and consequently the cells rupture (Savage, 2012). Hoarfrost occurs in the form of ice crystals forming from water vapour on plants, ground and other objects on the ground surface (Savage, 2012). The focus here is on hoarfrost, as this is the most common in South Africa and more specifically the study region, and “frost” will henceforth refer to hoarfrost alone.

3.1.2. Study aims

The aim of this study was to examine the effects of increased tree cover on the abiotic conditions at the level of the herbaceous layer at the local, stand-wide and landscape scale to examine how the local tree effects scale up with increased tree density. I quantified leaf area index (LAI), plant available light (photosynthetically active radiation and % transmittance), soil moisture and frost occurrence in the sub-canopy and inter-canopy micro-habitats at four sites along a tree canopy gradient at each of the four levels of encroachment.

I predicted that with increased tree cover the leaf area index (LAI) would increase, resulting in reduced light transmittance and thus photosynthetically active radiation (PAR) in both the sub-canopy and inter-canopy environments. At the local tree scale, the sub-canopy environment would be shaded by the tree canopy and at open to low tree canopy cover the inter-canopy environment would be completely unshaded. With increased tree canopy cover, the overlapping of tree canopies and shadows would result in the inter-canopy environment becoming shaded as well, reducing the amount of plant available light at least for parts of the day at the stand-wide and landscape level as the area becomes more encroached. To examine how the local ‘tree effect’ scales up in the landscape, the relationship between the observed abiotic values and tree cover was examined. Furthermore, to determine whether predictions about the stand-wide effect of various levels of tree cover can be based on the local tree effects, I examined how predicted values (extrapolated from the single-tree effect) compared to the observed values. The relationship between the expected values and tree cover is linear,

but observed values are expected to deviate from the expected values with increasing tree cover due to the effects of overlapping canopies (see Chapter 1, Fig 1.1 and 1.2).

Since the net effect of trees on soil moisture depends on the relative strength of the component effects (interception, evapotranspiration, competition), different outcomes are possible. I predicted that tree canopy interception of rainfall would result in lower soil moisture in the sub-canopy immediately after a rainfall event, and that this effect would be more pronounced at higher tree cover (and hence higher leaf area). Over the days following the rainfall event, I predicted that soil moisture would become higher in the sub-canopy relative to the inter-canopy due to reduced evapotranspiration, at least at low tree density. Increased root competition at higher tree density was predicted to counteract this effect and result in lower soil moisture under trees and overall at the landscape scale.

Temperature in the sub-canopy environment is lower than ambient temperature during the day and higher at night. The presence of tree canopies and the resulting changes in sub-canopy temperatures are not conducive to frost formation. I predicted that this effect would be more pronounced under large trees and at higher tree densities. I predicted that frost would be less likely to occur in the sub-canopy environment, and at the landscape level frost occurrence would become less frequent in the inter-canopy environment as tree densities increased due to overlapping of canopies in the inter-canopy area.

3.2. Methods

3.2.1 Data collection

At each of the four study sites (open grassland with no trees and low, medium and high levels of encroachment representing 21%, 45% and 72% tree canopy cover respectively; see Chapter 2), I measured light transmittance, photosynthetically active radiation (PAR), leaf area index (LAI), soil moisture and frost occurrence at 1 m intervals along four 50 m line transects. At the three encroached sites, sampling took place along the same fixed line transects used for sampling tree density and basal area (Chapter 2). At each site, four 50 m fixed line transects were set up. Transects were placed at least 10 m apart and ran parallel to one another. Markers (poles with flags) were placed at the start and end points of each

transect and GPS coordinates were recorded for each point. Markers were also placed at several points along each transect to facilitate re-sampling.

In addition, I selected four bush clumps at each of the low, medium and high levels of encroachment. These were dominated by *Acacia karroo* trees, although most had smaller *Scutia myrtina* shrubs in the understorey. I randomly selected bush clumps by choosing a starting point and then moving forward in a straight line and selecting the first clump intercepted. From this clump I moved 20 m to the left of the clump, and from that point the nearest bush clump was selected. This selection method was repeated until four clumps were selected. For each bush clump, I selected a paired open site that was situated next to the bush clump. Each open area chosen was large enough to have no trees within a 6m radius from the centre, and had continuous grass cover with no bare patches (as the main aim was to determine grass production (See chapter 4). Soil samples were taken in the middle under the bush clump, at least halfway between the edge of the canopies and the main stem, and in the middle of the open area. In this way, four pairs of sampling sites were set up at each of the three encroached sites. Four randomly placed sampling sites at least 20 m apart were set up at the open site.

3.2.1.1. Light measurements

Two different methods were used for light measurement. To measure the light transmittance and photosynthetically active radiation (PAR) at each of the sampling points, I used an AccuPAR LP-80 Ceptometer (Deacon Devices Inc.). Ceptometer readings were taken between 12:00 and 14:00 on cloudless days during the growing season along the fixed transects. Where tree canopies were present, I took light transmittance readings under the canopy as well as above the canopy to quantify the percentage light transmittance through the canopy. Points with no tree cover and points in the open site were recorded as having 100% transmittance.

The ceptometer records PAR (mols.m^{-2}) directly above the probe and does not reflect the effects of any object reducing transmittance from the side at any given point during a day. To account for the interception of morning and afternoon light incident at an angle, I used a hemispherical camera to measure light transmittance as well as leaf area index (LAI). Hemispherical photographs were taken at all the same points along transects at the four levels of encroachment. Hemispherical photographs were taken using a fish eye lens with a 180° field of view while the camera was stationed on a tripod at 30 cm above the ground to ensure

consistency between photographs. A compass was used to determine the point on the lens that was due north, and I placed a small marker that would be visible in the photograph on the lens to mark this exact point. The photographs were analysed using Gap Light Analyzer 2.0 (GLA; Simon Fraser University, British Columbia, 1999), which uses true colour fish eye photographs to extract light transmission indices. Images were imported into GLA and registered using the geographical orientation of the photograph. This was done by using the marker indicating north on the image as a starting point. GPS coordinates and elevation for each point was used to configure each image. The image was then classified to separate sky and non-sky pixels. A black and white image was then created with the sky area being white and the non-sky area black. I then calculated the percent non-sky area, which was used to calculate the LAI and percent transmittance. The final data set gave LAI in five concentric rings. For this study, the LAI for the 1st to 4th ring was used, which integrated the LAI over the zenith angle 0 to 60°. The 5th (outermost) ring contained mainly topographic features (especially mountains) at the edges of the photograph. Since these do not represent tree cover, data from the 5th ring were excluded from the analyses.

3.2.1.2. Soil moisture

Soil moisture samples were taken along the fixed transects and at the individual exclosures. Soil moisture samples collected along the transects were collected the day following a rainfall event of 22 mm, to determine the effect of tree canopies on soil moisture through rainfall interception. Soil moisture samples were collected at each point from the top 10 cm using a soil auger, placed in air tight bags and kept for further analysis.

At the selected bush clumps, soil samples were collected on two occasions after rainfall events, at each sampling site at the four levels of encroachment. The first set of soil samples were taken during the 2012/2013 growing season (December) and the second during the 2013/2014 growing season (December). This was to determine the net effect of competition and evaporation over time on soil moisture in the inter-canopy and sub-canopy. Sampling started a day after the rain stopped. The first set of soil samples were collected daily for 8 days following a rainfall event of 15 mm. In between days three and four, another 4 mm of rain was recorded. Soil sampling was done over an 8 day period and discontinued due to a heavy rainfall event on the 9th day. The second set of soil samples were collected every second day for 15 days after a rainfall of 27 mm. On day 8 of the second sampling period, 12

mm of rain fell during a thunderstorm. Soil samples were taken at three depths: 10 cm, 20 cm and 40 cm using a soil auger and kept in sealed air tight plastic bags for further analysis.

Soil moisture was determined by the gravimetric method. Each individual sample was weighed and placed in bag; this was then transferred to a drying oven at 70°C for 48 hours and re-weighed. The wet weight and dry weight were used to calculate the percentage soil moisture content of each sample.

3.2.1.3. Frost

Frost occurrence was recorded at all four levels of encroachment during one heavy and two lighter frost events. At each transect point, I recorded the presence (1) or absence (0) of frost on the grass at dawn, before the frost melted.

3.2.2. Data analysis

3.2.2.1 Tree cover and scale

The four sites representing different levels of encroachment, the 16 individual transects, and the 50 transect points at each transect, representing under- or sub-canopy micro-habitats were used to represent the different scales at which the data was analyzed. Tree cover at each of the four levels of encroachment (0%, 21%, 45% and 72% cover) represented the *landscape* scale or effect. The tree canopy cover (measured in a strip 50 x 4 m) along each of the fixed transects at the four sites was calculated and taken to represent *stand-wide* canopy cover (see Chapter 2 for quantification of canopy cover along each transect). Each sampling point was classified as either sub-canopy or inter-canopy based on the presence of a tree canopy. The sub-canopy and inter-canopy micro-habitats at each transect point represent the *local scale*, or *tree effect*, in the analyses. The landscape, stand-wide and local scales represent areas of one or more hectares, < 500 m² and a few m², respectively. From an ecological or farming point of view, the landscape scale represents a grazing camp or larger landscape unit that integrates several patches of denser bush and more open habitat. The stand-wide scale represents a smaller unit with a more homogeneous bush cover that integrates several sub- and inter-canopy patches. The local scale examines the difference in the shaded vs. open microhabitats, each of which is represented by a single sampling point.

3.2.2.2. Changes in LAI and plant available light at the landscape scale

To describe the light environment at the landscape scale, the distribution of light transmittance at each of the four levels of encroachment was examined using frequency tables and plotted as histograms. The classes were selected based on 10% light transmittance intervals ranging from 0 – 100% transmittance. The frequency of light transmittance in each category was calculated and plotted separately for each level of encroachment.

I used one-way analysis of variance (ANOVA) to examine the effect of the four levels of encroachment on the mean light transmittance, PAR and LAI at each site, using the values from all transect points at each site. A factorial ANOVA was used to determine the difference in light transmittance, PAR and LAI in the sub-canopy and inter-canopy habitats at each of the three levels of encroachment. The open site was excluded from this analysis as there were no data for the sub-canopy habitat. To examine whether the four sites and micro-habitats had significantly different effects on light availability, a post hoc Tukey (HSD) test was carried out. The results from the ANOVA test should be read, keeping in mind that the replicates of tree density are technically pseudo-replicates (Refer to Chapter 2).

3.2.2.3. Effect of micro-habitat on light transmittance, PAR and LAI across a tree density gradient

Mean observed values for light transmittance, PAR, LAI and soil moisture for each transect were calculated separately for the two micro-habitats (sub-canopy and inter-canopy) and plotted as a function of tree canopy cover. First the difference between the sub-canopy and inter-canopy light transmittance, PAR and LAI was examined. To determine whether the presence of the tree canopy significantly affects the abiotic factor in question, I used t-tests (paired by transect) were used to test for the effect of micro-habitat on the abiotic factors. A significant difference between sub-canopy and inter-canopy would indicate a ‘tree effect’ (Riginos *et al.* 2009; see Chapter 1, Figure 1.1). The open site was excluded from this analysis as there were no data for the sub-canopy habitat.

Secondly, the effect of stand-wide tree canopy cover on the abiotic factors at each micro-habitat was examined and will hereafter represent the ‘stand effect’ (Riginos *et al.* 2009). Linear regressions were fitted separately to the sub-canopy and inter-canopy habitats to assess the effect of tree cover on growing conditions in each micro-habitat. A significant result would represent a significant stand effect (See Chapter 1, Figure 1.1). To determine

how the local ‘tree effect’ changes with increased tree canopy cover, the difference between the mean observed values for the sub-canopy and inter-canopy was calculated for each transect. The difference between the observed sub-canopy and inter-canopy values at each point was then regressed against tree canopy cover. This would show whether the local ‘tree effect’ is altered by the change in tree canopy cover, and to what extent. A significant result indicates that there is an interaction between the micro-habitats and the stand-wide canopy cover. This means the local ‘tree effect’ has become more or less pronounced along the tree canopy cover gradient.

3.2.2.4. Observed vs. expected light transmittance, PAR and LAI across a tree cover gradient

To determine how the local ‘tree effect’ on light transmittance, PAR and LAI scaled up to light availability at the stand-wide scale, mean observed and expected values for each abiotic factor were calculated and plotted as a function of tree cover. First, the mean observed values for light transmittance, PAR and LAI were calculated for each transect, using data from both micro-habitats as the overall effect of tree cover was tested. Secondly, I calculated the mean expected values for the abiotic factors at each transect. When calculating the expected values it was assumed that the local ‘tree effect’ would scale up linearly. It was also assumed that the sub-canopy micro-habitat at the lowest level of tree canopy cover would best represent the effect of individual trees on the abiotic conditions. The inter-canopy at the lowest level of tree cover would represent the abiotic conditions without trees. Based on this assumption, the transect with 30% tree canopy cover was used to derive mean sub-canopy values of PAR, LAI and transmittance, and the 0% tree canopy cover transects were used for the mean inter-canopy values. As all the transects from the open site had 0% tree canopy cover the mean across the site was used. Tree cover from the individual transects represented the stand-wide tree cover and the expected values were calculated for each percent tree cover. This methodology and formula for calculating the expected values was adopted from Riginos *et al.* (2009).

The formula used to calculate the expected values was as follows:

$$\text{Expected value} = ((\text{mean sub-canopy value}) \times (\text{proportion stand-wide tree canopy cover})) + ((\text{mean inter-canopy value}) \times (1 - \text{stand-wide tree canopy cover}))$$

Both t-tests and linear regressions were used for statistical analysis of the data. Paired t-tests (by transect) were used to determine the difference between the stand-wide observed and expected values for each of the abiotic factors. Linear regressions were used to test the effect of tree cover on the mean observed values. The expected values were not regressed against tree cover as they were calculated as a function of tree cover and thus perfectly linear. The difference between the mean observed and expected values for each transect was calculated, and the difference was regressed against tree cover. A significant effect of the tree cover on the difference between the observed and expected values would show that the local ‘tree effect’ on the abiotic factors does not scale up linearly to the stand-wide level but rather increases (or decreases) with increased tree canopy cover (See Chapter 1, Figure 1.2).

3.2.2.4. Effect of tree density on soil moisture content

Soil moisture recorded along the transects at the four levels of encroachment at points in the sub-canopy and inter-canopy micro-habitats. This data was used to determine to what extent the tree canopies intercept rainfall. For each transect, mean soil moisture in the sub-canopy and inter-canopy micro-habitats was calculated and plotted as a function of tree canopy cover. A t-test (paired by site) was used to determine the difference between sub-canopy and inter-canopy soil moisture. A significant result would indicate whether there was a local ‘tree effect’ on soil moisture content. Significantly higher soil moisture in the inter-canopy would indicate that rainfall interception by the canopy plays a role in determining the soil moisture content in the sub-canopy environment. To determine how the stand-wide tree canopy cover affects soil moisture, linear regressions were fitted to the sub-canopy and inter-canopy data. Significant regression results would indicate that tree density affects soil moisture content and that there is a significant positive or negative ‘stand effect’. To examine how the local ‘tree effect’ is influenced by tree canopy cover, the difference between the inter-canopy and sub-canopy soil moisture content at each transect was calculated and regressed against tree canopy cover. This would give an indication of how the magnitude of the ‘tree effect’ changed with tree cover. A significant result would indicate that there was an interaction between the local ‘tree effect’ and the ‘stand effect’. This would mean that with the increase in tree canopy cover the local ‘tree effect’ was altered and either became more or less pronounced at high tree cover.

A two-factor ANOVA was used to determine how the level of encroachment affects soil moisture at three soil depths (10 cm, 20 cm and 40 cm) in the sub-canopy and inter-canopy

microhabitats at the selected bush clumps. The sub-canopy and inter-canopy data were analysed separately as the open site has no sub-canopy microhabitat. The soil moisture content on the last day of sampling after each of the two rainfall events was used (day 8 and day 15 respectively). The last day of sampling was used as this would give an indication of what the difference in soil moisture at the inter-canopy and sub-canopy would be in between rainfall events at this site. A post-hoc Tukey (HSD) test was carried out to test for a significant effect on the soil moisture content at the three depths and if there were any significant difference between the levels of encroachment. The soil moisture data from the first and last day of sampling for both rainfall events was then used to analyze the effect of competition and evaporation on soil moisture in the sub-canopy and inter-canopy environments. Again a two-factor ANOVA was used to test the effect of level of encroachment and soil depth on the soil moisture content at each of the micro-habitats on the two selected days. The analysis for each micro-habitat was done separately as the open site had no sub-canopy. A paired t-test (by enclosure) was used to determine whether there was a significant difference between the soil moisture in the sub-canopy and inter-canopy (regardless of depth and level of encroachment) on the first day and last day of sampling respectively. This would indicate whether the difference in soil moisture between the micro-habitats has become more pronounced over time. Data was analyzed separately for the two rainfall events.

3.2.2.5. Effect of tree presence and encroachment on frost occurrence

I recorded the number of times (0, 1, 2 or 3 times) each transect point had frost present, using the presence and absence of frost recorded at each transect point during the three frost events. These data were used to examine the overall effect of the canopy presence (inter vs. sub-canopy) and the difference canopy cover (four levels of encroachment and each transect). A Box and Whisker plot was used to show how often (0, 1, 2 or 3 times) it frosted at sub-canopy and inter-canopy transect points at the four levels of encroachment. As the data was not normally distributed, generalized non-linear regression was used to examine the effect of the micro habitat and tree cover at local and landscape scale on the occurrence of frost.

All statistical analyses were carried out in STATISTICA V10.0 (StatSoft. Inc., Tulsa, USA, 2010).

3.3. Results

3.3.1. *Effect of tree density on plant available light and LAI at landscape scale*

Figure 3.1 shows the frequency distribution of light transmittance at the four levels of encroachment. All sampling points at the open site had 100% transmittance as there were no trees in the surrounding areas. This also applied to the transmittance recorded with the hemispherical camera as there were no trees in the peripheral view of the camera. The number of observations for the low transmittance increased with the increased canopy cover at the site level. The number of observations at high transmittance (>90%), these including the inter-canopy areas, was lowest at the high level of encroachment. Thus the overall transmittance at landscape level decreased with increased canopy cover. There was a marked difference between the transmittance recorded with the ceptometer and the hemispherical camera. The light transmittance recorded using the ceptometer clearly has a bimodal distribution, reflecting the contrast in the light transmittance between the sub-canopy and inter-canopy micro-habitats. Whereas light transmittance recorded with the hemispherical camera was more continuous. This could be because the sub-canopy points receive light from beyond the canopy and the inter-canopy points are shaded by surrounding tree canopies. The reduction in transmittance beneath the canopy differed between the measurements recorded for the ceptometer and hemispherical camera with transmittance decreasing an average of 56% and 30% respectively. The reduction in transmittance recorded using the hemispherical camera is lower as the transmittance readings in the inter-canopy will be lower than that of the ceptometer (which were all 100%). This is because the hemispherical camera takes into account the surrounding objects that might shade the spot at some point during the course of the day. The mean transmittance in the sub-canopy, however, was more similar with 43% for ceptometer readings and 56% for hemispherical camera readings. The hemispherical camera never recorded 100% transmittance, as there were always trees in the peripheral view. Thus the distribution of light in the inter-canopy areas fell into categories with lower transmittance, whereas the ceptometer recorded 100% transmittance at all the points in the inter-canopy. This resulted in a higher number of observations in the middle of the range of light transmittance recorded by the hemispherical camera, as it included the inter-canopy data. At the low and medium levels of encroachment the hemispherical camera also did not record light transmittance less than 20%. Again this can be attributed to the field of view within which the hemispherical camera records light transmittance. As larger field of view and light transmitting from the edges of the view are taken into account the transmittance will be

higher than that recorded at a specific point in the sub-canopy habitat using the ceptometer. The hemispherical camera gives insight into the transmittance that the sampling point is likely to receive over the course of an entire day. The ceptometer reflects the transmittance at a given time (in this case between 12:00 and 14:00 in the afternoon) the sampling point receives.

At landscape scale, mean PAR and light transmittance readings taken with the ceptometer differed significantly between all four levels of encroachment, following the predicted decreasing trend with increasing tree cover (Figure 3.2 (a, c); PAR: $F_{(3,799)} = 62.153$, $p < 0.001$; transmittance: $F_{(3,799)} = 69.386$, $p < 0.001$). Tree cover also significantly affected landscape level mean LAI (Figure 3.2 (b); $F_{(3,599)} = 146.649$, $p < 0.001$) and light transmittance (Figure 3.2(d); $F_{(3,799)} = 217.99$, $p < 0.001$) values measured by the hemispherical camera, but the medium and high levels of encroachment did not differ significantly from one another. The high transmittance and PAR values at the open site compared to the encroached sites can be explained by the significantly lower sub-canopy values and the increasing proportion of sub-canopy habitats at these sites (Figure 3.3 (a, c, d), resulting in lower overall mean values. This is also the case for LAI, where the higher values in the sub-canopy resulted in higher overall mean values (Figure 3.3 (b)) When comparing transmittance, PAR and LAI between sub-canopy and inter-canopy habitats at the four sites, it is clear that there was a significant difference between the micro-habitats (Figure 3.3).

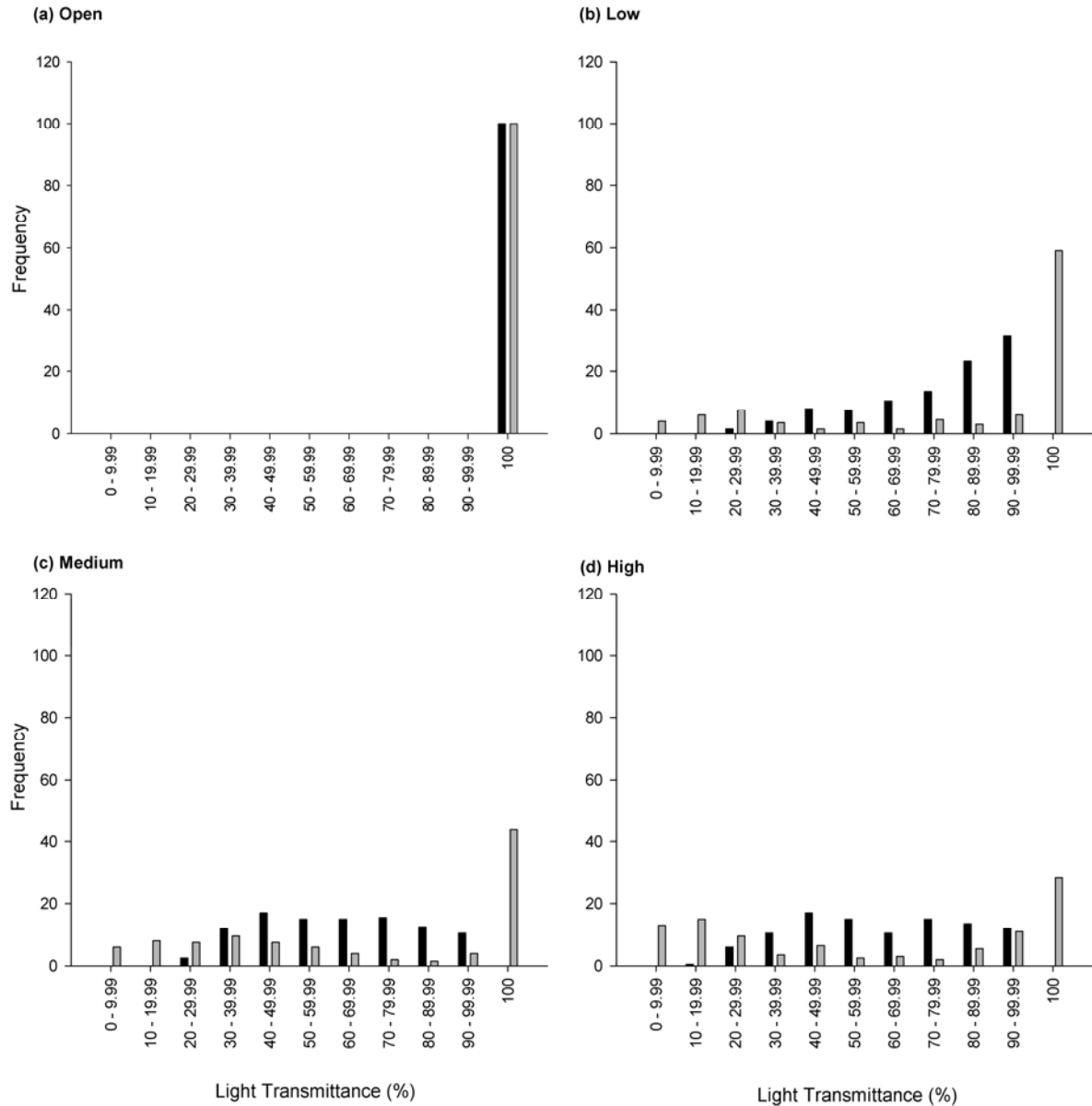


Figure 3.1: Frequency distribution of light transmittance (%) across the four levels of encroachment, open (a), low (b), medium (c) and high (d). The grey bars represent the light transmittance recorded by the ceptometer and the black bars the transmittance recorded by the hemispherical camera.

Excluding the open level of encroachment, the inter-canopy habitats had significantly higher transmittance and PAR than the sub-canopy habitat (Figure 3.3 (a, c, d); PAR: $F_{(3, 796)} = 825.33$, $p < 0.00001$; transmittance (c): $F_{(3, 796)} = 5389.37$, $p < 0.00001$; transmittance (d): $F_{(3, 796)} = 10076.76$, $p < 0.00001$). The lower values in the sub-canopy environment can account for the generally decrease in over transmittance and PAR, resulting in the overall significant decrease at landscape level. The inter-canopy values for LAI were significantly higher than

the sub-canopy values as expected (Figure 3.3 (d); $F_{(2, 793)} = 253.153, p < 0.0001$). There was no significant effect of encroachment on the inter-canopy and sub-canopy habitats.

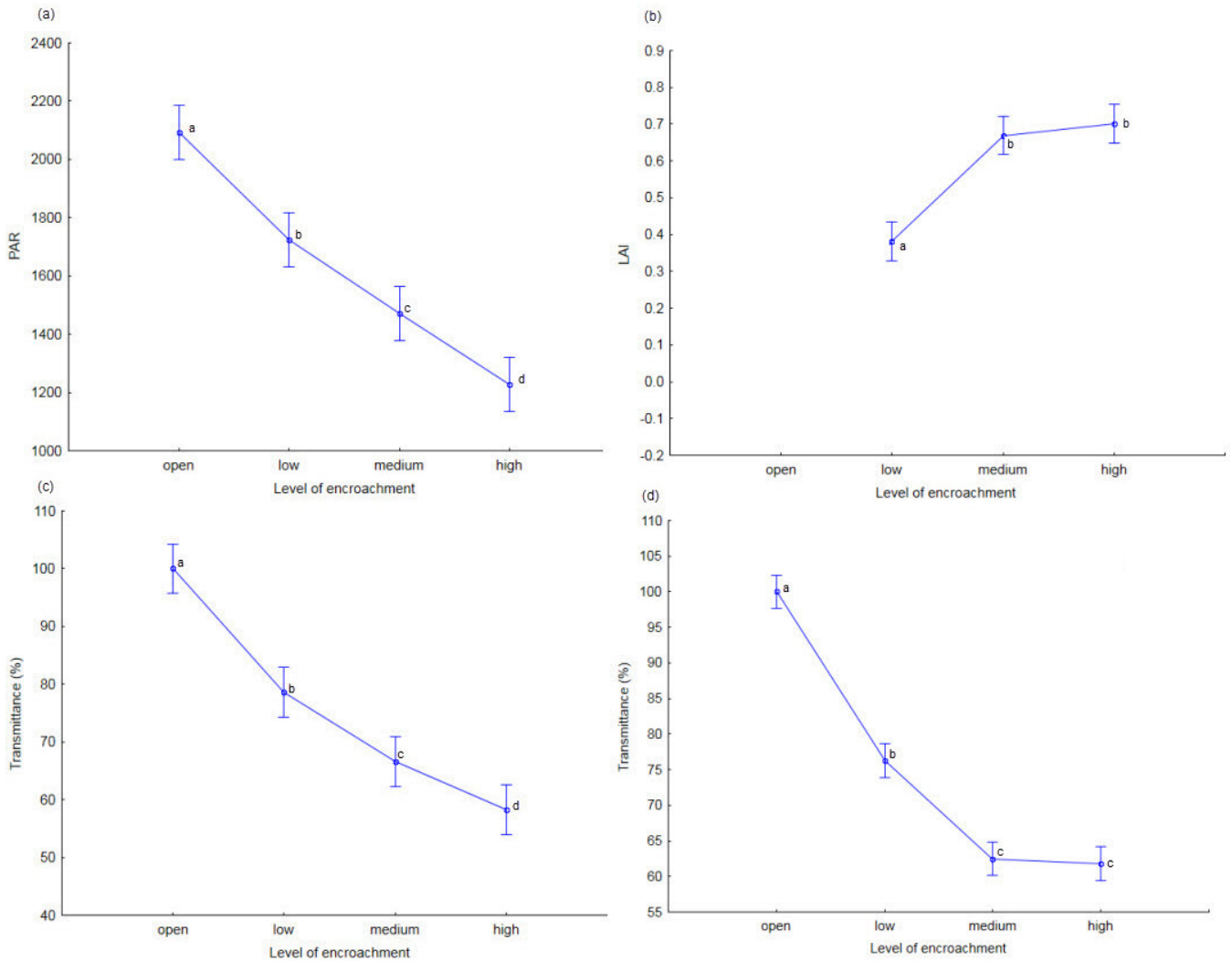


Figure 3.2: The effect of the level of encroachment on mean photosynthetically active radiation (PAR) (a), leaf area index LAI (b), and light transmittance recorded by the ceptometer (c) and the hemispherical camera (d) at the landscape scale. The letters indicate significant ($p < 0.05$) pairwise differences between means. $N = 200$ observations per site.

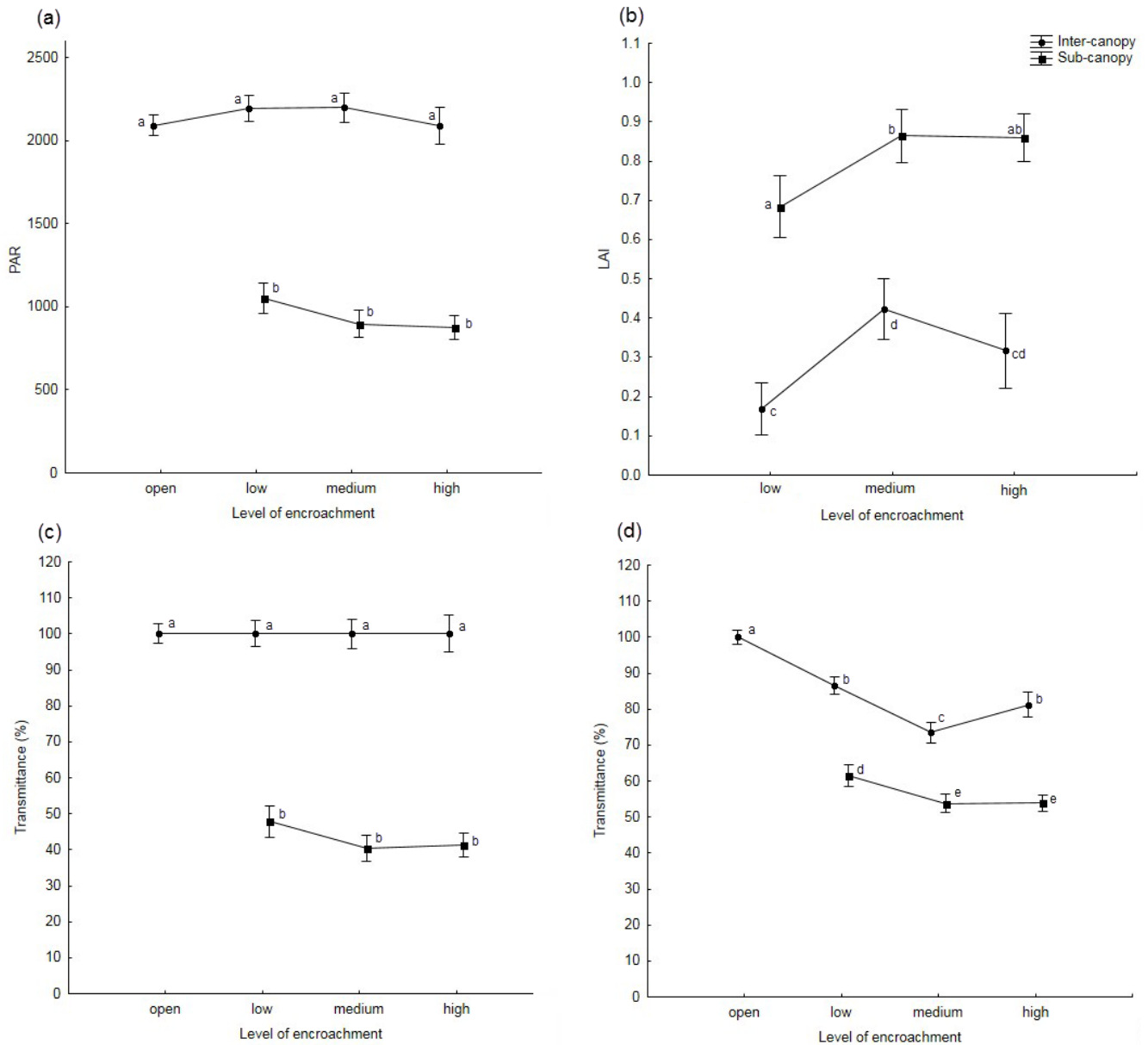


Figure 3.3: The effect of the landscape scale level of encroachment (open to high levels of encroachment) on the photosynthetically active radiation (PAR) (a), leaf area index (LAI) (b), and light transmittance from the ceptometer (c) and the hemispherical camera (d) at the sub-canopy and the inter-canopy. When comparing the two micro-habitats the open site was excluded. Letters indicate significant ($p < 0.05$) pairwise differences between the means. $N = 800$ for analyses comparing the effect of level of encroachment on the abiotic factors. $N = 200$ for all observations.

3.3.2. Plant available light and LAI across a tree canopy cover gradient

Transmittance and PAR was significantly higher, and LAI lower, in the inter-canopy than the sub-canopy habitats as expected (Figure 3.4; Table 3.1). These results show that tree canopies significantly reduce plant available light. While the PAR and transmittance values recorded

by the ceptometer and the sub-canopy LAI and transmittance recorded with the hemispherical camera did not change significantly with tree cover. The hemispherical camera data show an increase in LAI and reduction in transmittance in the inter-canopy habitat with increasing stand-wide tree cover (Figure 3.4 (b, d)). This shows that even though tree canopy cover does not alter the effect the tree canopy has on the plant available light, the inter-canopy habitat becomes increasingly shaded by surrounding trees as tree density increases. When the difference between the two micro-habitats was regressed against the tree cover (which necessarily excluded the inter-canopy data from the open site) there was, however, no significant difference in the magnitude of the local tree effect with increased tree cover (all $p > 0.05$).

Table 3.1: Paired t-test results for the difference in photosynthetically active radiation (PAR), leaf area index (LAI) and transmittance (%) between the sub-canopy and inter-canopy micro-habitats. $N = 24$ (12 pairs) for each case, they exclude the open site. Results significant at $p < 0.05$ are highlighted.

	d.f.	t-value	p-value
PAR	11	-23.48	<0.000001
LAI	11	-25.65	<0.000001
Transmittance (Ceptometer)	11	13.23	<0.000001
Transmittance (Hemispherical camera)	11	-39.61	<0.000001

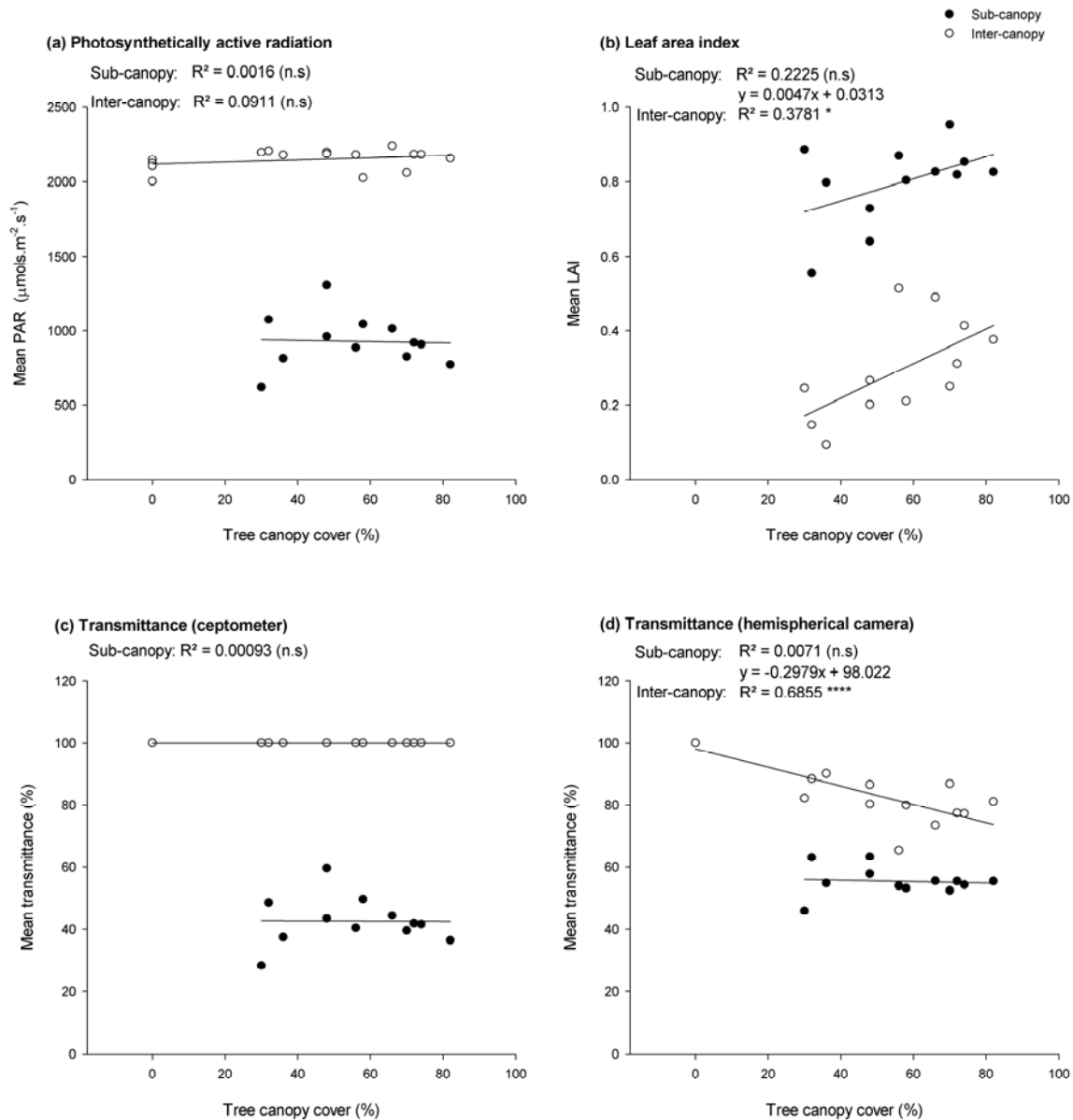


Figure 3.4: Mean observed PAR recorded with the ceptometer (a), LAI recorded with the hemispherical camera (b) and transmittance (c – ceptometer and d – hemispherical camera) in the sub-canopy and inter-canopy across a tree cover gradient. The regression results are shown for each graph. In (c), the inter-canopy transmittance values were not regressed against tree cover as they were all 100%. Significant regression results are indicated as $p < 0.05$ (*), $p < 0.001$ (**), $p < 0.0001$ (***) and $p < 0.00001$ (****). Results that are not significant are indicated as n.s.

3.3.3. Observed vs. expected stand-wide light transmittance, PAR and LAI in relation to canopy cover

With increased tree canopy cover, the observed stand-wide LAI increased and transmittance and PAR decreased significantly, indicating a negative effect of canopy cover on stand-wide

light availability (Figure 3.5). This effect is expected, as tree canopy cover becomes denser, the leaf area increases, and a greater proportion of the area falls within the sub-canopy micro-habitat. This suggests that the local negative tree effect do scale up at the stand-wide scale. The observed values for LAI and transmittance (both ceptometer and hemispherical camera) differed significantly from the calculated expected values (Table 3.2). Although, the mean observed values followed the same trend as the calculated mean expected values. Photosynthetically active radiation and transmittance (from the ceptometer) had similar or lower observed than expected values, with the transmittance from the hemispherical cameras lower than expected. Observed transmittance (recorded with the hemispherical camera) showed a deviation from the expected values at higher tree canopy cover. The difference between the observed and expected values for PAR and transmittance (recorded with the ceptometer) decreased significantly with increased tree canopy cover (Figure 3.6 (a, c)). The difference between the mean observed and expected values for transmittance (recorded with the hemispherical camera) increased significantly with increased tree canopy cover (Figure 3.6 (d)). Leaf area index showed no changes in the difference between the mean observed and expected values with increased tree canopy cover (Figure 3.6 (b)).

Table 3.2: Paired t-test results for the difference in photosynthetically active radiation (PAR), leaf area index (LAI) and percent transmittance (for both ceptometer and hemispherical camera readings) between the mean observed and expected values. $N = 32$ (16 pairs) for transmittance and PAR and $N = 24$ (12 pairs) for LAI as the open site is excluded. Results significant at $p < 0.05$ are highlighted.

	d.f.	t-value	p-value
PAR	15	-1.13	0.27
LAI	11	9.11	<0.00001
Transmittance (Ceptometer)	15	-2.46	0.025
Transmittance (Hemispherical camera)	15	-5.49	<0.0001

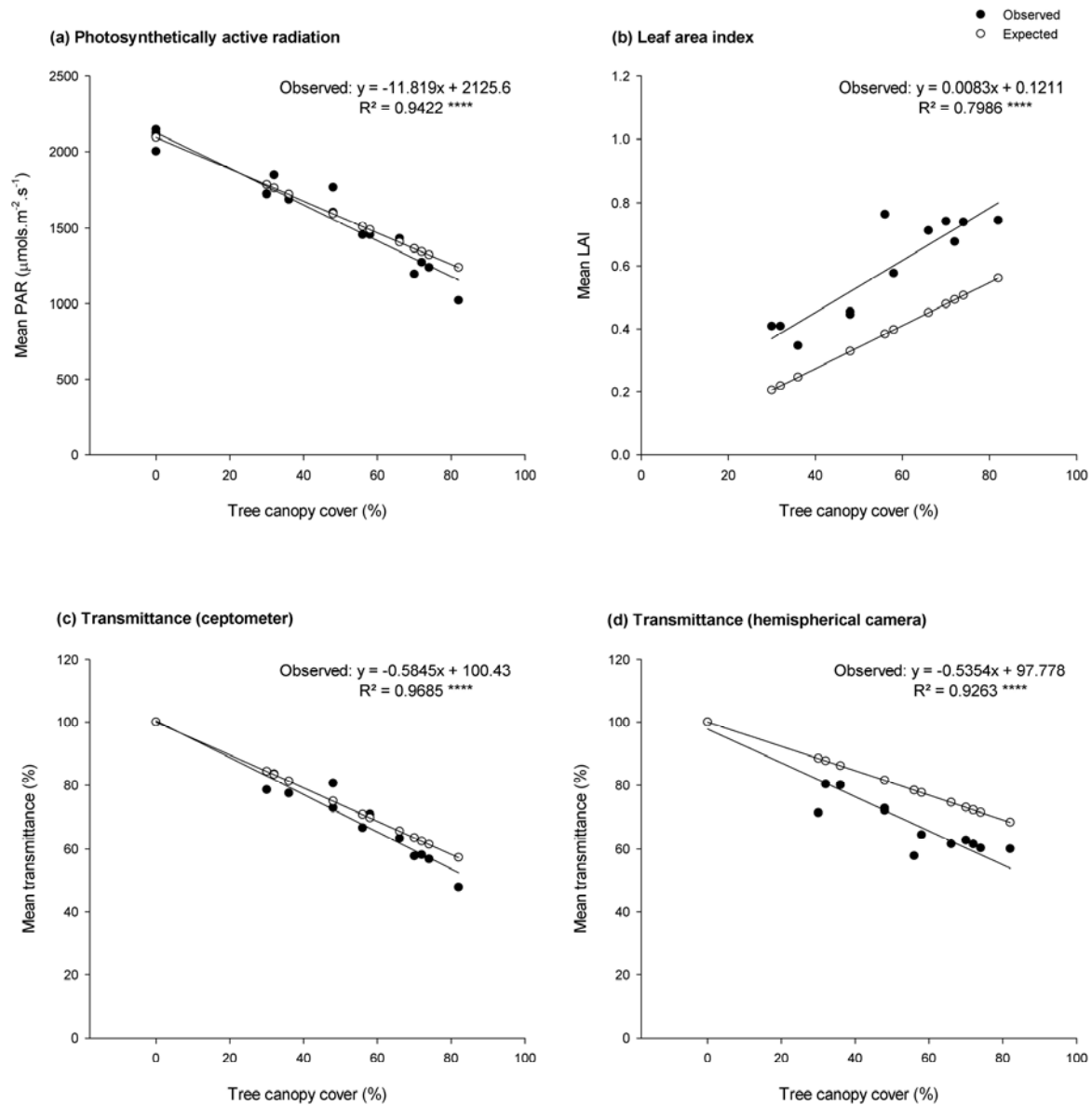


Figure 3.5: Mean observed and expected values for photosynthetically active radiation (PAR) (a), leaf area index (LAI) (b) and percent light transmittance (c – ceptometer and d – hemispherical camera) across a tree canopy cover gradient. The regression results for each graph are shown for the observed values; the expected values were not analysed as they are calculated and thus linear. Significant p – values are shown as $p < 0.05$ (*), $p < 0.001$ (), $p < 0.0001$ (***) and $p < 0.00001$ (****). $N = 32$ for PAR and transmittance and $N = 24$ for LAI as the open site is excluded.**

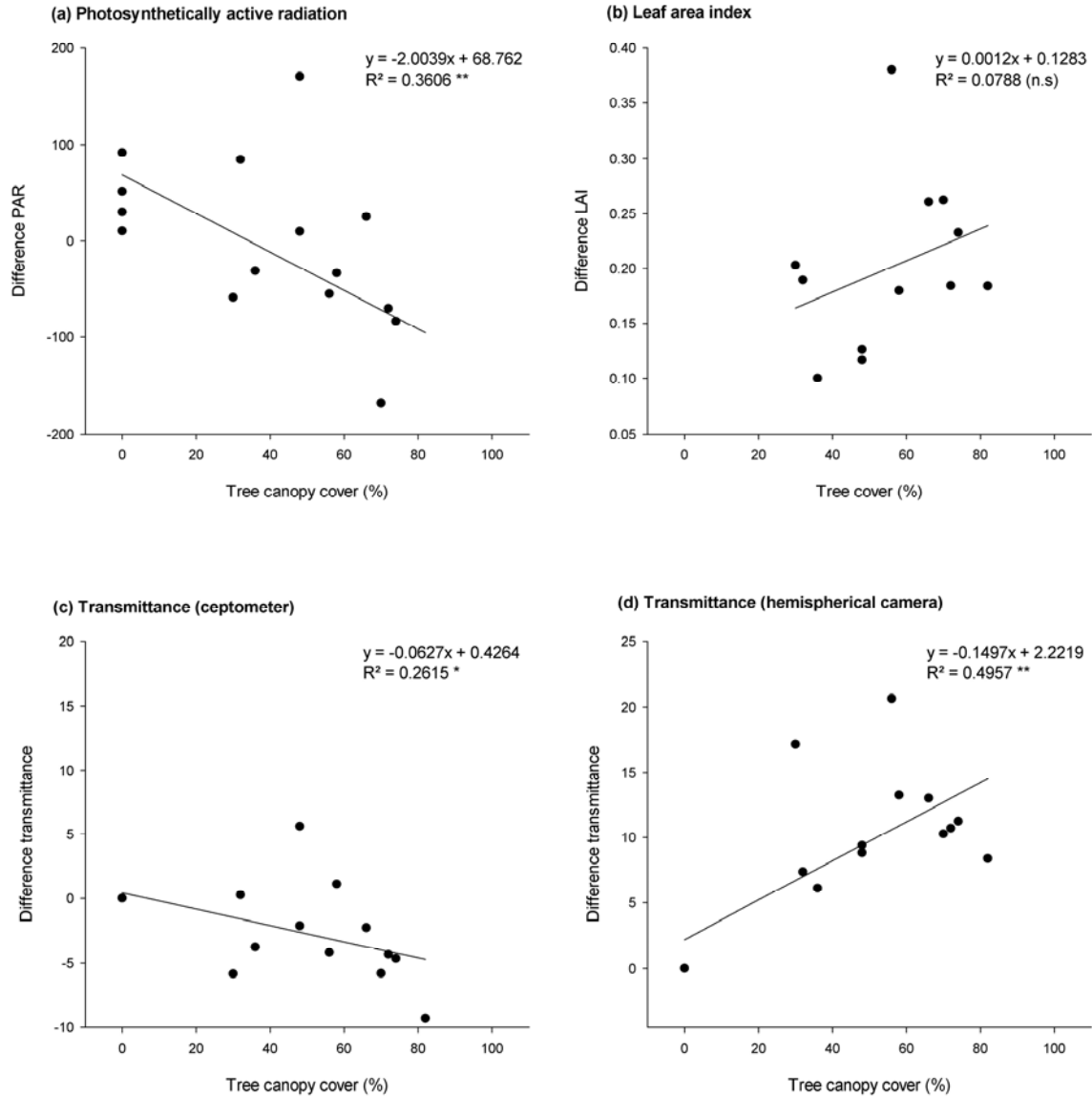


Figure 3.6: The difference between the mean observed and expected values for photosynthetically active radiation (PAR) (a), leaf area index (LAI) (b) and transmittance (c – ceptometer and d – hemispherical camera) across the tree cover gradient. The regression results for each graph are shown for the observed values; the expected values were not analyzed as they are calculated and thus linear. Significant p – values are shown as $p < 0.05$ (*), $p < 0.001$ (**), $p < 0.0001$ (***) and $p < 0.00001$ (****). Results that are not significant are indicated as n.s. $N = 32$ for PAR and transmittance and $N = 24$ for LAI as the open site was excluded.

3.3.4. Local and landscape effect of tree cover on soil moisture

At the open site, the average soil moisture content was higher than at the three encroached sites (Figure 3.7, graph a). This large difference suggests edaphic differences, such as soil structure or texture, and thus the site was excluded from the regression on inter-canopy soil moisture against tree cover and the soil moisture difference between the micro-habitats against tree cover. There was no significant difference between the sub-canopy and inter-canopy habitats on soil moisture content (Figure 3.7 (a); t -value = -0.66, d.f. = 11, p = 0.52). Suggesting there is no local tree effect on soil moisture content immediately following a rainfall event. Thus there is no evidence to suggest that rainfall interception by the tree canopies is a major factor in reducing soil moisture in the sub-canopy environment, at least not during a rainfall event of this size. The magnitude of the difference between the sub-canopy and inter-canopy soil moisture content was not significantly correlated with tree canopy cover either (Figure 3.7 (b)). There was also no significant change in the soil moisture content in either the sub-canopy or inter-canopy habitats with increased tree cover, indicating that there is no stand-effect on the soil moisture content following a rainfall event. This was a once-off measurement of rainfall immediately following a rainfall event, and thus could not provide insight into the effects of competition and evapotranspiration on soil moisture content which would have manifested over time.

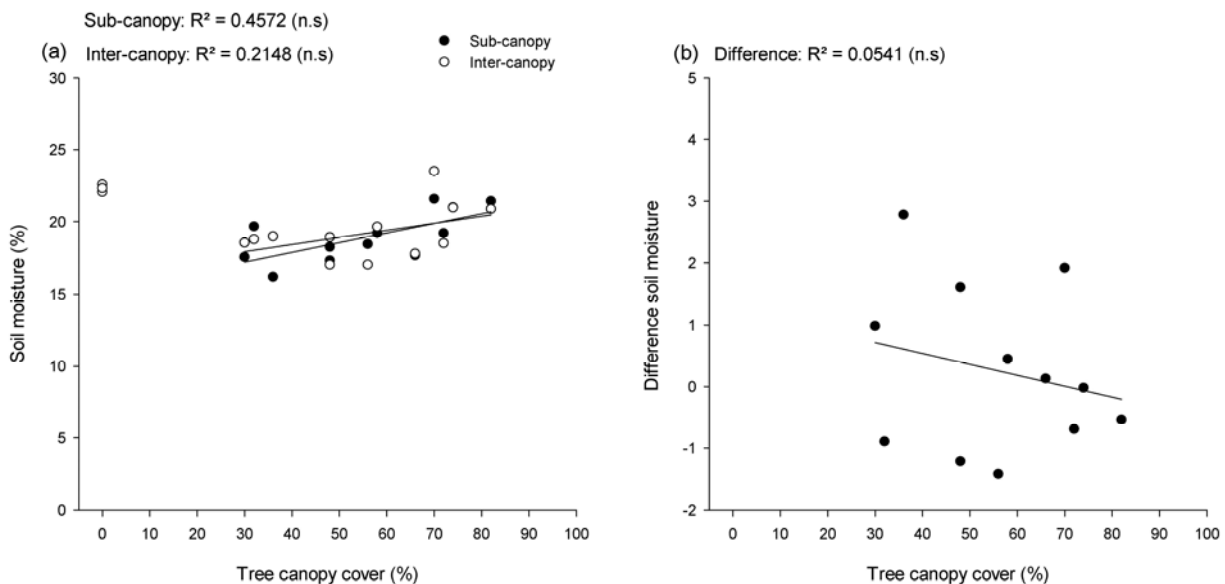


Figure 3.7: (a) Mean observed soil moisture at the inter-canopy and the sub-canopy micro-habitats the day after a rainfall event measuring 22 mm. (b) The difference between the observed inter-canopy and sub-canopy soil moisture content plotted against tree canopy cover. The regression for the observed soil moisture in the inter-canopy does not include the soil moisture content at the open site. None of the regression had significant results (n.s). N = 32 for the inter-canopy and N = 24 for the sub-canopy and difference (12 pairs).

Changes in soil moisture content over time at each of the four levels of encroachment are shown in Figure 3.8. Soil moisture at the open level of encroachment was again significantly higher than at any of the three encroached sites, suggesting that edaphic factors at this particular site are different from the other sites, although this was not tested. Soil moisture showed no significant changes with soil depth, and the data were thus analysed as mean soil moisture at each sampling point. Soil moisture on day one of the first sampling period was significantly higher than on day eight, the last day of sampling (t -value = 7.37, N = 24, d.f. = 23, p < 0.00001). This was also the case for the second sampling period where soil moisture on day one was significantly higher than the last day (t -value = 14.11, N = 24, d.f. = 23, p < 0.00001). The soil moisture was 2.3% lower during the first sampling period and 3.96% lower during the second sampling period. The difference is attributed to the longer sampling period, thus more water would have been lost through root competition and/ or evaporation.

Looking at the effect of micro-habitats on soil moisture at on the first and last days of the two sampling periods, regardless of the level of encroachment, there were significant differences between the sub-canopy and inter-canopy during the first sampling period but not the second (Figure 3.8). During the first sampling period, the inter-canopy had significantly higher soil moisture than the sub-canopy on the first day of sampling (t -value = 3.46, N = 4, d.f. = 3, p -value = 0.04), with the inter-canopy soil moisture increasing with 3.8% on average (Figure 3.8 (a, b, c, d)). This was the lower of the two rainfall events, and there is evidence here to suggest that the rainfall interception could have played a role in reducing soil moisture in the sub-canopy. On the last day of sampling the difference between the inter-canopy and sub-canopy was even greater (5.8%), and this significant difference was mostly due to a substantial decrease in mean soil moisture in the sub-canopy from 8.92% to 4.91% at the end of the sampling period (t -value = 9.53, N = 4, d.f. = 3, p -value = 0.002). Soil moisture was only 2.88% lower in the inter-canopy. This suggests that there was higher water loss due to root competition in the sub-canopy area. During the second sampling period there was a significant loss of water between the first and last day of sampling in both the sub-canopy and inter-canopy habitats. There was however, no significant difference between the two microhabitats on the individual days. There was a 4.8% loss in the sub-canopy over the 15 day period and 4.3% loss in the inter-canopy (Figure 3.8 (e, f, g, h)).

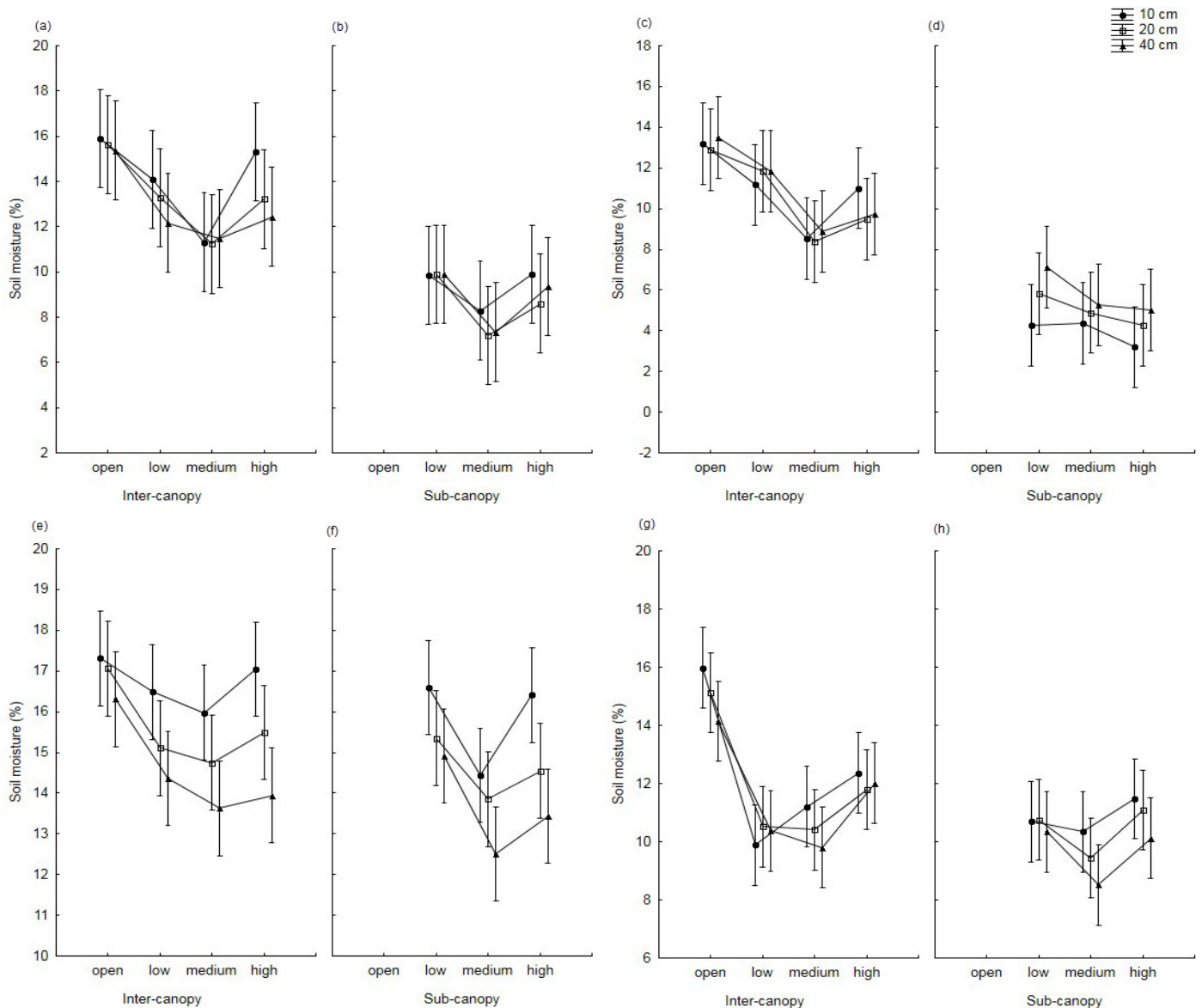


Figure 3.8: The Soil moisture content on the first and last day of sampling for two rainfall events (rainfall event 1: 1st day = a, b; last day = c, d; rainfall event 2: 1st day = e, f; last day = g, h), with the inter-canopy and sub-canopy soil moisture shown separately. The first rainfall event measured 15 ml of rain and the second 25 ml. The soil samples were taken at three depths: 10 cm, 20 cm and 40 cm.

3.3.5 The effect of woody encroachment on frost occurrence at the local and landscapes scale

With increasing tree cover, the incidence of frost decreased both in the inter- and sub-canopy micro-habitats. At the open site all transect points experienced frost during all three frost event. At the low level of encroachment, all transect point in the inter-canopy experienced frost during each of the three frost events, but the incidence of frost in the inter-canopy was

lower at the medium and high levels of encroachment (Figure 3.9). Frost occurrence was always lower in the sub-canopy environment than the inter-canopy. The low level of encroachment had the highest incidence of frost in the sub-canopy environment compared to the medium and high levels of encroachment, but frost only occurred in this micro-habitat during the more severe frost events (Figure 3.9). At the landscape level there was a significant difference between the sub-canopy and inter-canopy environment at each of the four levels of encroachment (Table 3.3). There was also a significant stand-wide effect of the micro-habitat across the tree canopy cover gradients (Table 3.4).

Table 3.3: Results of a general linear model (GLZ) comparing the number of frost incidence (0 – 3) at the inter-canopy and sub-canopy micro-habitats, for each of the four levels of encroachment. P-values are significant at $p < 0.05$.

	d.f.	Wald Stat.	p-value
Intercept	1	269.1165	<0.001
Level of encroachment	3	73.2163	<0.001
Micro-habitat (sub vs. inter-canopy)	1	190.3076	<0.001

Table 3.4: Results of the GLZ comparing the number of frost incidence (0 – 3) at the two micro-habitats across increasing tree canopy cover. The tree canopy cover taken from the individual transects. P-values are significant at $p < 0.05$.

	d.f.	Wald Stat.	p-value
Intercept	1	257.6546	< 0.001
Canopy cover	3	72.6884	< 0.001
Micro-habitat (sub vs. inter-canopy)	1	180.2944	< 0.001

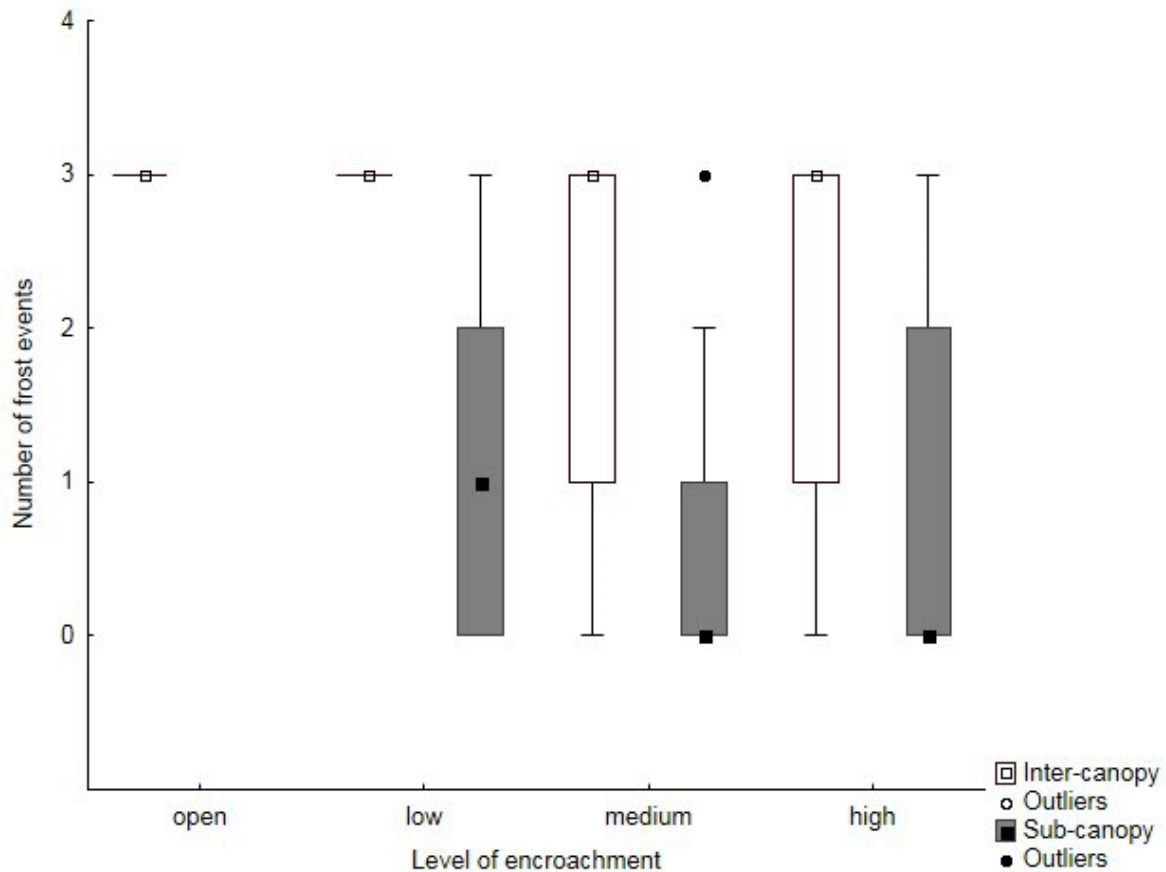


Figure 3.9: The number of times frost occurred (ranging from 0 – 3) at each sampling point at each of the four levels of encroachment (open, low, medium and high) in the sub-canopy and inter-canopy micro-habitats.

3.4. Discussion

3.4.1. Effect of tree cover on plant available light

Leaf area index in the sub-canopy environment can be up to six times higher than the average across the savanna (Scholes & Archer, 1997). At the sites studied here, LAI was 3.6 times higher in the sub-canopy environment than the inter-canopy, resulting in lower light transmittance and PAR in the sub-canopy environment across all levels of encroachment. The difference in LAI between the two micro-habitats was greatest at the low level of encroachment. We expected to find an increase in LAI in the sub-canopy habitat with increased tree canopy cover, once canopies start to overlap, but such an increase in the sub-canopy LAI (and accompanying decreases in PAR and transmittance) was not detected at this study site. Leaf area index in the inter-canopy, on the other hand, increased with increased

tree canopy cover, which can be explained by adjacent trees increasingly shading the inter-canopy areas at higher tree densities (Martens *et al.* 2000, Breshears, 2006). With increased tree canopy cover the areas that remain almost completely unshaded during the course of the day become fewer (Breshears, 2006) and the time during which the inter-canopy areas receive high light transmittance will become shorter. Bush encroachment thus reduces the amount of time plants can optimally use the light transmittance for photosynthesis. At the low level of encroachment there are several patches that receive high amount of transmittance, even when the adjacent canopies are taken into account (using the hemispherical camera). In the inter-canopy environment, the shading effect becomes evident from 50% transmittance upwards especially when looking at the hemispherical camera data.

The combined effect of tree canopies on sub-canopy light availability and of higher tree cover on the inter-canopy, overall plant available light decreased significantly at stand-wide tree cover. At the stand-wide scale at high tree densities, the stand-wide effect of trees plant available light is greater than can be accounted for just by scaling up the local tree effect. The predicted values using the ceptometer data were very similar to the observed values. While the observed values from the hemispherical data deviate from the expected values at higher tree densities. The reason for the difference between these measurements is that the ceptometer readings were taken around noon, and shading from surrounding trees (which would occur in the morning and/or afternoons) would not have been recorded. The hemispherical camera thus provides a more realistic and integrated measure of how the light environment in savannas is affected by different tree densities.

The amount of irradiation that infiltrates through the canopy has been shown to affect the herbaceous composition in the sub-canopy environment (Sage *et al.* 1999). If there is less than 15% transmittance under the canopy C₄ plants are likely to be excluded and the environment becomes dominated by C₃ plants (Sage & Kubien, 2003). In this study, I found that very few areas had less than 15% transmittance, with the high level of encroachment having the highest proportion. This suggests that at the levels of encroachment studied here there are few areas where C₄ plants are likely to be excluded. The hemispherical camera data revealed that even under canopies at the most densely encroached site, some incident light from the outside of the canopy in the morning and/or afternoon would reach the herbaceous layer, thus resulting in fewer records of extremely low transmittance than recorded by the ceptometer. In high light environments (>50% transmittance) C₄ plants dominate in tropical and subtropical grassy ecosystems (Sage, 2004). Light environments above 50%

transmittance (as recorded with ceptometer) comprise roughly 50% of the sampling points across all sites. This, however decreased moving from the low to high levels of encroachment (low: 77.5%; medium: 61.5% and high: 55.5%). It is thus very likely, even at 75% tree cover that C₄ grasses should dominate this system, at the landscape scale, with replacement by C₃ species being localised under bush clumps. The shifts from C₄ to C₃ grasses that is predicted to occur in areas where canopies become dense (Ratnam *et al.* 2011) is unlikely to occur in the case of *Acacia karroo* tree cover at these percentages. There is more likely to be a shift from shade intolerant to shade tolerant species (both C₃ and C₄), than a complete shift from C₄ to C₃. Thus species composition is likely to change moving from the inter-canopy areas to the sub-canopy and across the tree canopy cover gradient. This change could also be associated with phylogenetic changes in the composition of the C₄ grasses as well as changes in functional traits (Visser *et al.* 2012). Functional traits in shade adapted or tolerant C₄ species vary from sun adapted species for example higher specific leaf area has been recorded for species growing in the sub-canopy environment (Dias-Filho, 2000). This effect can possibly be seen in the inter-canopy at high tree densities as these areas become increasingly shaded. Thus it is even possible here that shade adapted species or species that can optimally use light transmittance over shorter period of time will become more prevalent. What will likely be affected at these light intensities is the primary production in the sub-canopy and inter-canopy areas as photosynthetic efficiency is reduced at lower light environments.

3.4.2 Effect of tree cover on soil moisture

I found some evidence of rainfall interception, where the soil moisture in the sub-canopy regions was lower than the inter-canopy immediately following the rainfall event. This however, only occurred after the lower of the two rainfall events. There was also no apparent effect of increased canopy cover on rainfall interception. Based on this, I conclude that the canopy intercepts rainfall between around 15 and 20 mm. This agrees with the conclusion from Belsky *et.al.* (1989) that during rainfall events with 20 mm or less rain canopy interception would become evident and this would become more pronounced with decreased rainfall.

For both sampling periods, there were significant decreases in soil moisture over time (from the first to last day of sampling). This was expected as soil moisture was due to be lost through evapotranspiration and/or root competition. If the increased shading in the sub-canopy environment contributed to lower evapotranspiration it would be expected that soil

moisture loss over time would be greater in the inter-canopy than sub-canopy region. This hypothesis however was rejected by my data, as soil moisture loss in the sub-canopy exceeded that in the inter-canopy during the first sampling period and was slightly greater during the second sampling period. The likely explanation for the difference and greater loss of soil moisture in the sub-canopy is root competition. As the roots of trees and herbaceous plant species compete for water, more water is taken up under the canopy than in the inter-canopy. Belsky *et al.* (1989) found that the soil moisture content was higher in the inter-canopy area than the sub-canopy, but that there was no significant difference during the rainy season. The results from this study agree with this, as the sub-canopy and inter-canopy soil moisture did not significantly differ. The difference between the two habitats became a bit more distinct after a few days without rain. It can be concluded that a combination of root competition and changes in soil properties in the sub-canopy resulted in the lower soil moisture compared to the inter-canopy. Soil moisture could not be observed over a longer period to observe to what extent soil dry out after rainfall, as rain kept falling. This would have given an indication of areas where the herbaceous layer could become water limited (Scholes, 1990). Thus, under the condition monitored in this study the areas were not truly water limited during that period in the growing season. Contrary to expectations however, soil moisture was higher at the most densely encroached site than the low and medium levels of encroachment. It is possible that at the higher levels of encroachment reduced evapotranspiration could have countered the negative effect of the root competition. The net effect of the tree canopies on soil moisture, however, was negative. Higher grass cover at the sites with lower tree cover to lower soil moisture at the low and medium sites. Grass is more efficient at utilizing the water in the top soil and thus can more rapidly deplete the soil moisture (Smit & Rethmna, 2000). This is predicted to impact the primary production in the sub-canopy (Scholes, 1990).

3.4.3 Effect of tree cover on the occurrence of frost

The presence of the canopy reduced frost occurrence and at the least severe frost event almost no frost occurred under the canopy and or the canopy edges. This effect was more pronounced at the medium and high levels of encroachment, where the inter-canopy also became less frost prone. There was thus a substantial stand-wide and landscape scale effect on frost occurrence, with frost occurrence decreasing with increased tree cover. The absence of frost under the canopy is likely to prolong the growth period of plants under the tree canopy as they are less likely to suffer die-back during a frost event. Thus herbaceous plants

growing under tree canopies will likely have an extended growing season compared to those growing in the open. Plants growing in the inter-canopy region experience top-kill during heavy frost event. This is likely to have a direct effect on tree recruitment, as frost top-kills *Acacia karroo* seedlings (L. Perumal, unpublished data). This could result in higher tree recruitment in the inter-canopy at high tree densities and in the sub-canopy areas at a range of tree densities. When seedling experience top-kill during frost it slows their growth rate, leaving them vulnerable to fire and herbivory, and reducing their survival rate (Wakeling *et al.* 2012). If there is a fire early in the winter season while the sub-canopy grasses are still green, the fire is likely to stop at the tree sub-canopy boundary. This effect will become more pronounced at higher tree densities as the inter-canopy area is smaller. Higher tree cover thus retards fire spread and trees are less exposed to fire damage. If there are seedlings or sapling in the sub-canopy region they could also escape the fire trap. This could lead to an increase in tree recruitment.

3.4.4. Conclusions

Plant available light and soil moisture was reduced in the sub-canopy habitat compared to the inter-canopy. Even though light transmittance was lower in these environments it was not low enough to necessarily exclude C₄ species as most areas had > 15% transmittance. The absence of frost during the early winter will result in a prolonged growing period under the canopy compared to the open areas. This effect is pronounced at the higher levels of encroachment compared to the low levels of encroachment. This effect will probably not be significantly greater with increased tree cover as the changes in the sub-canopy environment do not scale up linearly with increased tree cover. With the reduced shade and frost occurrence in the sub-canopy and inter-canopy (at higher tree canopy cover) could result in increase in seedling recruitment as these conditions are more favourable and *Acacia karroo* seedling have been shown to do well under tree canopies (O'Connor, 1995). Suppression of fire in this region will also assist seedling recruitment. The increase in green foliage in the sub-canopy region will result in herbivores favouring this area, although it is likely that the biomass and cover will be lower as a result of reduced light transmittance.

Chapter 4: The effect of tree density on the herbaceous layer

4.1. Introduction

Changes in the microclimate and resource availability associated with tree presence affect the herbaceous layer in the sub-canopy and inter-canopy regions. Trees can both suppress or enhance grass productivity (Dohn *et al.* 2013; Moustakas *et al.* 2013). Through competition with grasses for resources, trees suppress grass production. They also negatively affect grass productivity by reducing the plant available light (Martens *et al.* 2000; Funk & McDaniel, 2010). This effect becomes more prominent with increased tree density (Mordelet & Menuat, 1995). At higher tree densities the competition for resources will increase and trees may outcompete grasses in the sub-canopy and increase competition in the inter-canopy. With higher tree canopy cover, shading in the sub-canopy and inter-canopy is increased thus further reducing plant available light (Breshears, 2006). Trees can facilitate grass productivity by increasing the availability of soil nutrients (Augustine & McNaughton, 2006). In some cases, soil moisture enhanced by decreased evaporation under trees can therefore prolong the growing season of grasses (Ludwig *et al.* 2001; Vetaas, 1992). The changes in abiotic conditions under tree canopies can also result in species composition change moving from the inter-canopy to sub-canopy. This change is expected to include a shift from C₄ to C₃ species from the inter-canopy areas to sub-canopy areas at high tree densities (Sage & Kubien, 2003). With changes in global climate and CO₂ concentration influencing the tree-grass interactions (Buitenwerf *et al.* 2012), the effect of trees and tree density on the herbaceous layer becomes important from both a farming and conservation perspective (Angassa, 2012). Here the focus will be on how the herbaceous layer at the local and landscape scale is affected by different tree densities and the associated changes in light transmittance and soil moisture.

4.1.1. Effect of single trees on herbaceous productivity and composition

Herbaceous productivity under individual trees has been shown to be higher (Weltzin & Coughenour, 1990; Abdallah *et al.* 2008), and in some cases lower (Riginos *et al.* 2009; Smit, 2005) compared to open or inter-canopy areas. The primary production under individual trees may be enhanced by increased soil moisture and nutrients and lower evaporative demand (Ludwig *et al.* 2001), but suppressed by the decreased irradiance and competition with the tree for resources (Scholes & Archer, 1997; Treydte *et al.* 2007). The reduced

photosynthetically active radiation (PAR) in the vicinity of the tree will result in shade tolerant grass species being more productive in this microhabitat than shade intolerant species (Bond & Parr, 2010; Ratnam *et al.* 2011). Individual large trees at low density in savannas have been found to increase productivity of grasses under the canopies by as much as 25% (Stuart-Hill, 1987; Stuart-Hill & Tainton, 1989a). This effect differs with mean annual rainfall. Productivity under large trees in mesic savannas can be up to 50% higher in the sub-canopy compared to outside, but in more xeric areas the productivity under the canopies can be double that of the inter-canopy (Belsky *et al.* 1993). Mordelet & Menaut (1995) argued that the increase in productivity seen under individual trees can be attributed to the tree species under which these measurements were made. They argued that the higher productivity was measured underneath *Acacia* species and Baobab trees, and that these trees have sparse foliage which would not impede photosynthesis of the herbaceous layer. They also point out that the *Acacia* species have been shown to increase nitrogen thus increasing soil nutrient availability. In other cases, decreases in productivity have also been documented. Reasons for the decrease in herbaceous productivity under trees included tree density (bush clumps rather than individual trees) (Mordelet & Menaut, 1995), shading (Ludwig *et al.* 2001) and reduced soil moisture (Anderson *et al.* 2001).

The changes in the microclimate and resource availability can also result in changes in grass composition under tree canopies, including shifts in photosynthetic sub-types (Sage, 2004). This generally results in a shift in herbaceous composition, with shade intolerant species becoming replaced by more shade tolerant species, such as C₃ grasses (Ratnam *et al.* 2011) or more shade tolerant C₄ species such as *Panicum maximum* (Amundson & Belsky, 1995; Kunst *et al.* 2014). C₃ herbaceous species have higher quantum yield at low light intensities than C₄ grasses, which are generally adapted for high light environments (Still *et al.* 2014), and C₃ grasses are thus expected to perform better in shaded areas. In inter-canopy or open regions, C₄ plants have higher productivity as they outcompete C₃ plants, being more efficient at high light environments and higher temperature (Osborne & Freckleton, 2009). C₄ grasses are generally dominant in environments where they are exposed to more than 50% direct sunlight (Sage & Kubien, 2003). This would result in C₄ species being excluded at high tree densities and under bush clumps, but not necessarily at low to intermediate tree cover.

Whether the overall productivity in the sub-canopy environment will be higher than the inter-canopy also depends on factors such as soil moisture and nutrient availability, as these are two common limiting factors for productivity in savannas (Drescher *et al.* 2006; Dohn *et al.*

2013). The presence of trees can both increase and decrease soil moisture. The net effect of the tree on soil moisture depends on the interaction with herbaceous species in the sub-canopy as well as the size and architecture of the tree species. Water is a limiting factor in arid-and semi-arid savannas (Sankaran *et al.* 2005). Tree canopies intercept rainfall and reduce the amount of water that reaches the sub-canopy environment (Scholes & Archer, 1997); they also compete with grass roots for soil moisture (Smit, 2005). If soil moisture increases under individual trees, whether it is through hydraulic lift (Ludwig *et al.* 2004) or decreased evapotranspiration under the canopy (Breshears, 1993; Amundson & Belsky, 1995), it will benefit grass productivity in the sub-canopy environment compared to the inter-canopy environment, especially if the soil nutrient status is higher under the canopy. This can potentially result in higher productivity and herbaceous cover in the sub-canopy compared to the inter-canopy (Belsky, 1994). Water availability and temperature also determine the distribution and abundance of C₃ and C₄ grasses. C₄ grasses are more water use efficient, and thus occur abundantly in the open where evaporation is higher (Sage & Kubien, 2003; Pau *et al.* 2013). C₄ species are more productive than C₃ species under warmer growing conditions, though it is unlikely that the reduction in temperature under tree canopies results in low enough temperatures to directly favour C₃ plants (Stowe & Teeri, 1987).

The increase in herbaceous productivity and cover under trees can also be attributed to increased soil nutrient status under tree canopies. Tree presence has been known to create ‘islands of fertility’ in savanna ecosystems, with increased soil organic matter (Abdallah *et al.* 2008; Treydte *et al.* 2010), nitrogen (Belsky, 1994; Treydte *et al.* 2007), and phosphorus (Ludwig *et al.* 2008) being higher in the sub-canopy region compared to the inter-canopy. Increased soil nutrient status under canopies can improve herbaceous productivity compared to outside. The herbaceous layer in the inter-canopy has been documented to be N limited compared to grasses growing in the sub-canopy (Belsky, 1994; Treydte *et al.* 2007). Nitrogen from deeper soils can be redistributed to upper soil by trees (Priyadarshini *et al.* 2014) and leguminous trees increase soil nitrogen through N-fixation (Belsky, 1992; Smit & Swart, 1994). The increase in soil nutrients benefits the grass species found in the sub-canopy and as a result, these grasses have higher nutrient content and are more favourable for grazing (Ludwig *et al.* 2001; Treydte *et al.* 2009; Treydte *et al.* 2011). Leaf nutrient content of the herbaceous layer in the sub-canopy environment can be up to 25% higher than those of in the inter-canopy (Treydte *et al.* 2007).

4.1.2. Effect of tree density on herbaceous productivity and composition

Bush clumps or higher tree densities have a net negative effect on the herbaceous layer compared to the net positive effect of individual tree or tree at low or medium densities (Angassa *et al.* 2012; O'Connor & Chamane, 2012). At high tree densities net soil moisture and inter-canopy light availability decrease (Scholes & Archer, 1997), which leads to suppressed grass productivity (Abule *et al.* 2005; Riginos *et al.* 2009). At low to intermediate tree cover in arid and semi-arid savannas, herbaceous biomass in the sub-canopy does not significantly differ from that in the inter-canopy (Ludwig *et al.*, 2001; Ludwig *et al.* 2004; Sitters *et al.* 2013). In densely encroached areas the increase in tree cover and biomass results in significant decreases in grass cover and productivity (Jarvel & O'Connor, 1999; Ludwig *et al.* 2004). This effect is intensified under high grazing pressure (Angassa, 2005).

Species richness and composition is also affected by tree density. At intermediate tree cover (10 – 20%), species richness and abundance increases but decreases at higher densities (Ludwig *et al.* 2001; Angassa, 2014). At highly encroached sites more unpalatable species are generally found under canopies, and at sites that are heavily grazed, unpalatable species replace palatable species even faster as the pressure on these grasses increases (Angassa, 2005; Angassa *et al.* 2012). Herbaceous species richness and composition decreases with an increase in tree cover, and is highest at intermediate tree cover (Angassa, 2005; Angassa *et al.* 2012). In a semi-arid southern African savanna, Richter *et al.* (2001) found that high tree densities did not have a significant effect on species composition and concluded that changes in seasonal rainfall had a greater effect on herbaceous composition than tree canopy cover. The overall net positive effect that single trees have on their sub-canopy environments may or may not scale up at landscape level, and the net effect at the landscape level is likely to be influenced by tree density. Increased tree density generally results in lower herbaceous production and shifts in species composition, and the net effect of high tree density is often negative (Scholes & Archer, 1997; Riginos *et al.* 2009).

4.1.3 Study overview

The aim of this study was to examine the effect of increased tree canopy cover on the herbaceous layer productivity and composition at the local, stand-wide and landscape scale. I quantified herbaceous cover and productivity in the sub-canopy and inter-canopy micro-habitats at four sites along a tree canopy cover gradient. The effect of plant available light on grass species occurrence and dominance was also examined.

I predicted that increased tree canopy cover would decrease the herbaceous basal cover in the sub-canopy environment. As the inter-canopy micro-habitat becomes more shaded and more affected by root competition from tree, herbaceous basal cover is also predicted to decrease in the inter-canopy at high tree cover. Overall stand- and landscape-wide herbaceous productivity is thus expected to decline with increased tree cover.

The response of individual grass species abundance to increasing tree cover in the sub-canopy and inter-canopy was also examined. I predicted that basal cover of shade intolerant grass species would decrease with tree cover in the sub-canopy, and above a certain tree density also in the inter-canopy. The relationship between observed herbaceous basal cover and tree canopy cover was examined to determine how the local 'tree effects' scale up in the landscape for total basal cover as well as the abundance of individual grass species. To establish whether predictions about the stand-wide effect at various percentages tree canopy cover can be based on the local tree effect, predicted values (extrapolated from the local tree effect) were compared to the mean observed values. The relationship between the expected values and tree canopy cover is linear as this is calculated, but the relationship between the observed values and tree canopy cover is predicted to deviate from the expected values as tree canopy cover increases. Changes in species composition and shifts in photosynthetic sub-types from the inter-canopy to sub-canopy are likely with increased tree cover and changes in abiotic conditions. I also predicted that herbaceous species found in the sub-canopy would remain greener for longer at the end of the growing season and thus there would be an observed difference in the fractions of the living and dead biomass in the sub-canopy and inter-canopy environments.

As the tree canopy cover increased, light transmittance in the sub-canopy and inter-canopy environment decreased (Chapter 3). The low light environment can contribute to changes in basal cover and species composition in the encroached areas. I predicted that herbaceous species basal cover would decrease with increased canopy cover and reduced light transmittance. This effect would be more pronounced in the sub-canopy environment as the soil moisture in the sub-canopy was also lower in the inter-canopy environment. Grass productivity was also expected to be reduced in the sub-canopy environment as there would be increased root competition with higher tree cover and hence lower soil moisture availability.

4.2. Methods

4.2.1. Data collection

At each of the four study sites (open grassland with no trees and low, medium and high levels of encroachment representing 21%, 45% and 72% tree canopy cover respectively), I measured herbaceous basal cover and composition, light transmittance, photosynthetically active radiation (PAR) and leaf area index (LAI). Sampling was carried out along the same fixed transect and sampling points used for sampling abiotic variables in Chapter 3.

Paired sub-canopy and inter-canopy exclosures (1m x 1m) were set up at the start of the 2012/ 2013 growing season (31 October 2012), at each of the four sites (low, medium and high levels of encroachment). Four exclosures were also set up at the open site (see Chapter 3). The grass was cut to 10 cm above the ground before the exclosures were set up. The exclosures were left for the duration of the growing season. At the end of the growing season (31 March, 2013) the exclosures were removed and the grass was harvested to 10 cm above the ground. This gave a measure of grass primary production (1° production) at the four levels of encroachment. At each of the paired sub-canopy and inter-canopy exclosures light transmittance, photosynthetically active radiation (PAR) and leaf area index (LAI) was also measured.

4.2.1.1 Grass basal cover and composition

Herbaceous basal cover and grass composition were determined at each sampling point along the transects. The sampling points along the transects were chosen to relate the grass composition at that specific point to the light environment and soil moisture. I used a 16-pin sampling frame (4 x 4 points 4 cm apart, thus covering a square area of 144 cm²) with the transect point at its centre. For every pin that struck a rooted plant the species was recorded. Where a pin did not touch the base of a plant, I recorded bare ground. Plants were classified as grasses, herbs or woody species. All grasses were identified to species level. All herbaceous species other than grasses were recorded as 'herb' species. Data were collected once during December in the 2012/ 2013 growing season and once again in December during the 2013/ 2014 growing season. Both times the data were collected after the area had had sufficient rainfall for herbaceous growth. Grass species were identified using Guide to Grasses of Southern Africa (van Oudtshoorn, 2012) and identification was confirmed in the Selmar Schonland Herbarium Grahamstown, South Africa.

4.2.1.2 Grass biomass production

Grass biomass production was measured at the end of the 2102/ 2013 growing season (578 mm rainfall). Exclosures were removed and the grass was harvested to 10 cm above the ground. Grass harvested from the exclosures was separated by species and each species was then further separated into living and dead material. The grass samples were placed in a drying oven for 48 hours at 70°C. After 48 hours the grass was weighed and the dry matter weight (DM) was recorded for each sample. This gave an aboveground measurement of standing grass biomass accumulated during the growing season and hence reflects the annual net primary production (ANPP).

4.2.1.3 Light measurements

Light transmittance, photosynthetically active radiation (PAR) and leaf area index (LAI) were recorded at each sampling point on the fixed transects, and at the centre of each exclosure in the sub-canopy and inter-canopy using. Light transmittance was measured using both the ceptometer and hemispherical camera. The ceptometer was also used to measure PAR and the hemispherical camera gave LAI readings. Hemispherical photographs were taken at each sampling point along the transects and each exclosure in the sub-canopy and inter-canopy of each bush clump. This was the same data used for analyses in Chapter 3.

4.2.2. Data analysis

4.2.2.1 Effect of tree canopy cover on herbaceous basal cover at stand-wide and landscape scale

Total herbaceous basal cover was calculated as the number of pins that struck any herbaceous vegetation as a percentage of the 16 pins dropped at each sampling point. The percent total herbaceous basal cover at each transect was thus calculated as the mean herbaceous basal cover of all 50 sampling points. The percent total herbaceous basal cover at each level of encroachment was calculated as the mean herbaceous basal cover at all 200 sampling points per site. To examine the effect of the level of encroachment on total herbaceous basal cover a one-way ANOVA was carried out and a post-hoc test (Tukey HSD) was used to determine significant pairwise differences between the levels of encroachment. A simple linear regression plotting total herbaceous basal cover against tree canopy cover was carried out to determine the effect of stand-wide tree canopy cover on total herbaceous basal cover.

4.2.2.2 Effect of tree canopy on herbaceous basal cover and composition at local and stand-wide scales

The mean percentage cover of each grass species, ‘herbs’ and total herbaceous basal cover was calculated for the sub-canopy and inter-canopy micro-habitats at each individual transect. The percent basal cover of each herbaceous species was calculated as the number of pin striking this species as the percentage of the total 16 pins at each sampling point in the sub-canopy or inter-canopy micro-habitat. The same procedure was followed to calculate the percent cover the all plant species classified as ‘herbs’ and for total herbaceous basal cover.

To determine the tree effect at local scale, the mean observed percent grass basal cover for each species, ‘herbs’ basal cover and all herbaceous plants were calculated separately for the sub-canopy and inter-canopy micro-habitats at each transect and plotted as a function of tree cover. The open level of encroachment was omitted from these analyses as there was no sub-canopy. First, the difference between the sub-canopy and inter-canopy basal cover for individual grass species, ‘herbs’ and total herbaceous cover was examined. Based on the difference between the two micro-habitats it can be established whether the presence of the tree canopy significantly influences the herbaceous basal cover. This would represent the ‘tree effect’ (Riginos *et al.* 2009). T-tests (paired by transect) were used to test the overall effect of the sub-canopy and inter-canopy on the basal cover of each grass species, ‘herbs’ and total herbaceous cover. A significant result indicated that the tee canopy had a positive or negative ‘tree effect’ on the basal cover of a specific grass species, ‘herb’ or total herbaceous cover (See Chapter 1, Figure 1.1). Secondly, I examined the effect of the stand-wide (transect) tree canopy on the basal cover of individual grass species, ‘herbs’ and total herbaceous cover in the sub-canopy and inter-canopy. These results showed whether, and how, different percentages of tree canopy cover affect the basal cover in the sub-canopy and inter-canopy. The effect of increasing tree cover on the basal cover at each micro-habitat represents the ‘stand-effect’ (Riginos *et al.* 2009). To test the effect of tree cover on herbaceous basal cover, I used simple linear regressions that were fitted separately to basal cover in the inter-canopy and sub-canopy plotted against tree canopy cover. Significant regression results would represent a stand effect (See Chapter 1, Figure 1.1). Lastly, I examined changes in the magnitude of the local tree effect with increased canopy cover. The difference between the inter-canopy and sub-canopy environment was calculated and regressed against tree canopy cover at each transect. The results indicated whether, and to what extent, the magnitude of the local tree effect changed with increased tree canopy cover.

4.2.2.3 Observed and expected herbaceous basal cover at the stand-wide scale

To examine how the local tree effect on basal cover of individual grasses, ‘herbs’ and total herbaceous cover scales up along a gradient of increased tree canopy cover, mean observed and expected values for each variable were calculated and plotted as a function of tree canopy cover. First, the mean observed basal cover for each grass species, ‘herbs’ and total herbaceous cover were calculated at all sampling points at each transect, including both micro-habitats. Secondly, mean expected basal cover for each grass species, ‘herbs’ and total herbaceous cover was calculated. When calculating the expected values it was assumed that the local tree effect would scale up directly with increased tree canopy cover. It was assumed that the sub-canopy micro-habitat at the lowest tree cover would best represent the individual tree effect. It was also assumed that the inter-canopy effect would best be represented by the inter-canopy value at the lowest tree canopy cover. Based on this assumption, the transect with 30% tree canopy cover was used to derive mean sub-canopy values for basal cover (N = 15). The open site was excluded from the analysis as it is suspected that there are edaphic differences between this site and the encroached sites. Thus the 30% tree canopy cover transects were used for mean inter-canopy values as well. Mean expected values were calculated for each transect, using the tree canopy cover at the transect in question. The methodology and formula used for calculating the expected values were adopted from Riginos *et.al.* (2009). The formula was as follows:

Expected value = ((mean sub-canopy value) x (proportion stand-wide tree canopy cover)) + ((mean inter-canopy value) x (1 – stand-wide tree canopy cover))

To determine how the tree canopy cover affected the overall observed values, linear regressions were fitted to the data. The expected values were not analysed as these were calculated at thus perfectly linear. Paired t-test (paired by transect) were used to determine the difference between the observed and expected values for basal cover for each grass species, ‘herbs’ and total herbaceous cover. A significant difference indicated a stand-wide effect that could not be explained by the sum of single tree effects alone. Lastly, I examined the effect of tree cover on the difference between the observed and expected values. The difference between the observed and expected values was calculated and regressed against tree canopy cover at each transect. Significant decreases or increases in the difference between observed and expected values with tree cover would indicate that the local tree effect

on herbaceous basal cover did not scale up linearly at stand-wide level (See Chapter 1, Figure 1.2).

4.2.2.4 Effect of tree canopy cover on herbaceous primary production

To test the effect of micro-habitat on biomass, factorial ANOVAs were used to examine the effect of micro-habitat (sub-canopy and inter-canopy) and level of encroachment on the total biomass, dead biomass and living biomass. The open site was excluded from the analysis as there was no sub-canopy habitat. A post-hoc Tukey (HSD) test was performed to test for significant pairwise differences between micro-habitats and level of encroachment.

4.2.2.5 Probability of grass species occurrence at various light intensities

To determine how likely it was for the different grass species to occur at low or high light transmittance, the probability of occurrence for the most common grass species at different light transmittance classes was calculated. The light transmittance data collected using the ceptometer (See Chapter 3) was used to create categories of 10% transmittance. The percent light transmittance and grass species data from all four levels of encroachment was combined. To calculate the probability occurrence grass species was either assigned a 1 for “present” or a 0 for “absent” at each sampling point. The total number of times the grass species was classified at “present” in each light category was then divided by the total number of sampling points in that light category to give the probability of occurrence of a particular species in at a particular light transmittance class.

4.2.2.6 Change in grass species dominance with increased light transmittance

At each sampling point, species with the highest percent basal cover was recorded as being the dominant species. All sampling points for the four levels of encroachment were combined. From this data set the five most dominant grass species across all four levels of encroachment were selected. A box and whisker plot was used to show the median, quartiles and range of light transmittance at which each grass species was dominant. Since the data did not meet assumptions of normality or homogeneity of variance, I used a Kruskal-Wallis test to determine whether there was a significant difference between the light intensities at which grasses were dominant.

All statistical analyses were carried out in STATISTICA V10.0 (StatSoft. Inc., Tulsa, USA, 2010).

4.3. Results

4.3.1 Grass species composition at the study site

The grass species that were identified at the four level of encroachment were: *Themeda triandra*, *Sporobolus africanus*, *Pennisetum sphacelatum*, *Eragrostis chloromelas*, *Eragrostis plana*, *Digitaria eriantha*, *Panicum maximum*, *Cynodon dactylon*, *Panicum aequinerve* and *Helictotrichon turgidulum*. With the exception of the two latter grasses, all were C₄ grasses. *Setaria sphacelata* var. *sphacelatum* was also found at the site but only recorded once along the fixed transects. Other grasses such as *Eragrostis capensis*, *Eragrostis curvula*, *Paspalum dilatatum*, *Hyparrhenia hirta* and *Cymbopogon caesis* were identified on the farm but no encountered at the sampling sites or along the fixed transects. The grass species richness at this site appears to be low, this is also shown in other studies conducted in this area (Martens & Morris, 1994). The low species richness is also as a result of the sampling method and the fact that only grass species were identified. The sampling method used focused on small areas and only picked up the more common species in this area. This method is thus not suited to estimating the species richness and will likely miss rare species.

4.3.2 Herbaceous basal cover at the landscape level

Mean basal cover, including all herbaceous species identified in both microhabitats, was lower ($F_{(3, 799)} = 105.343$, $p < 0.001$) at the more encroachment sites. The open site had higher ($p = 0.00008$) basal cover than the three encroached sites (Figure 4.1). At the stand-wide scale, increased tree canopy cover led to a decrease in the herbaceous basal cover. ($d.f. = 15$, $r^2 = 0.25$, $p < 0.001$) (Figure 4.2), but again the higher cover at the open site strongly influenced this relationship.

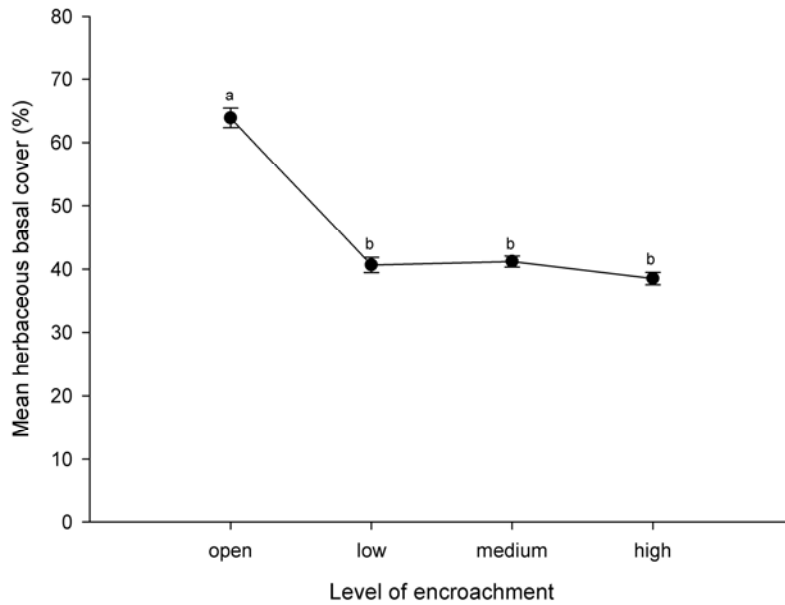


Figure 4.1: Mean herbaceous basal cover at each level of encroachment. Total herbaceous cover includes all grass species and species classified as ‘herbs’. The letters represent the pairwise differences (Tukey HSD), with different letter indicating significant differences. The bars indicate the standard error for each site. $N = 200$ for each site.

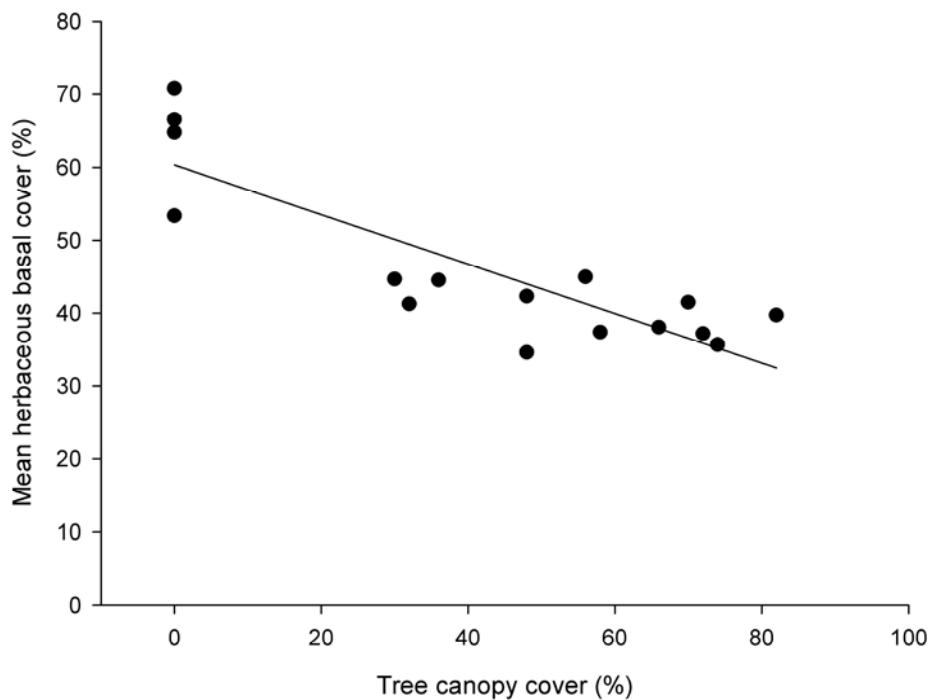


Figure 4.2: Regression results showing a significant decrease in mean herbaceous basal cover across a tree canopy cover gradient. This represents the mean total herbaceous cover along each fixed transect at the four levels of encroachment. $N = 16$ for all models.

4.3.3 Effect of micro-habitat on herbaceous basal cover across a tree cover gradient

Herbaceous basal cover varied greatly with micro-habitat and tree canopy cover for the individual grass species and ‘herbs’. Herbaceous basal cover along the transects in the open site differed greatly from cover found along the transects at the encroached sites. Thus these transects were left out of the analyses as they influenced the relationship between herbaceous basal cover and tree cover. Total herbaceous basal cover was significantly higher in the inter-canopy areas than in sub-canopy areas (Figure 4.3 (l); Table 4.1). This was also the case for *T. triandra* which was significantly more abundant in the inter-canopy than sub-canopy (Figure 4.3 (a); Table 4.1). The only grass species that had significantly higher basal cover in the sub-canopy environment compared to the inter-canopy was *P. aequinerve*, as well as species classified as ‘herbs’ (Figure 4.3 (f, h), Table 4.1). None of the other grass species showed any significant difference in abundance between the inter-canopy and sub-canopy environments (Figure 4.3; Table 4.1). Basal cover of *T. triandra* in the sub-canopy and *D. eriantha* in the inter-canopy decreased significantly with increased tree canopy cover, showing that there was a negative ‘stand effect’ on these species in the sub-canopy and inter-canopy respectively (Figure 4.3 (a, d); Table 4.2). *Eragrostis chloromelas* and *P. sphacelatum* showed an increase in abundance with increased tree canopy cover in the sub-canopy although it was only marginally significant ($p = 0.06$). No other grass species, ‘herbs’ or total herbaceous cover showed any significant stand-effect in either micro-habitat. There was no significant effect of stand-wide tree canopy cover on the difference between the sub-canopy and inter-canopy micro-habitats, indicating that the local tree effects on these species were not altered by increased tree canopy cover.

Table 4.1: Paired t-test results for the difference in herbaceous basal cover between the sub-canopy and inter-canopy for individual grass species, 'herbs' and total herbaceous basal cover. $N = 12$ for all cases. P-values significant at $p < 0.05$ are highlighted. Figures that were marginally significant are indicated with *.

	d.f.	t-value	p-value
<i>Themeda triandra</i>	11	-6.69	0.00003
<i>Pennisetum sphacelatum</i>	11	-2.06	0.06 *
<i>Sporobolus africanus</i>	11	-0.49	0.62
<i>Panicum aequinerve</i>	11	3.22	0.008
<i>Panicum maximum</i>	11	-0.23	0.82
<i>Helictotricon turgidulum</i>	11	0.83	0.42
<i>Eragrostis chloromelas</i>	11	-2.05	0.06 *
<i>Eragrostis plana</i>	11	-0.62	0.55
<i>Cynodon dactylon</i>	11	1.03	0.32
<i>Digitaria eriantha</i>	11	-2.46	0.03
'Herbs'	11	3.09	0.01
Total herbaceous basal cover	11	-7.88	0.000008

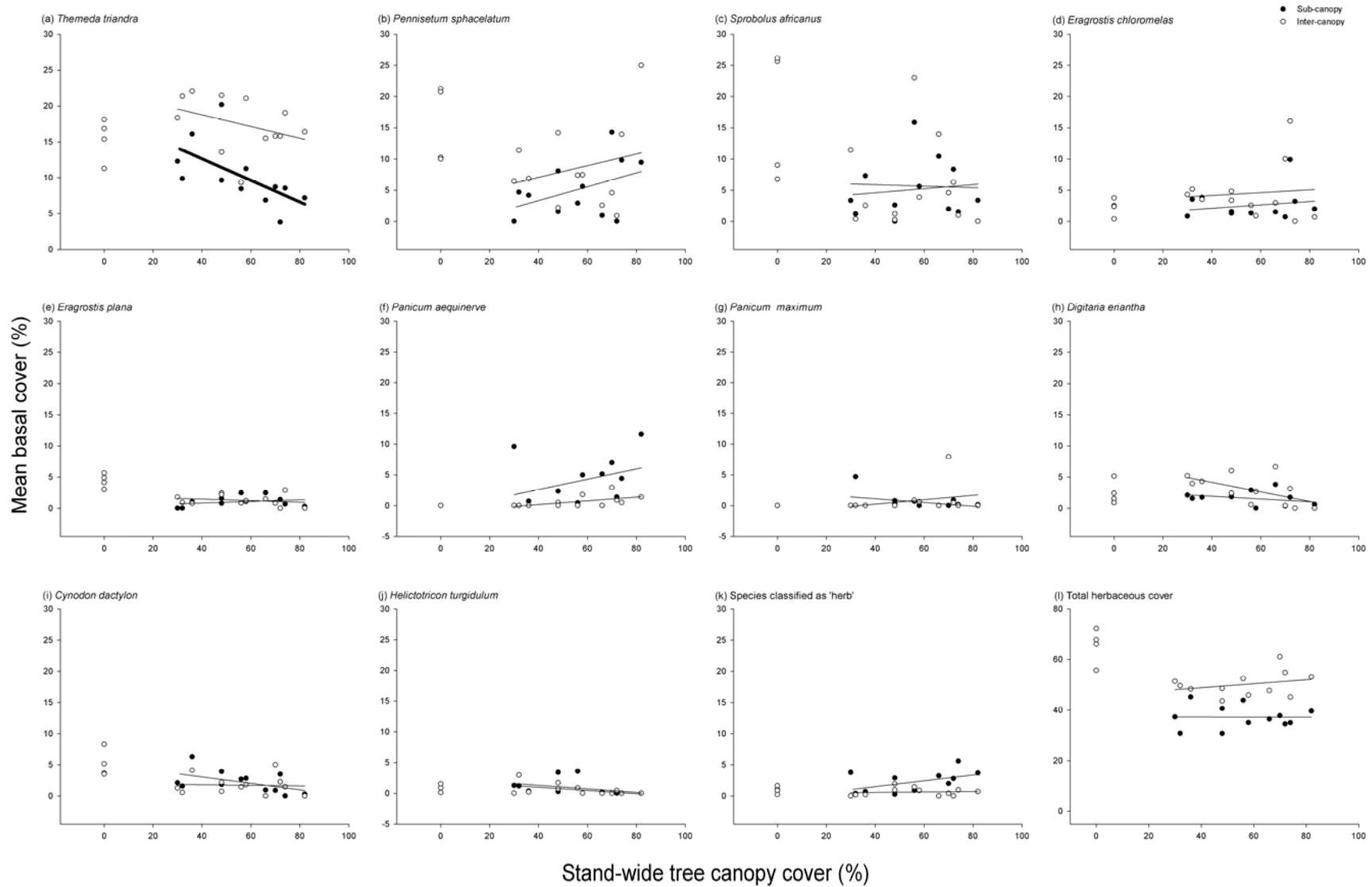


Figure 4.3: The mean observed inter-canopy (open symbols) and sub-canopy (solid symbols) values for herbaceous basal cover of identified grass species (a – j), ‘herb’ plant species (k) and total basal cover (l) plotted as a function of tree canopy cover. $N = 12$ for all models, significant regression results ($p < 0.05$) are highlighted.

Table 4.2: Regression results for the relationship between tree canopy cover and mean basal cover of grass species, ‘herbs’ and the total herbaceous basal cover in the sub-canopy and inter-canopy micro-habitats. $N = 12$ for all models. Significant ($p < 0.05$) and near-significant ($p < 0.1$) results are highlighted.

	r^2	Slope	p-value
<i>Themeda triandra</i>			
Sub-canopy	0.361	-0.150	0.03
Inter-canopy	0.130	0.080	0.23
<i>Pennisetum sphacelatum</i>			
Sub-canopy	0.184	0.110	0.16
Inter-canopy	0.058	0.090	0.44
<i>Sporobolus africanus</i>			
Sub-canopy	0.015	0.030	0.70
Inter-canopy	0.0008	-0.0100	0.92
<i>Eragrostis chloromelas</i>			
Sub-canopy	0.030	0.026	0.50
Inter-canopy	0.007	0.022	0.78
<i>Eragrostis plana</i>			
Sub-canopy	0.070	0.012	0.39
Inter-canopy	0.050	-0.012	0.46
<i>Panicum aequinerve</i>			
Sub-canopy	0.140	0.083	0.22
Inter-canopy	0.300	0.029	0.06
<i>Panicum maximum</i>			
Sub-canopy	0.15	-0.03	0.20
Inter-canopy	0.070	0.030	0.31
<i>Cynodon dactylon</i>			
Sub-canopy	0.260	-0.051	0.09
Inter-canopy	0.002	0.004	0.86
<i>Digitaria eriantha</i>			
Sub-canopy	0.100	-0.021	0.30
Inter-canopy	0.320	-0.076	0.05
<i>Helictotricon turgidulum</i>			
Sub-canopy	0.140	-0.028	0.22
Inter-canopy	0.240	-0.026	0.09
‘Herb’			
Sub-canopy	0.230	0.040	0.10
Inter-canopy	0.009	0.003	0.76
Total grass basal cover			
Sub-canopy	0.0001	-0.003	0.97
Inter-canopy	0.080	0.079	0.36

4.3.4 Observed vs. expected stand-wide herbaceous basal cover in relation to tree canopy cover

Observed stand-wide herbaceous basal cover did not differ significantly from the expected values for most of the grass species or total herbaceous basal cover. Three grass species showed a significant difference between observed and expected basal cover, *P. aequinerve*, *E. plana* and *C. dactylon* (Table 4.3). The difference between the observed and expected values for *P. aequinerve* was greatest at higher tree canopy cover where the difference for *E. plana* was greater at low tree canopy cover. In the case of *C. dactylon* the difference remained similar regardless of tree canopy cover (Table 4.3). Observed values for total herbaceous basal cover also significantly differed from the expected values (Table 4.3). Observed total herbaceous basal cover was much lower than the calculated expected, although the difference decreased with increased tree cover (Figure 4.4).

In most cases the observed basal cover followed similar trends as the expected basal cover with the exception of *T. triandra*, *P. sphacelatum*, *S. africanus* and *P. aequinerve* (Figure 4.4 (a – c, f)). Observed stand-wide *T. triandra* decreased where the expected values remained the same with increased tree cover. The difference between observed and expected values for *T. triandra* varied with tree cover, at the lower tree canopy cover observed values were greater than expected, but was lower than the expected values at higher tree canopy cover. The magnitude in the difference between observed and expected values, however, became greater at higher tree canopy cover (Table 4.4). Expected values for *P. aequinerve* also showed no change with tree cover but the observed values showed an increase. The difference between the two values for *P. aequinerve* increased with tree canopy cover (Table 4.4). In the case of *P. sphacelatum* and *S. africanus* the expected values decreased with tree cover and the observed values showed hardly any change. Observed stand-wide basal cover for *T. triandra* and *D. eriantha* decreased significantly with tree canopy cover (Figure 4.4 (a, h); Table 4.4), while observed *P. aequinerve* basal cover increased with tree canopy cover (Figure 4.4 (f); Table 4.4). For *T. triandra*, *P. aequinerve*, *D. eriantha*, *C. dactylon* grass species there was a significant negative effect of tree canopy cover on the difference between the expected and observed values (Table 4.4). This indicates that the difference between the expected and observed values was lower at higher tree cover. The difference between expected and observed basal cover for ‘herb’ species and total herbaceous basal cover showed significant positive effect of increased tree canopy cover, indicating a greater difference at high tree cover (Table 4.4).

Table 4.3: T-test results for the difference between the observed and calculated expected values for herbaceous basal cover for grass species, 'herbs' and total basal cover. $N = 12$ for all cases. P-values significant at $p < 0.05$ are highlighted.

	d.f.	t-value	p-value
<i>Themeda triandra</i>	11	-1.15	0.27
<i>Pennisetum sphacelatum</i>	11	-1.93	0.07
<i>Sporobolus africanus</i>	11	-1.91	0.08
<i>Panicum aequinerve</i>	11	2.72	0.02
<i>Panicum maximum</i>	11	-1.03	0.32
<i>Helictotricon turgidulum</i>	11	-1.06	0.31
<i>Eragrostis chloromelas</i>	11	1.39	0.19
<i>Eragrostis plana</i>	11	-5.51	0.0001
<i>Cynodon dactylon</i>	11	-6.09	0.00007
<i>Digitaria eriantha</i>	11	0.39	0.70
'Herb'	11	1.75	0.11
Total grass basal cover	11	-5.25	0.0002

Table 4.4: Linear regression results for the relationship between the observed herbaceous basal cover and tree canopy cover. The difference between the observed basal cover and calculated expected basal cover was also regressed against tree canopy cover. $N = 12$ for all cases. P-values significant at $p < 0.05$ are highlighted.

	r^2	Slope	p-value
<i>Themeda triandra</i>			
Observed	0.59	-0.02	0.003
Difference	0.433	0.148	0.01
<i>Pennisetum sphacelatum</i>			
Observed	0.31	0.04	0.58
Difference	0.109	-0.084	0.29
<i>Sporobolus africanus</i>			
Observed	0.001	0.010	0.91
Difference	0.0001	0.004	0.96
<i>Eragrostis chloromelas</i>			
Observed	0.0030	0.0090	0.85
Difference	0.030	-0.028	0.58
<i>Eragrostis plana</i>			
Observed	0.013	-0.003	0.72
Difference	0.004	-0.002	0.84
<i>Panicum aequinerve</i>			
Observed	0.43	0.10	0.019
Difference	0.404	-0.102	0.026
<i>Panicum maximum</i>			
Observed	0.006	0.003	0.80
Difference	0.042	0.008	0.52
<i>Digitaria eriantha</i>			
Observed	0.43	-0.06	0.01
Difference	0.235	0.038	0.11
<i>Cynodon dactylon</i>			
Observed	0.02	-0.02	0.28
Difference	0.22	0.01	0.04
<i>Helictotricon turgidulum</i>			
Observed	0.10	-0.027	0.12
Difference	0.21	0.03	0.134
'Herb'			
Observed	0.52	0.05	0.007
Difference	0.486	-0.046	0.01
Total grass basal cover			
Observed	0.24	-0.11	0.09
Difference	0.003	-0.010	0.86

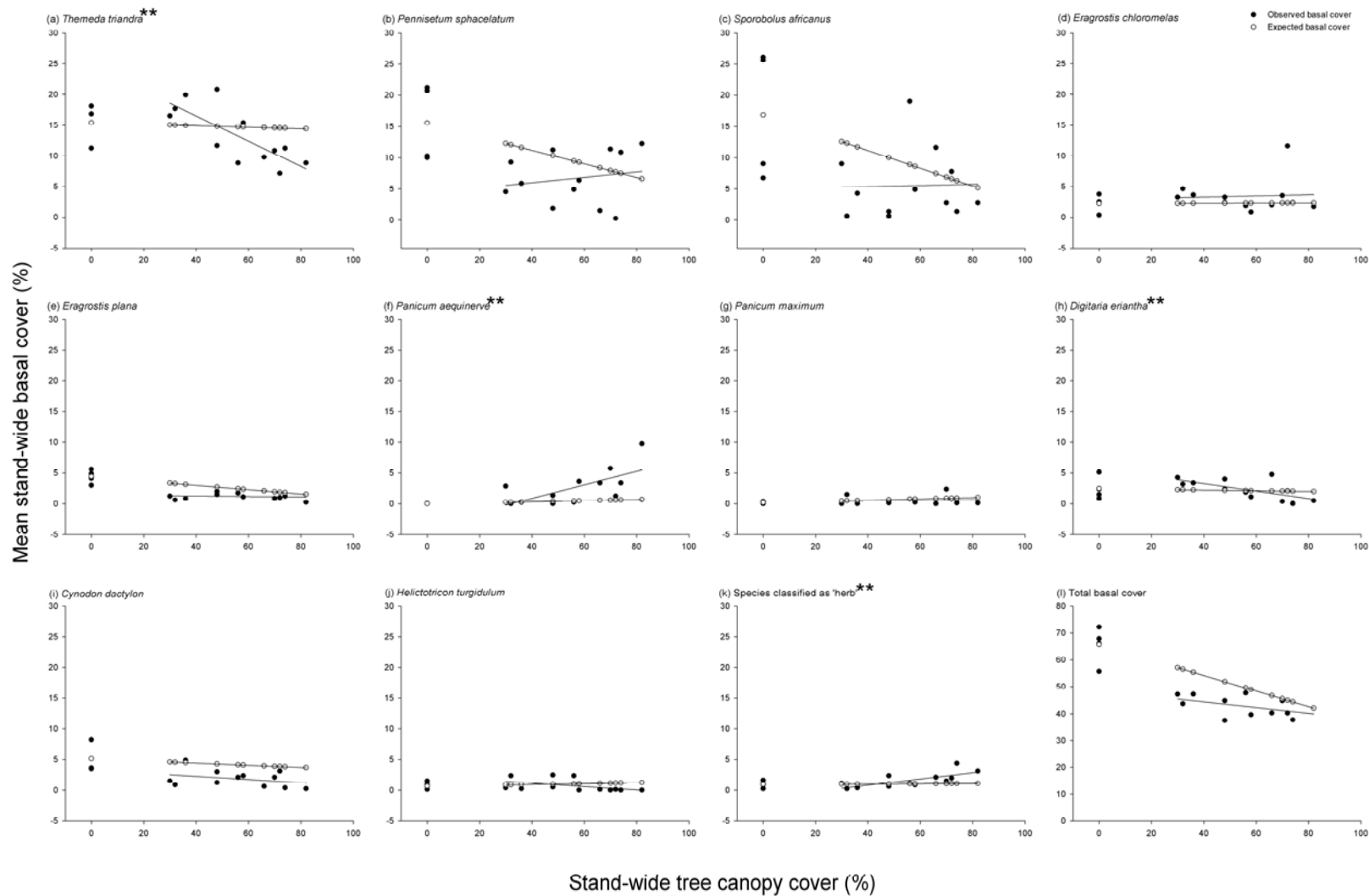


Figure 4.4: The mean (solid symbols) and calculated expected (open symbols) values for herbaceous basal cover plotted against tree canopy cover. The observed and expected basal cover for identified grass species (a-j), 'herb' plant species (k) and total basal cover (l) is shown. $N = 12$ for all models. Regression results for observed values are significant at $p < 0.05$ (*), $p < 0.01$ (**) and $p < 0.001$ (***) .

4.3.5 Effect of encroachment on herbaceous production

Mean total biomass at the end of the growing season was significantly ($F_{(2, 23)} = 3.58$, $p = 0.04$) affected by the level of encroachment. Level of encroachment did not have a significant effect on mean dead biomass ($F_{(2, 23)} = 0.55$, $p = 0.58$) and mean living biomass ($F_{(2, 23)} = 3.21$, $p = 0.07$). Micro-habitat across the three encroached sites had a significant effect on dead biomass, but not total and living biomass (dead biomass: $F_{(2, 23)} = 5.67$, $p = 0.02$; Figure 4.5). The post hoc results showed there was a difference between in biomass in the inter-canopy at the medium level of encroachment and the sub-canopy of the high level of encroachment. There were no significant differences between the sub-canopy and inter-canopy for the individual levels of encroachment. This was due to the large variation around the mean biomass in each micro-habitat at each of the levels of encroachment. The interaction between micro-habitat and level of encroachment was not significant for any of the variables.

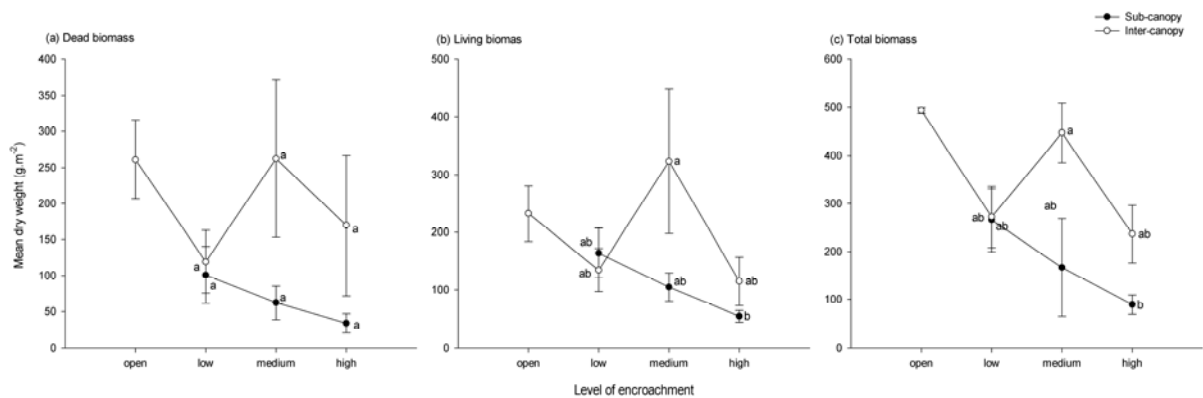


Figure 4.5: The results from the two-way ANOVAs comparing micro-habitats and level of encroachment for Dead (a), Living (b) and Total biomass (c). The letters represent the pairwise differences (Tukey HSD), with different letter indicating significant differences between the micro-habitats. Bars represent standard error. $N = 24$ for all cases as the open site was excluded from analysis but included in the graph.

4.3.6 Effect of plant available light on grass species occurrence and dominance

Grass species occurrence varied considerably with changing in light transmittance, but none of the species were excluded at any of the light intensities. *Themeda triandra*, *P. sphacelatum*, *S. africanus*, *E. plana* and *C. dactylon* exhibited slight increases in the probability of occurrence at higher light transmittance (Figure 4.7 (a, b, c, g, i)). The only grass species that showed major changes in occurrence with increased light transmittance was *P. aequinerve*, which decreased at higher light intensities (Figure 4.7 (d)). The other grass species showed no discernible trends with changes in the light transmittance. The probability of *T. triandra*,

P. sphacelatum and *S. africanus* occurring at any of the given light transmittance categories was high, with the probability of *T. triandra* occurring anywhere on the light spectrum being more than 50%. *Panicum maximum* and *H. turgidulum* were rarely encountered anywhere along the transects (Figure 4.7 (e, h)).

Themeda triandra, *P. sphacelatum*, *S. africanus*, *E. chloromelas* and *P. aequinerve* were the most commonly dominant grass species at the four levels of encroachment. The occurrence of these grass species spanned the range of light intensities (Figure 4.7), but the light intensity range at which they were dominant was less broad (Figure 4.8). *Themeda triandra* had the smallest range at which it was dominant, although this grass was the most common along the four levels of encroachment. It was dominant mostly between 85% and 100% light transmittance. There were some outliers, sampling points where *T. triandra* was dominant at lower light intensities between 40% and 60%. *Pennisetum sphacelatum* and *S. africanus* were found to be dominant in areas where light transmittance was between 65% and 100%, with a couple of outliers, where they were dominant at very low light intensities. This suggests that these three grass species are dominant in the inter-canopy areas, the sub-canopies of small trees or the edges of canopies. *Eragrostis chloromelas* was locally dominant across a very large range of light intensities, ranging from 35% to 100%. This grass was dominant in inter-canopy and sub-canopy micro-habitats. The only grass species that was dominant at low intensities is *P. aequinerve*, which was found to be dominant in the range between 8% and 57% light transmittance, indicating it is dominant in the sub-canopy environments. The range within which *P. aequinerve* was dominant was significantly different to the three other grass species ($H_{(4, 661)} = 96.72$, $p < 0.0001$).

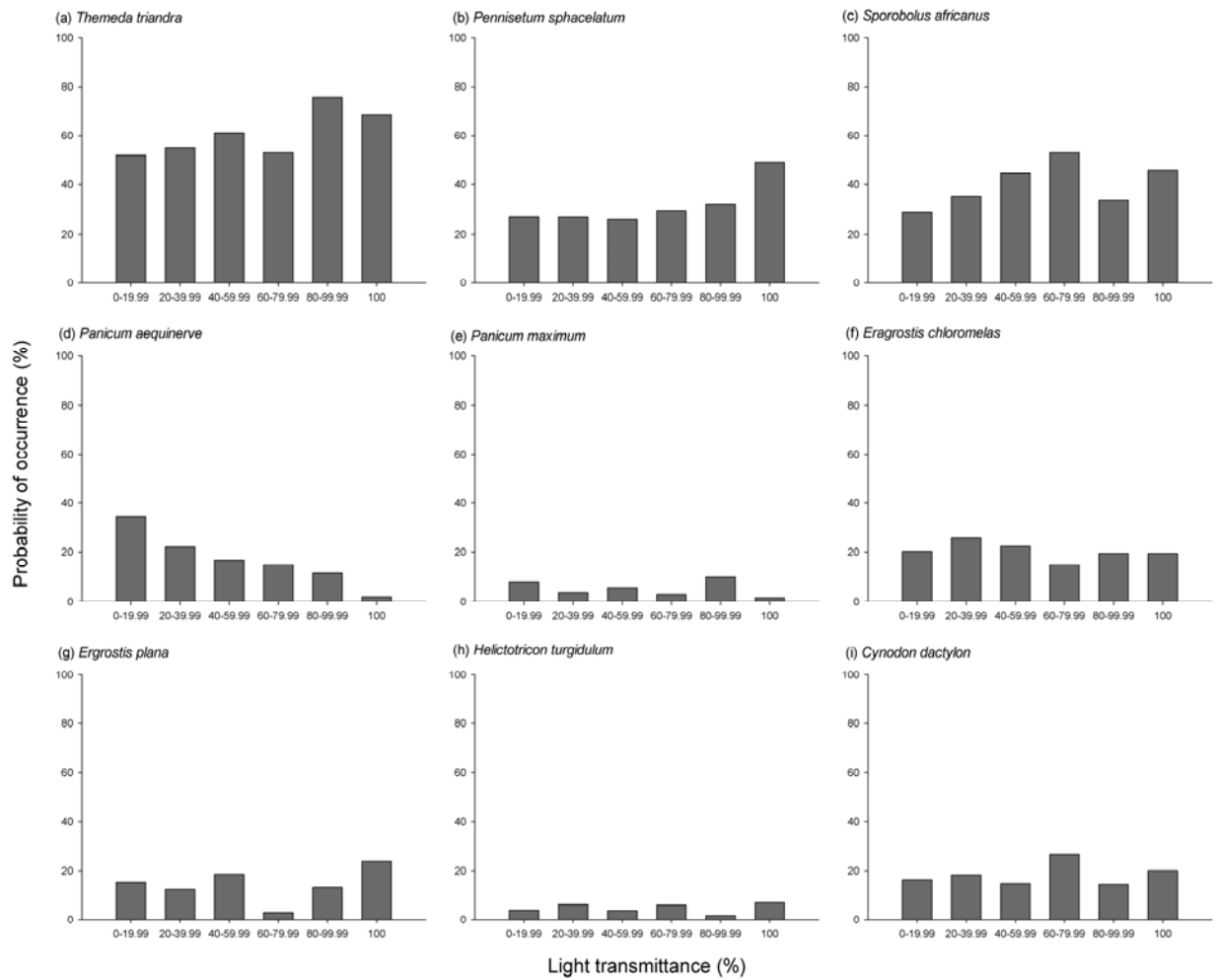


Figure 4.7: The probability of the dominant grass species occurring within a given light transmittance category. The grasses shown here are *Themeda triandra* (a), *Pennisetum sphacelatum* (b), *Sporobolus africanus* (c), *Panicum aequinerve* (d), *P. maximum* (e), *Eragrostis chloromelas* (f), *E. plana* (g), *Helictotrichon turgidulum* (h) and *Cynodon dactylon* (i). Data across all four level of encroachment were combined for each grass species.

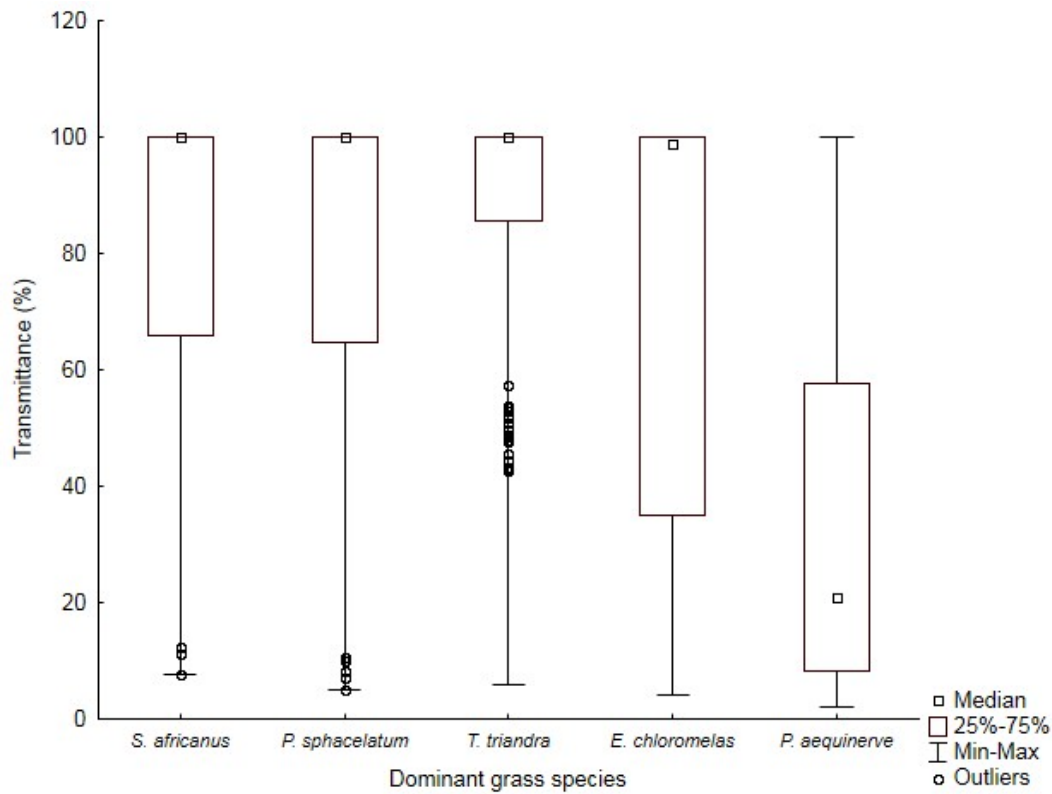


Figure 4.8: Range of light intensities at which the five most dominant grass species identified at the study site occurred.

4.4 Discussion

4.4.1 Herbaceous cover and composition

At the landscape level there was a significant decrease in total herbaceous basal cover moving from the open to high level of encroachment. This was expected as it was predicted that at increased landscape tree cover (or at more encroached sites) basal cover would be reduced. An unexpected finding was that only the open site had significantly higher basal cover and the encroached sites did not differ significantly. When looking at this trend at the stand-wide scale (individual transects), a similar relationship between herbaceous basal cover and tree canopy cover was observed. From this, and the different species composition, I concluded that the open site differs in its edaphic characteristics from the three encroached sites, possibly due to its higher position at the top of a very gentle slope. If this is the case, then the degree of encroachment did not significantly change the overall herbaceous basal cover at the landscape scale, up to the 70% tree canopy cover included here. Bush encroachment has previously been

shown to decrease herbaceous cover and productivity (Smit & Rethman, 1999; Richter *et al.* 2001).

Only one of the grass species, *Panicum aequinerve*, had significantly higher cover in the sub-canopy habitat than the open. The positive local tree effect on this species could be the result of several factors. *Acacia karroo*, like other *Acacia* species, is known to increase the nitrogen content in their sub-canopy environment through nitrogen fixation (Belsky *et al.* 1993). The other explanation could be that as this grass is a C₃ grass, it is more shade tolerant than the other grass species (all C₄, with the exception of *H. turgidulum*) which is why the cover of this grass species has increased with increased tree cover. *P. aequinerve* also showed a positive response to increased tree cover in the sub-canopy and overall observed cover; even though the expected results showed that this species should decrease with tree cover. This demonstrates that the local positive tree effect on *P. aequinerve* scales up to landscape level, and this effect were greater than the sum of the individual tree effects on *P. aequinerve* basal cover. *Themeda triandra* cover was significantly higher in the inter-canopy region. Total basal cover was also significantly higher in the inter-canopy region, and this was mainly due to the high basal cover of the three most common grass species *T. triandra*, *P. sphacelatum* and *S. africanus*. These species were all expected to perform better in the inter-canopy environment as they are all generally shade intolerant C₄ species. Some studies however, have shown that at the local tree scale *T. triandra* does not show any significant differences between the two micro-habitats (Treydte *et al.* 2007; Riginos, 2009). The similar expected values for each percent tree canopy cover agrees with this, as there is not a great difference between *Themeda triandra* cover in the sub-canopy and inter-canopy at the low level of encroachment. The other species showed no difference between the micro-habitats, even though *P. maximum* was predicted to increase under the tree canopy as were the ‘herb’ species as these were mainly C₃ species. *P. maximum* usually exhibits an increase in cover and biomass under trees shown in other studies (Roos & Allsop, 1997; Abule *et al.* 2005). Studies have found that *D. eriantha* showed no significant difference between the canopies, which was also the case at the sites investigated here (Smit & Swart, 1994; Treydte, 2007). It does however show an increase in the inter-canopy with increased tree canopy cover. *Themeda triandra* decreased significantly in the sub-canopy environment as the tree density increased, although it showed no effect of tree density on the cover in the inter-canopy. This suggests that the factors that are influential under the canopy affect *T. triandra* for example the decrease in light transmittance that was observed with increased tree cover. It is possible

that at very high tree canopy cover (<100%), when canopies start overlapping, *T. triandra* might decrease considerably although it will not be excluded. *P. sphacelatum* and *S. africanus* exhibited a negative stand effect in the inter-canopy region as well as total basal cover in the inter-canopy. As the tree cover increases, rooting zones start overlapping, increasing competition for soil resources in the inter-canopy region, and shading also increases in the inter-canopy (Breshears, 2006; Chapter 3). This could explain the decrease of these species in the inter-canopy zone with increased tree cover. Increased tree canopy cover does not seem to have as great an effect on species composition as would be expected. Most species were not excluded in the sub-canopy or at higher tree densities, the basal cover of individual species just changes. As only one grass species seemed to scale up from local to landscape level, it is clear that predicting how these species perform at local tree effect and how they perform at the landscape level is not always as simple as scaling it up. Abiotic factors such as changes in light availability and soil moisture content changes with tree density and the net effect at landscape level will not be the same as local level. These changes can alter species cover and composition at the landscape scale even if there is not necessarily a negative or positive interaction at the tree level. These species can be affected by other factors in the landscape level other than the tree itself as interactions with herbivores as disturbances such as fire may override the tree effect. The rather small overall effect that tree canopies and tree density has on herbaceous basal cover and abundance is probably influenced by the low grazing pressure at the study site (Abule *et al.* 2005; Angassa 2014). These authors also showed that pressure increased on the remaining palatable species and at high tree densities this resulted in the loss of these species (Ludwig *et al.* 2004; Abule *et al.* 2005; Angassa *et al.* 2012). There is no evidence of this occurring at this study site. The high cover of *T. triandra* is one indication of this as this grass species can be eliminated under high grazing pressure especially when combined with bush encroachment (Carter & O'Connor, 1991). At this site a strong selection for *T. triandra* has been found (Gower, unpublished data; Carruthers, unpublished data). Thus higher grazing intensities on this farm would very likely disadvantage this grass species and prove detrimental to its abundance.

4.2.2 Herbaceous productivity

Level of encroachment had a significant effect on herbaceous biomass production, but this was not simply a decrease in biomass with increase tree cover. The medium level of encroachment had the highest biomass and the high level of encroachment lowest. This was unexpected as I predicted that biomass would significantly decrease with increased tree cover

as the trees would start suppressing the productivity of grasses at higher densities. Bush encroachment has been shown to significantly lower the herbaceous production compared to unencroached areas (Angassa, 2005). This effect was probably due to the fact that the chosen bush clumps consisting of different number of trees and tree size which would have influenced the biomass in these areas. Biomass was higher in the inter-canopy than sub-canopy habitats, and biomass in the sub-canopy region decreased significantly with increased tree cover. In bush encroached areas biomass under the canopy is generally lower than the inter-canopy region (Richter *et al.* 2001). One possible reason for biomass being higher in the inter-canopy compared to the sub-canopy is the slight observed increase in soil moisture in those areas (See chapter 3). This has generally been cited as a reason for higher biomass under canopies of individual trees in other studies (Belsky *et al.* 1993; Amundson & Belsky, 1995), but in this case it is the inter-canopy that had slightly higher soil moisture content at the time of sampling. Another possibility could be the distance away from the stem where the samples were collected. The exclosures were placed in the middle of the canopy, meaning not directly next to the base of the tree. Individual *Acacia karroo* trees have been shown to enhance grass productivity immediately within 1 m from the stem but suppress grass between 2 to 4 m away from the stem in the sub-canopy and inter-canopy via canopy and root effects (Stuart-Hill & Tainton, 1989a). This effect could be enhanced in bush clumps, where the individual tree effect on grass productivity is higher as there are more trees competing and suppressing grass. Living biomass was higher in the sub-canopy than inter-canopy regions at the end of the growing season. Thus the herbaceous layer in the sub-canopy may remain greener longer into the start of the winter season. The higher dead biomass was expected as the vegetation was predicted to remain greener under high tree cover than in the open (Mordelet & Menaut, 1995). Thus grass species in the sub-canopy are expected to be productive longer into the growing season. The higher dead biomass in the inter-canopy can provide fuel for fires and promote establishment and growth of fire tolerant C₄ species in the following growing season. Even though fire had not been implemented on this farm, fires are a frequent disturbance in savannas and play a vital role in savanna maintenance. C₄ species are adapted to fire systems; they have higher productivity and die quickly at end of the growing season and dry out but decompose slower than other grass species. Thus they provide fuel that drive fires in these systems and help maintain the tree-grass equilibrium. To support a suitably intense fire in this system, a grass fuel load of 3 ton. ha⁻¹ is required (Trollope, 1980). This will be effective in killing off small *Acacia karroo* tree and branches and stem of adults (Trollope, 1980). At the four levels of encroachment studied here the inter-canopy in the open, medium and high

levels of encroachment would support a fire, but not the low level of encroachment. The sub-canopy environment at all the encroached sites would exclude fire. Thus at these levels of encroachment the grass biomass is sufficient to support fires, but fires may not carry through the sites as they will stop at the sub-canopy regions. Archibald *et al.* 2009 reported that fires spread is stopped at 40% tree cover, this may be due to the sub-canopy region not supporting fire spread as it would be in this case. If fires are excluded at tree cover above 40% (such as medium and high levels of encroachment here), seedling recruitment under tree canopies would increase as they won't be top-killed. Grass productivity did not decrease with increased tree cover up to about 50% and only showed a decrease at the highest level of encroachment. Thus grazing capacity at the low and medium level of encroachment would not be negatively influenced; even at the high level of encroachment as inter-canopy biomass productivity was still high. It seems that the presence of the trees increases the biomass productivity in the inter-canopy but not the sub-canopy environment. This contradicts other studies that have shown that herbaceous biomass was higher in the sub-canopy than inter-canopy environment but decreased with increased tree cover (Stuart-Hill *et al.* 1987). At low *Acacia karroo* densities biomass production was shown to be higher in the sub-canopy environment (Aucamp *et al.* 1983) compared to areas where there were no trees. These findings support the data from this study where the open site had lower productivity than the encroached areas.

4.4.3 Species response to changing light intensity

Light availability is considered one of the most important factors restricting plant productivity under tree canopies (Mordelet & Menuat, 1995). The three most common grass species found at all four levels of encroachment were *T. triandra*, *S. africanus* and *P. sphacelatum*. The probability of encountering all of these grass species was relatively high across the full range of light transmittance, from < 20% to 100%. This was unexpected, as it was hypothesized that these C₄ savanna grasses would become less prominent at the lower light intensities. This contradicts the view that these species would become excluded at low light intensities (<20 % transmittance) (Sage *et al.* 1999). If these cut-off values are considered, it is surprising that these C₄ grass species are still being encountered at these light intensities. They generally had a higher probability of occurring at the high light intensities from 80 % to full light transmittance. The other grass species also showed no distinct trends with increasing light intensities. The only exception was *P. aequinerve* which decreased considerably from the lowest light intensity to higher light intensities. The reason for this is the *P. aequinerve* is a shade adapted plant and does not fare well at high light intensities. This species is probably

also outcompeted by the C₄ grasses at higher light intensities. It has been shown that C₄ plants do poorly at low light intensities below about 15% transmittance. They can grow at intermediate light intensities 25% - 50% (Sage *et al.* 1999; Sage & Kubien, 2003). This does not support these findings as this shows that C₄ grasses can occur at the lower light intensities. Their dominance at the low light intensities however shifts from C₄ grasses to C₃ and shade tolerant grasses. *T. triandra*, *P. sphacelatum*, *S. africanus*, *E. chloromelas* are all shown to be dominant at light intensities higher than 50%. C₄ grasses are generally dominant at light intensities higher than 50% to full light exposure (Weltzin & Coughenour, 1990; Sage & Kubien, 2003). Again *P. aequinerve* is the only grass that shows a clear preference for low light intensities. This supports the hypothesis that a shift in dominance can occur at low light intensities from C₄ dominated at high light to C₃ or shade tolerant species at low light.

4.4.4 Conclusion

At the local tree scale total herbaceous basal cover and productivity was significantly different between the inter-canopy and sub-canopy as expected. Tree density even at the highest level of encroachment had very little effect on the cover and composition of the herbaceous layer. Herbaceous productivity increased with tree cover up to 45% and decreased at the higher tree canopy cover, this could be an indication of the limit of tree cover at which the tree presence positively influences herbaceous productivity. Individual grass species responded differently to tree canopy cover, but none were excluded at high tree canopy cover. Even at high levels of encroachment in the sub-canopy and inter-canopy C₄ species such as *T. triandra* were still prevalent (though much less dominant) which was unexpected. These species occur at light levels as low as 15%, where it has been previously suggested they would be excluded. This raises the question whether this is a unique situation on this farm or a general occurrence in areas encroached by *Acacia karroo*. There is still a lack of predictive understanding of what determines the relative fitness of different grasses under increasing shading (and hence shorter and more fragmented period of full sunlight) with increased tree cover. This could be the combination of low stocking rates and local positive influence of the trees on grass species. The low stocking rates could be the reason why grass productivity of palatable species is still being maintained. This begs for more research on the effect of bush encroachment on the herbaceous layer across a range of stocking rates is needed. This understanding would be vital in management planning, especially when facing the inevitable problem of bush encroachment.

Chapter 5: Summary

5.1. Effect of tree density on abiotic factors and the herbaceous layer at different scales

At the three encroached areas, tree presence at the local scale had a net negative effect on plant available light and soil moisture. Plant available light at the local tree scale also significantly decreased with increased tree canopy cover, though this effect primarily occurred in the inter-canopy regions. Increased tree density thus resulted in a significant reduction in stand-wide scale light availability. Soil moisture was also lower in the sub-canopy environment than the inter-canopy environment, through root competition and interception of smaller rainfall events. The shade adapted C₃ grass, *P. aequinerve*, became more common at higher tree canopy cover and low light environments and was generally the dominant grass in these low light patches. This was also the case for the ‘herbs’ recorded at the site, which were all C₃ plants. *Themeda triandra* basal cover was reduced in the sub-canopy environment and was negatively affected by stand-wide tree cover. Thus a switch in dominance from *T. triandra* and other sun-adapted C₄ grasses to *P. aequinerve* and forbs occurred, but at these levels of *Acacia karroo* canopy cover found at my site study site, I did not observe a wholesale shift from C₄ to C₃ species with bush encroachment at the landscape scale. Such a shift is likely to be highly localised, moving from the inter-canopy to the sub-canopy where the density of trees in patches in the landscape might exclude C₄ species due to low light intensities.

Herbaceous productivity was lower in the sub-canopy compared to the inter-canopy. This can be attributed to lower soil moisture and light under the canopies and the resultant reduction in herbaceous basal cover. The C₄ grass species found in the sub-canopy would experience reduced photosynthetic capacity as they are not adapted to optimally use the low light and sun flecks under tree canopies. Lower soil moisture would also result in lower biomass production under the canopies (Scholes, 1990). The data in this study were limited to the growing season, and more soil moisture data at different times of the year, including late in the wet season and into the dry season, would be useful to get a better idea of the magnitude of this effect. Basal cover and productivity were affected by the level of encroachment at the landscape scale and decreased at the high level of encroachment.

The open site had significantly different results from the encroached areas. Based on the findings at this site, I concluded that there were edaphic differences between this site and the

encroached sites. Thus at the landscape scale it also important to consider how the different patches influence the environment, as net effect at the landscape scale is not necessarily the same as that of the tree patches or inter-canopy area. This was illustrated in this study as the net negative effect of tree canopy cover at the smaller scales (local tree effect and stand-wide effect) was not reflected at the landscape where the effect between the levels of encroachment did not differ significantly. Studies have shown both positive and negative effects of increased tree cover. They have also shown that the local positive effects of trees sometimes scale up positively and sometimes negatively with increased tree cover (Riginos *et al.* 2009; Soliveres & Eldridge, 2013). In the case of the positive effect on herbaceous productivity that is still seen at higher levels of encroachment (up to 50% encroached) two explanation were given: one was that the addition of nitrogen fixers would alter the tree grass relationship, they add nitrogen which at lower tree cover facilitates grass productivity but at higher tree densities they limit P, which then suppresses grass productivity. The second explanation was grazing intensity. At low grazing intensity the positive local effects remain at higher tree densities. With increased grazing intensity the positive effect are subdued (Abule *et al.* 2005) and grasses losing their competitive ability (Jelstch, 1996).

5.2. Prediction about local and landscape effects on abiotic environment and herbaceous layer

The effect of the tree canopy on the plant available light in the sub-canopy and inter-canopy environments did no scale up predictably to the stand-wide scale; this was also the case for soil moisture. Herbaceous basal cover, with the exception of *P. aequinerve*, also did not scale up as predicted from the local scale data alone. The positive local tree effect in the sub-canopy on this grass species scaled up at the landscape level. Based on these findings it was concluded that prediction about how the local tree effect will change with increased tree canopy cover cannot be made. The effect at different percentages of tree canopy cover has to be examined before any conclusion can be drawn.

Based on these finding it can be concluded that prediction about how plant available light will be affected by various tree canopy cover densities can be made, as the LAI will directly influence light availability (Scholes & Archer, 1997). Thus this relationship, although not linear, will be highly correlated. What has to be considered is the tree species in question as different tree species will influence light availability differently (Skarpe, 1992; Vetaas, 1992). Thus predictions made based on one species may not extrapolate to other tree species.

Another factor that has to be considered that these areas are only encroached by *Acacia karroo*, thus areas where several tree species occur, would have different outcomes. Where more than one tree species is involved predictions about how light will be affected become more complicated as each one will have different effects and the density of the different tree species at sites may vary. Unlike plant available light, herbaceous cover did not simply scale up and herbaceous basal cover could not be extrapolated from the local to stand-wide scale based on the cover at a specific tree canopy cover. The reason for this is that it is not tree canopy cover alone that influences the herbaceous layer but also abiotic factors such as light, water and nutrient availability (Scholes, 2003; Sage, 2004; Treydte *et al.* 2007). In order to made prediction about how increased tree canopy cover influence the herbaceous layer a multi-factor model will have to be implemented that take other factors into consideration, thus it becomes very complicated to make accurate predictions.

5.3. Impact on fire, herbivory and tree recruitment in savannas

In the savanna biome, feedbacks such as fire and herbivory play an important role in maintaining the tree-grass balance by suppressing tree recruitment or growth (Bond, 2008). Changes in tree densities and resultant changes in abiotic factors and the herbaceous layer can alter these feedback effects and potentially have serious impacts on the tree-grass balance. The suppression of the herbaceous layer will also affect use by herbivores and carrying capacity. If stocking rates are not reduced as herbaceous productivity declines under high tree cover, pressure on the few remaining grass species increases and less palatable species will become dominant (Abdallah *et al.* 2008). This will result in a further reduction in carrying capacity of the herbaceous layer, which could in the long run have negative impacts on livestock farming and conservation. The reduced vegetation cover under high grazing pressure could also result in increased tree recruitment via reduced root competition and reduced fuel loads that lower the frequency of fire or exclude it completely (Roques *et al.* 2001). Thus the suppression of the grass layer leads to less frequent or less intense fires, which could also result in increased tree recruitment and shifts in herbaceous layer composition. Fire is considered a dominant process for preventing tree recruitment and maintaining the savanna structure (Sanakaran *et al.* 2008) as tree saplings are prone to top-kill by fires (Bond & Midgley, 2012). I found that herbaceous biomass was significantly reduced in the sub-canopy habitats and that herbaceous cover decreased with increased tree cover. In the sub-canopy, standing biomass (even with herbivory excluded) was less than the 3 ton.ha⁻¹ considered necessary for fire spread in an average rainfall year. I also found that the

herbaceous layer in the sub-canopy environment had more living (green) biomass at the end of the growing season compared to the inter-canopy environment. This could potentially result in fires being excluded from the sub-canopy region and at higher tree canopy covers even parts of the inter-canopy. With frost being excluded under most canopies the change of species in the sub-canopy habitat remaining greener longer into the winter is also possible, when the vegetation in the inter-canopy is likely to die back. Suppression of the grass layer (especially under high grazing intensities) can lead to higher tree recruitment (Jeltch et al, 1996). This has a possible knock-on effect of increasing the tree densities in the near future. Increased shading in the case of *Acacia karroo* does not necessarily stop tree recruitment (O'Connor 1995; O'Connor *et al.* 2010).

5.4. Conclusions

I showed that the effects of bush encroachment on the abiotic environment and herbaceous layer change depending on the degree of encroachment. Thus local effects do not necessarily scale up linearly with increased tree cover or sometimes it does depending on which variable is considered. But it was concluded that generally one cannot extrapolate the effect of tree canopies based on single measurement at the local tree scale. The changes in the light microclimate and abiotic environment, as well as increased tree cover, resulted in lower herbaceous cover and productivity in the sub-canopy environment but not the inter-canopy. This does not negatively affect herbivory as the inter-canopy region can still support this, but will have impact on fire spread and seedling recruitment. This study can provide insight into the ecological consequences of *Acacia karroo* encroachment at various stages of encroachment and how this affects specific grass species which should give insight into how the grazing capacity could be influenced. It is important when looking at the impacts of bush encroachment or tree densities that one considers the species in question and the grazing intensity in the area that is being studied.

Southern Africa is predicted to be vulnerable to climate change. CO₂ fertilization has very likely resulted in increased woody cover in savannas, and further increases in atmospheric CO₂ may intensify this effect (van Jaarsveld & Chown, 2001; Wigley *et al.* 2010; Buitenwerf *et al.* 2012). This is due to C₃ trees benefiting from the increased CO₂; they can increase their leaf area at less expense and grow rapidly after disturbances such as fire or herbivory (Higgins & Scheiter, 2012). This tips the balance in favour of C₃ trees instead of C₄ grasses in savannas. Under current climate change models, it is predicted that mean annual rainfall in

semi-arid savannas in South Africa can decrease by between 10 – 15% (DEAT, 2004). With the decrease in mean annual rainfall it is predicted that forage production in South Africa may be reduced by as much as 20% (van Jaarsveld & Chown, 2001), thus carrying capacity is likely to decline due to a loss of perennial grasses (Lohmann *et al.* 2012). With these prediction of climate change for South Africa it becomes clear that a good understanding of how changes in tree cover impacts its environment and subsequently feedback mechanisms becomes critical. This will impact management decision in the agriculture and conservation sectors.

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