Quantifying the impacts of tree densification on the grassy understorey: a trait-based approach

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Abstract

Understanding how trees limit light will advance theories of bush encroachment and tree-grass coexistence in savannas and it will enable us to explore how we can best conserve fire maintained, fire-dependent vegetation systems in South Africa and how our biome boundaries may shift. In order to understand how fire maintains the boundary between closed canopies and open grassy environments, the aim of this research was to test the hypothesis that; tree traits affect light that passes through the canopies of trees to the ground, by influencing the threshold tree density at which grass stops growing under trees. Using the Point-Centered-Quarter method I estimated tree density using a proxy, mean PCQ distance, to reflect changes in inter-tree distance across the gradient of tree density. At the same plots I used dry-weight ranking to record changes in grass cover, species composition and abundance, a balance scale to weigh wet and dry grass biomass, in tandem with densiometer measurements and hemispherical images to obtain canopy cover and the amount of sunlight received by the ground, in addition to the tree density data. To elucidate the interaction between tree traits and sunlight (correlation, boxplots, `ANOVA`, post-hoc test, `MRD`, quartile-regression analyses and linear modelling) as well as response of grass species to light (regression analysis, boxplots, `ANOVA` and `GAMs`), respective passable analyses were employed using `R`. The results show that biomass declines with changes in grass species composition and abundance, that are in turn driven by decline in light transmittance; when horizontal and compound leafed trees, especially on short, umbrella shaped trees with horizontal spheroids prevail. Consequently reducing light loving grass species with characteristics that lead to high fire frequency and intensity; high cover, height and biomass, that prevail when tall trees with vertically angled leaves and spheroids dominate, leading to higher light transmittance. This succinct understanding highlights variation in the tree-grass relationship across savanna ecosystems, suggesting site-specific interventions and recommendations to bush encroachment. Findings reveal value in monitoring tree canopy cover across savanna ecosystems; using it as an early warning proxy for changes in primary production and fire regimes. Conclusions challenge assumptions about the minimum light tolerance of grass, and provide important clues to help disantangle mechanisms by which grasses may persist at low light levels.

Key words: Savanna, South Africa, light transmittance, trees, grass, bush encroachment

Dedication

To my daughters – Olo-thando and Hlal'umi, for allowing me to use time I should have spent with them, to pursue this degree. To my family – my parents; Mr and Mrs Lungana and Nokwakha Nondlazi, my brothers, Linda and Mkhuseli as well as my sisters, Siyasanga and Wandisiwe for their support, and many people who allowed me to "sleep on their couches". This one is for all of you.

Declaration

By my signature, I declare that this dissertation is my original, unaided work, including artworks and text herein, except in form of advice from my two supervisors; therefore all intellectual property rights are reserved. This work, was done during the course of my MSc candidature at the University of the Witwatersrand and has never, nor any of its parts, been submitted to any institution for any qualification. It has been prepared in accordance with the requirements and guidelines of the Faculty of Science of University of the Witwatersrand. This dissertation does not exceed 100 pages (including all pages but front matter).

Signed in .....at.....

On date .....

Signiture.....

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Acronyms and definitions

C_4 ..... a 4-carbon molecule.

C_3 ..... a 3-carbon molecule.

C ..... Carbon = an abundant nonmetallic tetravalent element occurring in three allotropic forms: amorphous carbon, graphite, and diamond; occurs in all organic compounds.

CO_2 ..... a Carbon dioxide = a heavy odourless colourless gas formed during respiration and by the decomposition of organic substances – absorbed from the air by plants in photosynthesis.

et al. .... *et aliae* = and others ("*et al.*" is a general abbreviation of '*et alii*' (masculine plural) or '*et aliae*' (feminine plural) or '*et alia*' (neuter plural), when referring to a number of people).

e.g. ..... = as an example or for instance.

etc. ..... *etcetera* = additional unspecified odds and ends; more of the same or and so on.

E ..... East = the cardinal direct 90˚to the right of planet earth's north pole (when facing towards earth)[1]

GPS ..... Global Positioning System = navigational system involving satellites and computers that can determine the latitude and longitude of a receiver on Earth by computing the time difference for signals from different satellites to reach the receiver.

LAI ..... Leaf Area Index = one sided leaf area per unit area of ground surface.

Light Transmittance ..... Actually in this dissertation this refers to constrained light transmittance – the result of total light from the sun minus light obstructed by clouds and minus light obstructed by vegetation.

m ..... meters = denotation for standard international (SI) unit of a metric for measuering linear distance that is too long for centimeter units but too short for kilometer units.

Missingness ..... a statistical term used in this dissertation, to refer to observations that were not included in the analysis due to incoplete pairs in covaraites where interpolation was not applicable.

N ..... Nitrogen = a common nonmetallic element that is normally a colourless, odourless, tasteless, inert diatomic gas; constitutes 78 percent of the atmosphere by volume; a constituent of all living tissues.

[1] All directions hereafter are expressed from the perspective of facing towards earth.

n ..... = statistical representation of the value for sample size, similar to population size *N*.

N ..... North = the cardinal direction in the direction of planet earth's true north pole, relative to the magnetic north.

NE ..... North-East = the inter-cardinal direction exactly halfway between Northerly and Easterly main cardinal directions.

NW ..... North-West = the inter-cardinal direction exactly halfway between Northerly and Westerly main cardinal directions.

PAR ..... Photosynthetically Active Radiation = radiation in the 400 to 700 nanometer waveband. It represents the portion of the solar spectrum which plants use for photosynthesis.

PCQ ..... Point Centered Quarter = a method employed in vegetation ecology for estimating the average distance between trees at a stand or plot.

SOM ..... Soil Organic Matter = the amount of decomposed former live material in the soil.

S ..... South = the cardinal direct to the direction of planet earth's south pole.

SE ..... South-East = the inter-cardinal direction exactly halfway between Southerly and Easterly main cardinal directions.

SW ..... South-West = the inter-cardinal direction exactly halfway between Southerly and Westerly main cardinal directions.

Tree density.....Meaning the number of individual trees within a unit area of ground surface.

^{TM} ..... Registered trade mark.

W ..... West = the cardinal direct 90°to the left of planet earth's north pole (when facing towards earth).

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Chapter 1

Introduction

1.1 Rationale of the research

This exposition describes research conducted to understand how encroaching trees become protected against the popular tool used to manage bush encroachment in Southern Africa: fire. The project was designed to test whether the local-scale savanna dynamics are driven by the quantity and quality of sunlight that penetrates to the understorey of trees. The rate of bush encroachment depends on fire presence (frequency and intensity), which in turn depends on the amount of grass growth. In savanna, grass growth is in turn determined by the amount of light that trees intercept, given adequate moisture reaches the ground.

I hypothesized that if trees limit more light, they indirectly limit fire because less light limits grass, which is the ignition fuel for fire. It follows that, if differences in tree species transmittance[1] exist, it could be due to their leaf and whole tree architectural characteristics. This differencing in light transmittance across tree species would mean tree species inherently differ in their ability to exclude grass, encroach on grasslands and exclude fire. This differencing is an important question because it relates to bush encroachment, a current global socioeconomic challenge with trajectory of its projection suggesting that it will intensify in the future.

Understanding how trees limit fire will be a new and meaningful advancement of bush encroachment and tree-grass coexistence theories in savannas because it will enable us to explore how we can best intervene and conserve fire maintained, fire-dependent vegetation systems in South Africa, and potentially elsewhere.

[1] Light transmittance as used here refers to the amount of light that penetrates a tree's canopy and gets transmited to the ground below. In this dissertation light transmittance and light penetration are used interchangeably, as used here.

1.2 Background

1.2.1 Coexistence of woody and grassy ecosystems

A savanna is a vegetation structure that is characterised by codominance of trees and grass (Higgins *et al.* 2000), with a continuous grass layer which covers the ground surface and a discontinuous layer of trees and shrubs above it (Ludwig *et al.* 2004). Bond (2008) describes grass composition of grassy ecosystems as spatially heterogeneous [2]. Furthermore, Mutanga *et al.* (2004) consider understanding spatial variations of grass across scales as an important step towards understanding future distributions of grassy ecosystems, as well as identifying crucial areas for conservation and intervention. Although the relative proportion of trees and grass in savannas is indeed very variable; in general, maximum tree cover increases with increasing rainfall (Sankaran *et al.* 2005), but various factors (fire, grazing, wood harvesting) can act to reduce tree cover below the climate predicted maximum (Bond & Keeley 2005).

While, response of grass biomass to tree cover has been shown to be convex — at low tree cover, trees have very little impact on grass biomass, but as cover increases, a threshold is crossed where grass biomass declines rapidly (Scholes & Archer 1997; Scholes 2003). This convex relationship is a crucial fact because grass is the main fuel for fire in savannas and fire is an important factor controlling tree recruitment (Higgins *et al.* 2000; Hoffmann *et al.* 2003). Therefore, increase in tree cover, that reduces light transmittance, can feedback to tree recruitment, because it would reduce grass biomass, which would in turn reduce fire frequency and intensity, which would eventually support tree recruitment. Feedbacks to tree recruitment, from the relationship between grasses and fire have been suggested to be one of the main factors controlling tree-grass dynamics at landscape scale — and at larger scales, the distribution of forest and savanna biome states (Staver *et al.* 2011a).

In C4 plants, photosynthesis is more efficient at low intercellular CO_2 concentrations (Hatch & Slack 1968) and higher temperatures (Mantlana *et al.* 2008) hence they are highly efficient in assimilating carbon (C) while exposed to full sunlight (Piedade *et al.* 1991). Therefore, as the climate changes, CO_2 concentrations and temperature change globally — to a CO_2 rich and warmer, wetter climate; causing tree cover to increase and reduce the exposure of grass to sunlight, the distribution of grass species will likely shift due to differences in ecophysiological requirements *e.g.* photosynthetic pathways (Ehleringer *et al.* 1997; Bond & Midgley 2000).These changes may include small-scale shifts in grass species composition along the light gradient from outside tree canopies to the shade under individual trees; that is not yet well understood. Yet understanding these

[2] Differing in space or changes with change in sites or positioning

small-scale shifts is critical knowledge for understanding equilibrium of tree-grass coexistence over larger scales in savanna, thus the distribution of savanna, grassland and forest biomes.

Current understanding on tree-grass coexistence offers three alternative theories that explain persistence of tree–grass assemblages: (1) niche differentiation hypotheses (Tilman 1987; Higgins *et al.* 2000; Sankaran *et al.* 2004; Caylor & Shugart 2006; Wiegand *et al.* 2006; Scheiter & Higgins 2007; Bond 2008; Stokes & Archer 2010), (2) the demographic bottleneck hypotheses (Higgins *et al.* 2000; Higgins *et al.* 2007; Bond 2008; Hoffmann *et al.* 2012c; Hoffmann *et al.* 2012c) and (3) neutral theory (Hubbell 2001; Hubbell 2006). These theories differ in how they explain effects of lifeform competition and response of grasses to increase in tree cover through the life history stages of trees (Sankaran *et al.* 2004), and thus highlight the need for a unifying theory.

Past studies on tree-grass coexistence have focused on different stages of tree growth and tree densities (Scholes & Archer 1997). However, they considered bigger scales without necessarily quantifying tree density and tree age at small scales such as plot level (Eldridge *et al.* 2011). They also considered different limiting factors of tree establishment like fire, grazing and rainfall (Bond 2008; Archibald *et al.* 2009; Vadigi & Ward 2013; Staver *et al.* 2011b). They, however, ignore many other potential interactions such as sunlight and tree leaf traits (Supérieure *et al.* 1995; Wiegand *et al.* 2006; Meyer *et al.* 2007a; Meyer *et al.* 2007b). In this study, I quantify understorey light environments created by trees with different architectures and leaf traits in order to understand its effect on, and relationship with understorey grass.

1.2.2 Fire: a woody plant control yet a support for grassland structure and richness

Fire frequency in savannas is largely controlled by grass productivity. In regions of high rainfall where grass regrows quickly, fires can occur annually (Higgins *et al.* 2000; Roques *et al.* 2001; Archibald 2010). This rapid grass growth represents an important control on the growth and recruitment of woody species in these savannas. Frequent fires can prevent recruitment of juvenile woody savanna individuals (Higgins *et al.* 2000; Bond *et al.* 2008) by repeatedly burning these saplings when they resprout. These fires have also been shown to prevent invasion of grassy ecosystems by neighbouring forest species (Hoffmann *et al.* 2003; Hoffmann *et al.* 2012a). However, if fire is excluded, woody species mature quickly resulting in closed canopies, causing a switch to forest tree species. This process of switch to forest tree species has been documented in fire-exclusion experiments (Swaine *et al.*

1992; Titshall *et al.* 2000; Bond & Keeley 2005; Shackleton 2012); modelling experiments (Higgins *et al.* 2000; Scheiter & Higgins 2007), and regional analyses (Sankaran *et al.* 2005; Staver *et al.* 2011a). Although recently cited literature shows a good mechanistic understanding of the processes by which grassy systems prevent canopy closure, there is less information available on exactly how closed-canopy ecosystems prevent herbaceous growth and therefore fire when a lanscape is already encroached.

For example, regional scale analyses of the distribution of fire in Africa have identified a threshold tree canopy cover of 40% above which fire cannot spread, and above which woody cover will rapidly increase to its climatic limit (Archibald *et al.* 2009; Staver *et al.* 2011a; Staver *et al.* 2011b). It is likely that this threshold is related to the decline in grass biomass under woody canopies, but these processes have not been well investigated in the field. Hennenberg *et al.* (2006) showed that the point at which fire stops on a forest-savanna boundary is correlated with a decline in grass biomass. Also, Hoffmann *et al.* (2012a) showed that fuel moisture content increases under closed canopies, potentially slowing fire spread. Therefore, the fuel load and moisture content of surface fuels are likely to be the two main controls of fire spread under woody plant canopies.

Trees intercept light before it reaches the grass layer. This interception has two effects: *1)* it reduces the light available for photosynthesis, allowing only shade-tolerant grass species to grow under tree canopies, and *2)* it reduces the amount of evapotranspiration below the canopy, resulting in more moist grass fuels. For both of these reasons light plays a primary role in determining the exact threshold where fire drops off. Understanding light transmittance would be very useful in understanding and managing tree-grass dynamics. Hence investigating these thresholds is the focus of this work.

1.2.3 Tree architecture and light transmittance

The degree to which the over-storey intercepts light depends on a range of tree architectural and leaf traits in addition to stem density: the height and branching level of the trees, the angle and type of leaves and the density of leaves (Lieffers *et al.* 1999; Montgomery & Chazdon 2001; Archibald & Bond 2003). For example, a tall tree would cast less shade than a short tree with the same canopy diameter, and a tree with leaves that hang vertically downwards, would cast less shade than a tree that holds its leaves horizontally (Hikosaka & Hirose 1997; Valiente-Banuet *et al.* 2010; Mc Millen & Mc Clendon 2011). *Terminalia sericea* can grow at relatively high densities but still carries a grassy understorey — *T. sericea* leaves have a near vertical angle, and its leaf area index (LAI) is low. Thus, even quite dense canopies still allow sufficient light penetration for

grass to grow. In contrast, *Spirostachys africana* has a much higher LAI, and holds its leaves at all leaf angles, effectively cutting out much of the light before it reaches the understorey (Zhao *et al.* 2003).

Due to differences in leaf angle, leaf structure, and tree architecture the same density of trees could result in different light transmittance (Lieffers *et al.* 1999; Montgomery & Chazdon 2001; Lhotka & Loewenstein 2006). For this reason, the point at which grass biomass drops off under increasing tree densities would depend very strongly on the type of tree. A short, dense, highly encroaching species might prevent grass growth at much lower densities than a tall species with a small crown cover. Villegas *et al.* (2010) demonstrated the importance of these traits where they show large differences in evapotranspiration rates for the same tree density across different tree species, but the feedbacks to grassy fuels and fire remain to be demonstrated. Hence this work intended to investigate the importance of these traits.

1.3 Research problem: bush encroachment

1.3.1 Why is bush encroachment a problem?

Forests and thickets differ from the grassland biome (Huxman *et al.* 2005) in the impacts they each have on the biogeochemical cycles, the suites of fauna and flora they each support, and the ecosystem services they provide. Trees are not a problem necessarily, they are very important as carbon sinks, and for human use as wood fuel as well as food for browsers, which includes most game or wildlife (almost all antelopes). A major problem is that an increase in the number of woody plants reduces the carrying capacity of livestock farms (Wiegand *et al.* 2006), resulting in loss of income for farmers (Hudak & Wessman 1998). The underlying problem is that ecosystems with woody plants are very different from grassy ecosystems.

Bush encroachment suppresses grass productivity and alters soil moisture (Pressland 1973), nutrient and microclimate conditions (Belsky 1992), as well as grass diversity, favouring shade tolerant grass (Stuart-Hill & Tainton 1989; Cingolani *et al.* 2005). Bush fragments the grassland habitats and causes a decline in rodents, small mammals, carnivores and birds (Seymour 2006; Thiele *et al.* 2008) leading to loss of biological diversity (Milton & Dean 1995; Herremans 1998; Meik *et al.* 2002; Blaum & Wichmann 2007; Blaum *et al.* 2007).

Given the global area covered by savanna, 20% of earth and 40% of Africa (Tews *et al.*

2006), an increase in savanna tree density that influences atmospheric C [3], may shift relationships of global C pools, sources, and sinks. Shift in C flux could have significant implications on biogeochemistry, both regionally and globally (Hudak & Wessman 1998; Bond & Midgley 2001; Bond & Midgley 2000; Bond & Keeley 2005; Bond 2008; Bond *et al.* 2008; Eldridge *et al.* 2011; Poulter *et al.* 2011; Bond & Midgley 2012). Soil C sequestration declines with increasing tree density and decline in grass production in semiarid rangelands (Hudak & Wessman 1998; Houghton *et al.* 2001; Roques *et al.* (2001). At global scales changes in C flux could influence the global C cycle feedback used to predict 'global warming' and can alter the amount of C sequestered, potentially leading to negative biogeochemical processes and consequences for tree-grass interactions (Archer *et al.* 2001; Pacala *et al.* 2001; Jackson *et al.* 2002).

Rates of decomposition of plant material and plant production are crucial because they are also linked to soil C and nitrogen levels (Ojima *et al.* 1993). Therefore, increase in woody plants in savannas may alter long-term C and N pools (Hudak *et al.* 2003). Given these conspicuous changes in savanna vegetation structure and functioning as well as litter inputs, the implications could be far-reaching and permanent. Tree cover increases with rainfall over continental scales resulting in a plant litter decomposition gradient associated with a moisture gradient (Sankaran *et al.* 2005). Litter becomes wetter, decomposing faster as environmental conditions become wetter and warmer (Ojima *et al.* 1993). The distribution of soil organic matter (SOM) globally suggests moisture and temperature as major environmental constraints balancing primary production and decomposition (Ojima *et al.* 1993; Hudak *et al.* 2003). Therefore, an increase in tree cover may alter soil nutrient conditions and shift grass species composition(Cramer *et al.* 2012; Vadigi & Ward 2013). However, at local scales, like under individual tree canopies; where moisture as an environmental influence maybe less limiting than on areas outside tree canopies, light transmittance becomes a major environmental constraint. Changes in light transmittance, evaporation of soil moisture and the nutrient status of soil are explanations for small-scale changes in grass species composition, hence the focus on light transmittance in the current study.

1.3.2 The extent of bush encroachment

Bush encroachment is wide spread and has devastating outcomes to many life forms. In South Africa, it has been estimated that 13 million hectares, including savanna, have been

[3]Increase in tree cover can change albedo, which can result in a rise in average surface temperature on the planet, but can also affect microclimate by affecting evapotranspiration rates and thus rainfall patterns and more importantly increase in tree cover can alter the input of carbon into the atmosphere through changing patterns of biomass burning.

subject to bush encroachment (Trollope *et al.* 1989). O'Connor and Crow (1999) reported the rate and patterns of bush encroachment in the grasslands and savannas of the Kei Road, Komga region of the Eastern Cape, South Africa (see figure 1.1, Section 1.6.2 Study sites, Table 1.1). In 1994 the Madikwe Development Task Team noted that bush encroachment had depleted the grazing potential of Madikwe Game Reserve a portion of the North West Province of South Africa, over the past several decades (Hudak & Wessman 1998).

As early as 1857, Andersson noted bush encroachment in Namibia (Andersson 1857). Since then abundance of bush in African savanna has been widely documented (van Vegten 1983), including recent reports from Roques *et al.* (2001) of severe encroachment by thorny shrubs, especially *Dichrostachys cinerea* (L.) Wright & Arn. in the Lowveld savanna of South Africa and the savanna of Swaziland. Parr *et al.* (2014) have detailed the spread of this increase in tree cover across Tropical Grassy Biomes (TGBs) globally.

1.3.3 Bush encroachment: a socioeconomic problem

In South Africa bush encroachment is potentially a serious socioeconomic problem because it has potential to threaten the profitability of grass-based farming practises, which in turn threaten human wellbeing. South Africa faces serious food security challenges (Koch 2011). Livestock production is fundamental to food security in South Africa because only a small proportion (13%) of the total land area is arable, and only a small (22%) portion of the 13% has high potential. Although the World Bank reviewed the arable portion down to 9.92% in 2011 by excluding abandoned or old lands and back up to 10.3% in 2013, as a result of shifting cultivation (data.worldbank.org, 2016), the remainder (89%) is rangelands that support both wild and domestic livestock production (South African Department of Agriculture 2007). Since wildlife conservation occupies approximately 7% of the national land area, approximately 82% of the land remains for livestock production, but is not necessarily suitable for livestock production (South African Department of Agriculture 2007).

These rangelands occur within considerably homogenous vegetation assemblages called biomes. Biomes are Savanna, Thicket, Grassland, Forest, Fynbos, Nama Karoo, Succulent Karoo. Grasslands and Savannas are the main areas where livestock production takes place. Their carrying capacity is of great significance because savanna is home to a large and rapidly growing proportion of the world's human population — including many pastoralists (Lamprey 1983; Scholes & Archer 1997). Savanna also provides a range of important ecosystem services, *e.g.* tourism (Higgins *et al.* 2007). Savanna accounts for

approximately 13% of global net primary production (Grace *et al.* 1998), affects approximately 20% of the world's population (Turner *et al.* 1989) and contributes between 40 and 50% of Africa's surface area to form the most extensive vegetation type in Africa (Scholes & Walker 1993).

Simply put, if savanna is such a fundamental vegetation structure of Africa's landscapes, then bush encroachment will have devastating consequences for those whose livelihoods depend on ecosystem services produced by savanna ecosystems. Savannas in good condition provide: grazing for livestock and wild animals; water; including wood fuel and all goods and services extracted from savanna species as well as 'big-five' game viewing experiences. When savannas become encroached, the quality of these services declines with negative consequences for people and entire enterprises. These negative consequences are exacerbated by slow adaption to imminent changes inherent in social-ecological systems.

1.3.4 Bush encroachment: a scientific problem

Bush encroachment links to the question on biome distribution. The question of what determines the distribution and abundance of woody plants in woody biomes like savanna and forest is of global interest (Roques *et al.* 2001). Accordingly, ecologists have long been preoccupied with understanding the factors that govern the distributions of biomes, particularly focusing on how fire limits tree recruitment or how trees adapt to fire presence. Focusing on this scientific problem is a formidable challenge, especially because savannas have multiple interacting factors, like climate, hydrology, herbivory, fire and soil characteristics that influence its distribution (Tinley 1982; Furley *et al.* 1992; Ruggiero *et al.* 2002; Bond 2008). However the bulk of literature on bush encroachment, does not consider the other side of the fire feedback, of how trees limit fire. In this dissertation, I propose that the amount of light that trees transmit is also the primary and arguably most primary determinant of bush encroachment, because:

– Differences in how trees hold their leaves in the canopy, the shape of the canopy or how far the canopy is from the ground (architecture), and how the leaf material is arranged (leaf type), all influence the area of the ground under the trees that receives light and radiation, which are factors for moisture and nutrient balance with potential to affect understorey plant composition.

– Differences in optimal light levels, due to differences in leaf traits of different understorey species, influences grass species survival at different regions along the light gradient.

Therefore, I suggest that light transmittance (*as determined by tree traits, canopy cover,*

and stem density) should also be considered as one of the primary determinants of bush encroachment. Just as other determinants can have dynamic interactions such as the rainfall-fire interaction mechanism that has been invoked to explain some of the dynamics at the prairie–forest ecotone in the northern United States (Grimm 1983; Jeltsch *et al.* 2000), such is light transmittance. Zhang *et al.* (2001) provides an analysis of the influence of vegetation cover on evapotranspiration based on data from over 250 locations globally; to highlight, but one way, radiation thus light transmittance can affect key plant physiological processes.

Defoliation pressure, interacting with high drought frequency, suppresses fire frequency and encourages high tree cover, which is well investigated in the Eastern Cape (Hudak & Wessman 1998). Most drivers of savanna vegetation change are correlated (Archer *et al.* 2001; Roques *et al.* 2001).

1.4 Aim of the study

The aim of this research was to investigate how tree traits influence the threshold tree density at which grass stops growing under trees, in order to understand how the boundary between closed canopies and open grassy environments is maintained by fire.

1.5 Objectives of the study

1. To assess how the amount of light that is transmitted to the understorey of trees changes along a gradient of increasing tree cover. More specifically:
    - To determine the relationship between light transmittance and *(i)* tree density and *(ii)* tree canopy cover.
    - To determine whether the relationship between tree density and light transmittance differs across different tree species (Table 1.2).
    - To investigate whether tree characteristics affect the amount of light transmittance by different tree species (Table 1.2).
2. To assess how grass biomass changes along gradients of increasing tree density and canopy cover and whether the 20% threshold for C4 grass growth is apparent in the field. More specifically:
    - To test if grass becomes limited at 20% light transmittance.
    - To asses response of grass species abundance in response to light availability.

- To investigate whether grass characteristics can explain changes in grass biomass and composition along a gradient of increasing light transmittance.

1.6 Study sites, species and sampling design

This section decribes the overview of the sampling design at the study sites. Since in my project, I needed to link my tree density measurements to light interception and grass biomass data at each plot, at each site (Table 1.1). I desribe how I designed a protocol that combined all the methods, including those for collecting data on tree density, canopy cover, light transmittance, grass biomass and tree species (Table 1.2) composition across all sites (Table 1.1). Detailed methods for collecting tree density, canopy cover and light transmittance are described in Chapter 2, while methods for collecting data on grass variables are detailed in Chapter 3.

1.6.1 Study sites

Response of grass biomass to increasing tree densities was studied at nine sites in South Africa (Table 1.1). Sites were selected to represent different over-storey tree species — ranging in height, leaf architecture (Table 1.2), as well as their perceived potential to encroach. I also chose one site, which had over-storey of *Eucalyptus grandis* to include a common introduced Australian species which has low potential to encroach in South Africa. A pilot study was conducted at Kwalata Nature Reserve to test the methods (shown in map Figure 1.1 — located north of Pretoria in Gauteng). Before use in the main study, necessary adjustments were made and a trial was run at Pullen Farm prior to the start of sampling. The sites were situated (Figure 1.1) at the Eastern Cape [Fort Beaufort and Kei Road], in KwaZulu-Natal [Giant's Castle], in Gauteng [Midrand at Allandale], in Mpumalanga [Pullen Nature Reserve, University of the Witwatersrand], in Kruger National Park [Limpopo and Mpumalanga] (Figure 1.2). Areas of forest-grassland mosaics in KwaZulu-Natal and the Kruger National Park were also sampled (Figure 1.2 MS 5 & MS 3). I selected sites that represented a gradient of tree densities — from open to totally closed canopies. This selection criterion was possible at most sites, but was difficult at some sites that represented true forest-savanna boundaries [Eastern Cape] and areas of forest-grassland mosaics [KwaZulu-Natal] (Figure 1.2).

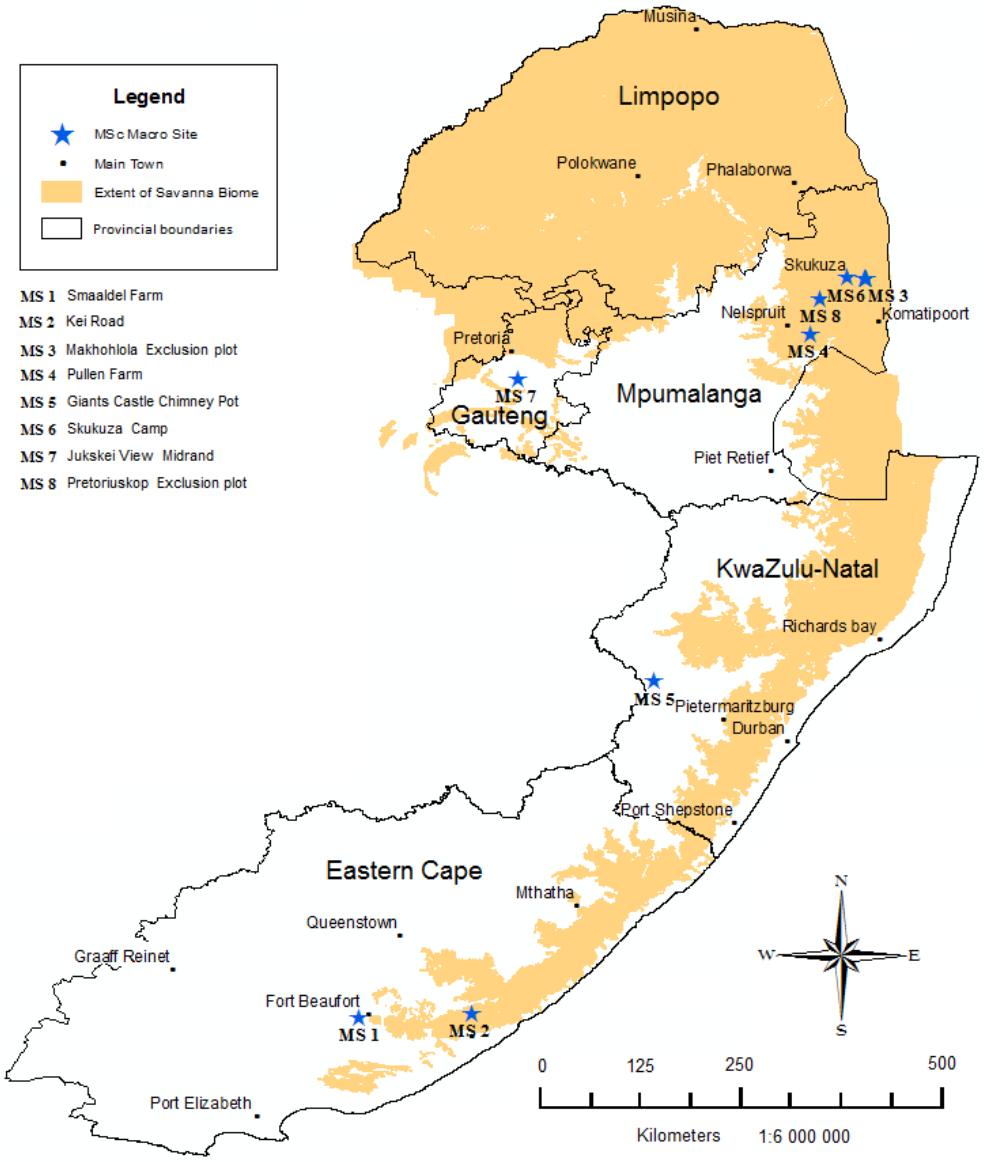
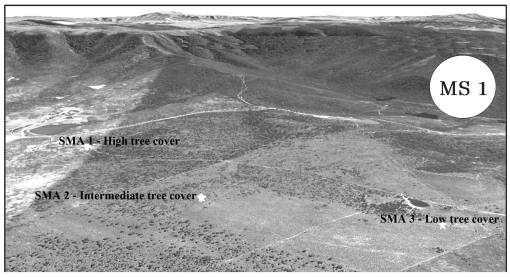


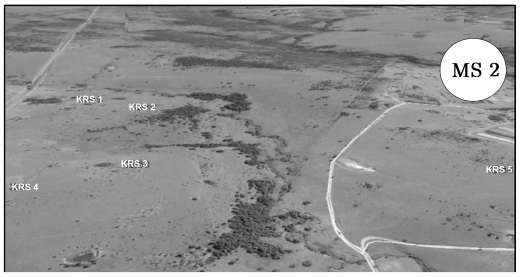
Figure 1.1: Study sites (stars) mapped with provincial boundaries and relative to major cities and towns (undifferentiated; all black dots). The distribution of the sites spans the savanna region of South Africa, which covers the eastern mesic region of the republic (shaded area, excluding the Norht West Province). Site codes MS1 – MS8 correspond with Table 1.1, for cross-referencing purposes [Nondlazi 2015].

During planning, with the assistance of the local land-managers, the general localities of the potential sites were selected on a Google Earth™ aerial image or a map. The approach of using aerial images allows ease of targeting or avoiding features or anomalies on sampled landscape (*e.g.* dykes and riparian zones, as well as ease of identifying targeted levels of tree cover and for locating tree species. Farms and nature reserves were selected for sampling. Within the perimeter of the target farms and nature reserves, monospecific stands of the targeted tree species (Table 1.2) were identified and their GPS locations were

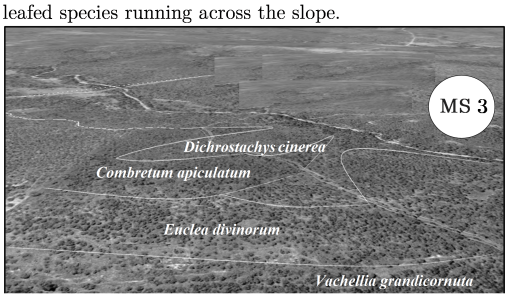
generated. As far as possible, only unburnt, ungrazed sites during the years of data collection (2013/2014), were targeted, otherwise, the intensity of defoliation was recorded. The peak growing season grass biomass measurements that I took represented actual productivity under those conditions.



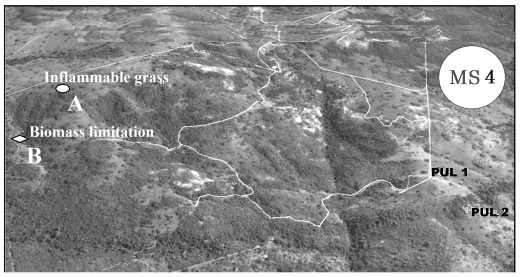
MS 1 (Macro Site 1): The Fort Beaufort macro site, at Smaaldel, eKrumi, with three of the four micro sites labelled SMA 1 to SMA 3. SMA 4 is located roughly between SMA 1 and 2. These micro sites were surveyed to sample the gradient of roughly 20%, 40%, 60%, and 80% tree cover, SMA 1 to 4 respectively. Almost all the trees in the image are ***Vachellia karoo,*** which dominates this savanna that adjoins Andrew's Forest, forming a savanna-forest boundary that starts at the foot of the mountain slope, with pockets of mixed broad-leafed species running across the slope.



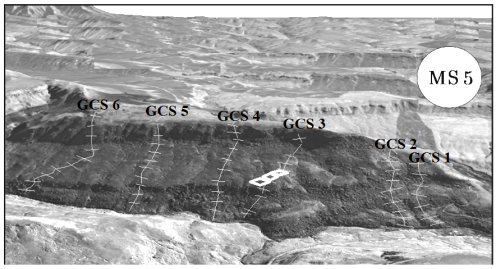
MS 2 (Macro Site 2): At the Kei Road macro site, five micro sites were sampled and labelled KRS 1 to KRS 5. These micro sites also sampled an increasing gradient of tree cover. At these sites, the aim was to sample transects from closed to open tree cover but targeting the low (>0% to 20%) and the higher (>80%) ends of tree canopy cover. KRS 4 was sampled on an area that is completely open with zero tree cover in order to sample plots at the low end of the range of tree cover. This site also sampled the ***Vachellia karoo*** species.



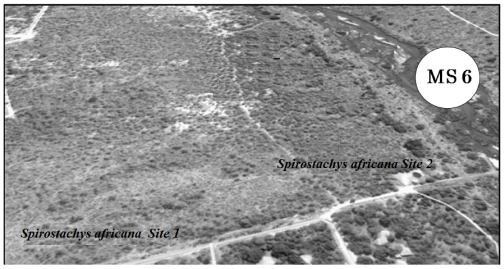
MS 3 (Macro Site 3): Four of the tree species that were targeted in the research were sampled from the Makhohlola Exclusion Plots (MEP). MEP is a series of three plots, conventionally known as the Sabi Exclusion plots (full exclusion = FE, partial exclusion = PE, and control the plot). The tree species sampled at this site were ***Vachallia grandicornuta, Euclea divinorum, Combretum apiculatum*** and ***Dichrostachys cinerea.***



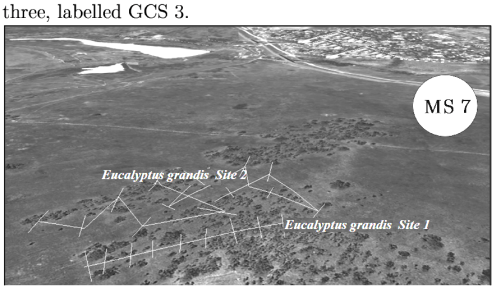
MS 4 (Macro Site 4): Pullen Farm is an experimental farm of the University of the Witwatersrand situated southeast of Nelspruit. The first site PUL 1, runs from open to closed tree cover of mixed species but PUL 2 site, samples a ***Dichrostachys cinerea*** stand. At Pullen, two permanent fire boundary experimental plots were established and sampled by the author in 2012 to test if fire would stop due to low grass biomass (MS4 B) & nonflammability (MS4 A).



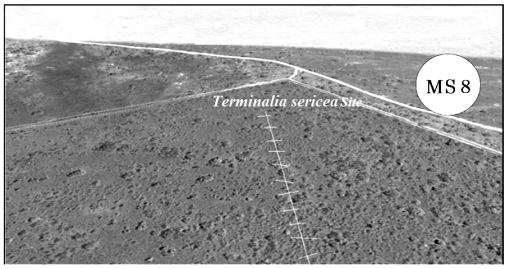
MS 5 (Macro Site 5): Chimney Pot (uMaqomfa) one of the Giant's Castle Peaks located in the Witteberg area of the uKhahlamba - Drakensberg World Heritage site Park. This mountainside has had fire excluded from it for over 45 years. Although six transects were sampled as shown on the image (GCS 1 - GCS 6). The *Morella serrata* tree was the focus and was sampled from transect three, labelled GCS 3.



MS 6 (Macro Site 6): *Spirostachys africana* was sampled next to the staff village at the Skukuza camp in the Kruger National Park. The areas where monospecific stand of the tree species could be found were few. This area was mainly heavily browsed by impala and rhino with considerable elephant damage.



MS 7 (Macro Site 7): In Gauteng, Midrand, there is a graveyard called Juskei View with stands of *Eucalyptus grandis*. This is where two sites of the species were sampled in 2013 growing season. This site had no grazing, however it had signs of recent fire activity, burnt plant parts and a thin black top soil.



MS 8 (Macro Site 8) : Pretoriuskop site is located in a plot fenced off from large herbivores. This site is situated in an area that is dominated by *Terminalia sericea* and is surrounded by a well maintained fire break to prevent it from burning outside prescription.

Figure 1.2: The images show the locality of macro sites, mainly the distribution of trees at these sites. Each image shows the position of the sample plots or the vicinity of tree species samples (Table 1.2). MS 3 had several species sampled on it and the image shows where these tree species were found within MS 3. The two sites where the "fire boundary experiment" was conducted are shown in MS 4. The two sites demonstrate the two main ways in which fire can be stopped by woody plants, through changes in grass characteristics, amount of biomass and flammability. At MS 4 (A) fire was stopped by non-flammable grass that was present under the tree canopies. At MS 4 (B) fire was stopped by low or absence of grass biomass. The geographical positioning of these sites can be see on Figure 1.1, Table 1.1

Table 1.1: Summary of sites, their GPS locations, provinces in which they are located, tree species sampled at the sites and the number of plots sampled at each location.

Tree Species	**Macro Site**	**Region**	**Site Code**	**GPS**	***n***	**MAP**$_{mm}$	**Alt.**$_{m.a.s.l}$	**Management**	**Landscape Position**
Combretum apiculatum	Makhohlola Crest	Mpumalanga	MS 3	24°59'03.2"S 31°46'35.7"E	25	563	400 – 480	SA National Park	Crest, flat loamy to sandy loam
Dichrostachys cinerea	Makhohlola Midslope	Mpumalanga†	MS 3	24°59'01.8"S 31°46'27.8"E	8	563	270 – 839	SA National Park	Midslope, sandy loam, well drained
Diospyros whiteana	Pullen Farm	Mpumalanga	MS 4	25°35'04.0"S 31°10'34.7"E	13	667	600 – 640	Was livestock, now game	Valley side, close to river bank, loamy
Eucalyptus grandis	Jukskie View Midrand	Gauteng	MS 7	26°02'46.8"S 28°07'44.1"E	21	537	1700 – 1750	Cemetery grounds	Flat, sandy, periodically waterlogged
Euclea divinorum	Makhohlola Footslope	Mpumalanga†	MS 3	24°59'01.3"S 31°46'19.2"E	11	563	260 – 839	SA National Park	Sodic area, foot slope silt loam, well drained
Mixed site	Pullen Farm	Mpumalanga	MS 4	25°34'25.8"S 31°11'33.7"E	7	667	610 – 640	Was livestock, now game	Flat, loamy, along a dyke rocky out crop
Morella serrata	Giants Castle Chimney Pot	KwaZulu-Natal	MS 5	29°13'02.0"S 29°32'57.4"E	11	1650	1380 – 3350	Game Nature Reserve	Plateau summit, forest edge, sandy loamy, rocky
Spirostachys africanas	Skukuza Camp	Mpumalanga	MS 6	24°58'30.2"S 31°34'49.3"E	17	553	400 – 480	SA National Park	Valley, sandy to loam, moist
Terminalia sericea	Pretoriuskop	Mpumalanga	MS 8	25°18'38.3"S 31°34'49.6"E	13	746	560 – 640	SA National Park	Flat, sandy, well drained
Vachellia grandiconuta	Makhohlola Footslope	Mpumalanga†	MS 3	25°01'08.1"S 31°47'50.0"E	9	563	260 – 839	SA National Park	Sodic area, foot slope silt loam, well drained
Vachellia karroo	Fort Beaufort	Eastern Cape	MS 1	32°70'08.1"S 27°50'50.0"E	20	500	200 – 350	Livestock farming	Hillside, gentle to flat slope, loam soil, dark soil.
Vachellia karroo	Kei Road	Eastern Cape	MS 2	32°42'47.5"S 27°38'13.1"E	15	476	640 – 700	Livestock farming	Valley side, flat, clay loam to loam

Alt.: Altitude, D. cinerea was also sampled at Pullen Farm, PUL 2. Coordinates that are almost identical are for micro sites that are located in the same macro site. GPS: Global Positioning System. MAP: Mean Annual Precipitation. *m.a.s.l.* = meters above sea level, *n*: Number of plots sampled, Game = wildlife, † = $Samelocality(samemacrositedifferentmicrosites)$.

1.6.2 Study species

Table 1.2: A list of tree species sampled in the study and the range of traits and variables measured directly from these species from the different savanna ecosystems. Other variables measured directly include canopy cover; using two methods concomitantly, and the two perpendicular canopy diameters. I only used data on tree canopy cover because they were showing patterns. Tree individuals of the target tree species (Table 1.2) of varying ages were selected for sampling, but juveniles, diseased or damaged trees were avoided.

		Vars.						
		Cat.Vars				**Num.Vars**		
Genus Species Name	**Phenology**	**Leaf Angle**	**Leaf Type**	**Plant Height**	**Plot LAI**	**Plot Light Trans.**	**Stand LAI**	**Grass Biomass**
(factor)	*(cata.)*	*(cata.)*	*(cata.)*	*(m)*	*(g/m^2)*	*(%)*	*(g/m^2)*	*(g/m^2)*
Combretum apiculatum	Deciduous	Horizontally	Simple	2.30±0.70	00.73±00.31	56±15.95	NA*	414±374.23
Dichrostachys cinerea	Deciduous	Vertically-up	Fine	2.44±1.15	00.78±00.32	56±18.36	03.63±00.89	243±078.67
Diospyros whyteana	Deciduous	Vertically-up	Simple	1.03±0.44	00.85±00.73	60±27.54	NA*	297±205.78
Eucalyptus grandis	Evergreen	Vertically-down	Simple	6.18±2.48	00.65±00.24	59±13.19	NA*	208±108.64
Euclea divinorum	Evergreen	Horizontally	Simple	1.67±0.59	00.44±00.44	74±25.29	01.74±00.32	185±171.00
Mixed site	Deciduous	Horizontally	Simple	0.91±0.68	01.09±00.97	50±34.91	NA*	312±227.01
Morella serrata	Deciduous	Vertically-up	Simple	1.43±0.35	00.34±00.45	81±22.44	NA*	832±417.39
Spirostachys africana	Evergreen	Vertically-down	Simple	1.35±0.94	01.13±00.57	42±19.60	10.77±06.34	198±115.70
Terminalia sericea	Deciduous	Vertically-up	Simple	2.71±0.60	00.76±00.50	59±17.61	27.56±11.12	305±253.73
Vachellia grandicornuta	Evergreen	Horizontally	Fine	1.81±0.29	00.51±00.32	69±19.32	01.87±00.32	230±149.72
Vachellia karroo	Deciduous	Vertically-up	Fine	2.51±1.21	75.88±27.01	69±21.51	NA*	NA

Cat.Vars = Catagorical variables, Cata. = Catagorical, LAI = Leaf Area Index, Lf = Leaf, Num.Vars. = Numerical variables, NA* = Unobtainable due to overcast cloud conditions, Trans. = Transmittance, Vars = Variables, *Spirostachys africana* is actually semi-evergreen and *Terminalia sericea* is actually semi-deciduous, but these were included in the dichotomous catagories.

1.6.3 Sampling design

I aimed to collect data from 20 sample plots at each study site (Table 1.1), in order to represent the range of tree densities that were present at each site using the **Point-Centred-Quarter method (Mitchell 2007).**

- In preparation for the sampling, two lists of random numbers were generated using R's random number generator. One list had a range of 1-8 (n=8) and another a range of 5-20 (n=50); but really it can be any number of values as long as there are enough to accommodate numbers that will be scrapped because of undesirable placement.
- If a site had a gradually increasing gradient of tree density from an open to a closed woodland canopy, I established a straight PCQ transect (Figure 1.3b), steps outlined below.
- However, if a site did not present a gradual transition from an open to a closed woodland canopy, rather sporadic distribution, then the wandering variation of the PCQ method was used, (Figure 1.3a).
- From the second list of random numbers (with 50 numbers) each number was considered as an inter-plot distance, making 50 possible random inter-plot distances ranging from 5 to 20[4].
- After sampling the first 10 plots, I then plotted the data to see regions of the mean PCQ distance range (1 m to 20 m) that had not been sampled. I then selected plots purposefully to cover missing regions of the tree density range by skipping each randomly selected plot that was not sampling the missing regions.
- Even with this precaution of purposefully sampling, due to time constraints and working without field assistance, collecting data from 20 plots at each site was not always possible (see Figure 1.3). Also since the search effort for the missing range took up more time that could have been otherwise used for sampling, nonetheless, that sampling would have saturated the data with a narrower range of values that does not even cover the range.

[4]A PCQ plot has been illustrated in Figure 1.3 and refers to the area within which all the inter-tree distances belonging to one PCQ centre point where collected.

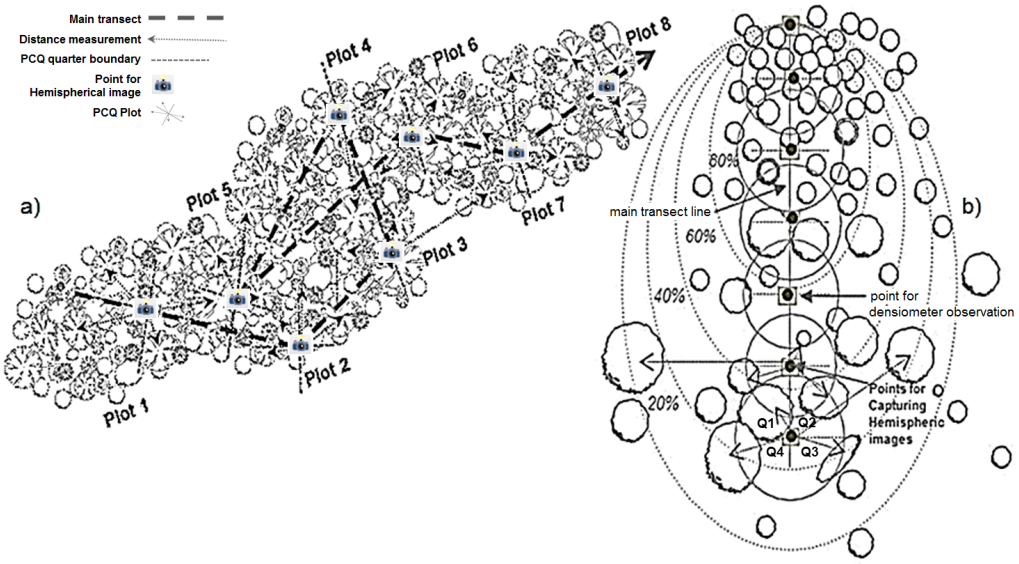


Figure 1.3: An aerial view of two variations of the Point-Centred-Quarter method (PCQ). In 1.3.*a*) a wandering PCQ (with key) and the right of it, 1.3.*b*), the straight line PCQ plotted along a gradient of increase in tree cover (upward direction). The circles around each plot 1.3.*b*) represent possible overlaps between plots considering the sampled individuals [Nondlazi 2015].

Straight Point-Centred-Quarter method

- A point is selected from an aerial image.
- From the selected point the first plot is established by selecting the first random number from a list of random numbers and pacing from the selected point a number of steps that is equal to the selected number and considering it as meters, then making the last step the centre of the first PCQ plot of the transect.
- After collecting the data on the first plot the maximum distance measure was noted and the distance to the next plot was determined as the nearest number to the maximum distance measure, choosing from 5 m, 10 m, 15 m and 20 m.
- As a result, at sites where the boundary between an open grassy system and the closed woodland canopies was abrupt the inter-plot distances tended to be shorter typically 5 m. Things were designed in this way because it was not expected that sampling away from the boundary too far into the closed forest or grassy area would help to explain how trees limit light and grass on the boundary between grassland and forest.
- The chosen inter-plot distance would be maintained from plot to plot along a straight line (also see section 2.2 page 22 – 23).

Wandering Point-Centred-Quarter method

- Similarly for the wandering PCQ transect the first plot is established by selecting the first random number from the list of random numbers and pacing the distance that is equal to the selected number in meters, then making the last step the centre of the first PCQ plot of the transect.
- To select the next plot using the first set of random numbers with n=8, each number was allocated due directions, where 1=N, 2=NE, 3=E, 4=SE, 5=S, 6=SW, 7=W and 8=NW bearings as possible random directions.
- From the 50-number-lists I selected values sequentially and started sampling at a random point, and then walked a random inter-plot distance, in a random direction (selected from 2 above) and established the next sample plot.

Light transmittance data

- Light transmittance was measured directly above each quadrat where grass biomass, cover, and height samples were collected, using a hemispherical fish-eye lens mounted on a Nikon™ D600 camera, to capture a sky image from 30 cm above the ground (between the base of the camera and the ground).
- Each hemispherical image was analysed using the Gap Light Analyzer™ (GLA) software to obtain a value of light transmittance.

1.7 Structure of the dissertation

This introductory chapter, **Chapter 1**, gives the background literature review, the structure of the dissertation, information on the study sites, sampling design and species. **Chapters 2** and **3**, form the body of this dissertation and are each written as stand-alone scientific papers.

In **Chapter 2**, I extracted empirical relationships between increase in tree density and changes in light transmittance across tree species in order to determine the tree density where grass growth is limited and the tree species that cut out sunlight more effectively from their understorey amongst the eleven tree species sampled (Table 1.2). I present differences in thresholds for grass growth across tree species and use differences in the leaf traits of trees to explain the empirical differences across the thresholds. These thresholds pointed out new insights on how and why tree species are markedly different in this relationship between tree density and light transmittance.

In **Chapter 3** I explore how differences in light interception across tree species influences grass biomass, composition, cover and height. I extracted thresholds for grass growth, which fitted with current understanding of the light level at which grass is limited, but raised contradicting evidence that, some important mechanism or characteristics exist among grass species by which some grasses are able to persist even below this 20% threshold, owing to variation in optimum light levels of grass species.

The synthesis chapter (**Chapter 4**) draws out the key findings and discusses what has been achieved from the findings in **Chapters 2** and **3** and it focuses on the interpretation of these findings from the two chapters, and how they contribute to improving our understanding of tree-grass coexistence, bush encroachment and the fire feedback. This concluding chapter also shows how this dissertation complements the substantial body of work, which already exists on these scientific theories with empirical evidence from diverse savanna environments in South Africa.

Chapter 2

Tree architecture and leaf traits alter the impacts of tree density on light transmittance

2.1 Introduction

An increase of woody plants at the expense of grass in savanna and grassland is commonly referred to as 'bush encroachment'[1] (Trollope 1974; O'Connor & Crow 1999; Hudak *et al.* 2003; Mlambo *et al.* 2004; Govender *et al.* 2006; Meyer *et al.* 2007a).

Although the ratio of trees to grass can vary quite widely across savannas (Sankaran *et al.* 2005), and within a savanna (Wiegand *et al.* 2005), dense bush is a concern — because once woody species become too dominant, affected ecosystems have the potential to switch to non-savanna states with very little grass — a state that is difficult to reverse back to an open grassy ecosystem again (Archer 1995; van Auken 1993; Roques *et al.* 2001).

This system switch occurs because an increase in tree density reduces cover and biomass of understorey plants (Shackleton & Scholes 2011), which suppresses fire. This sequence of events leads to repression of plant and animal diversity (Meik *et al.* 2002; Riginos 2009; Vadigi & Ward 2013), reduction in forage for livestock (O'Connor & Crow 1999) and ecosystem services that are derived from the open savanna ecosystems (Dougill *et al.* 1998; Hudak *et al.* 2003). One of the reasons for this system switch is the reduction in light that occurs as tree stems and canopies become denser, limiting light for the grass layer growing

[1] Following O'Connor & Crow (1999) also Wiegand *et al.* (2005) as used here, but it is also known as 'Woody plant encroachment' (Hudak & Wessman 1998); 'Shrub encroachment' (Roques *et al.* 2001); 'Thicketization' or 'Woody plant expansion' (Archer *et al.* 1995)

beneath the trees (Kroon & Herbert 2001).

Clearly some trees intercept more light than others — depending on their leaf area index (LAI), their growth form, and their leaf traits (Villegas *et al.* 2010). Therefore, we would expect that while there is a general relationship of decreasing light and increasing tree canopy cover and stem density, the exact shape of this relationship should vary depending on the tree species involved, and its vegetation traits. This variation in the shape of this relationship means that some tree species would be more effective at excluding understorey grassy plants than other species; by excluding grass at lower tree densities. Accordingly, Sage (2004) identified a threshold of 20% light transmittance below which most C4 grassy species would struggle to grow. The tree density at which this threshold is reached could be considered a tipping point, and it would be valuable to be able to quantify this tree density threshold for a range of important tree species.

The ability to predict changes in tree cover is very important and the accuracy by which we do that largely depends on the models that we build to predict these changes and the data we use to develop and test our models. Numerous attempts to study, predict, and quantify changes in woody cover have been seen over the years. Scientists have been preoccupied with understanding changes in land cover, incorporating increase in woody cover as one land cover change, using remote sensing (Baldi *et al.* 2008) and GIS (Iverson *et al.* 1999; Dougill *et al.* 1999; Hudak *et al.* 2003). Others (Archer *et al.* 2001; Archer 1995; Jeyaseelan 2004; Wiser & Rose 1997; Moran *et al.* 1997; Jakubowski *et al.* 2013) have based their work on historical ground and aerial imagery. However, none of these approaches can replace empirical observations and measurements.

A plant functional trait is any measurable morphological, biochemical, physiological, structural, phenological, or behavioural characteristic or averaged property of a plant species that is expressed in the phenotype of the individuals of that species. Functional traits are relevant to the response of a species to its ecosystem or the influence of a species on the properties of its ecosystem (Cornelissen *et al.* 2003; Díaz *et al.* 2013).

Plant traits can be used to assess differences in function between different species and across environments (Díaz *et al.* 2004), and to group species into 'functional types' which show similar responses to environmental conditions (response functional types) or effects on the environment (effect functional types) (Lavorel *et al.* 2007). Vegetation traits which potentially influence light interception range from tree height and architecture, to leaf size, shape, and arrangement (Falster & Westoby 2003; Westoby & Wright 2006). Tree architecture plays a big role in influencing the amount of light those trees intercept.

A tree canopy (the branches and twigs) only carries leaves, and therefore leaf traits are as

such a primary factor in the relationship between trees and light and can be used to model light transmittance. We understand how trees intercept light at the individual level very well (Niklas *et al.* 2007; Westoby *et al.* 2000) but the way that these individual trees aggregate to cut out light at a canopy level is limited (Niklas *et al.* 2007; Westoby 1998; Niklas 1994). As leaves are designed to intercept light for photosynthesis, one would expect most trees to be maximising light interception. However, trade-offs with water loss, temperature regulation, and issues around competition, defence from fire and herbivory, and resource allocation mean that trees display a variety of architectures and leaf characteristics, which vary in their ability to intercept light individually and at a stand level. I identified several vegetation traits that might be important in the ability to intercept light:

a) **Leaf area index (LAI)**: defined as the ratio of leaf area per square meter of ground surface (Kitajima *et al.* 2005), indicates the amount of photosynthetic leaf material carried by a tree canopy. The more leaves there are on a tree and the larger the leaves and the higher the LAI; the more the interception of light will be under individual trees (Figure 2.11).

b) **Leaf phenology**: the study of seasonal plant activity or seasonality of maximum production of photosynthetic tissue (Díaz 1998) is considered here as the number of months in a year that a tree retains its green leaves. This seasonal plant activity is important because tree species which drop their leaves in the dry season intercept light effectively only for some period of the year — but since the time of the year when the leaves are flushed is the same time of year that grass grows, it might or might not have a strong impact on understorey biomass.

c) **Leaf type**: the arrangement of leaf material of a single leaf can be used to evaluate the effect of leaf type on light transmittance. I distinguished between compound-leaved and simple-leaved species. This differencing in the arrangement of leaf material is important because compound leaves may intercept light differently from simple leaves.

d) **Leaf angle**: the predominant angle of tilt in the leaves of a canopy relative to zenith or 90˚angle. Leaves held more vertically transmit more light for more of the day than leaves held horizontally.

e) **Tree height**: could be important as taller trees can hold more leaves if the vertical spread of the canopy is wide and the branches start very close to the ground (*have a higher LAI*). However, when considering light interception at a stand level it

is possible that short trees block out light more effectively, as the distance between their canopies and the ground is smaller.

It is therefore crucial to understand the tree traits that cause different tree species to intercept different light levels. For more details on these traits and an explanation on exactly what each trait means, and how it might influence light transmittance, *see Chapter 1 sections 1.2.3, page 4 - 5* and *page 24; subheading 'Sampling tree trait data'.*

The current chapter presents the results on tree traits that explain the behaviour of light transmittance along a gradient of increasing tree density for different tree species.

I tested three hypotheses: a) The relationship between tree density and light transmittance is different between tree species; b) Tree traits, including LAI, phenology, leaf angle, leaf type and tree height, can be used to explain variation in the relationship between tree density and light transmittance between tree species; and c) The threshold of 40% tree canopy cover proposed in literature, which coincides with the threshold of 20% light, beyond which grass is excluded from the understorey of trees is supported by my data.

A better understanding of these theories would help explain the traits that make some tree species more prone to encroachment than others and the different threshold tree densities where tree species begin to prevent grass growth.

The aim of this chapter was to examine how changes in woody biomass (*tree density and canopy cover*) influence light transmittance in South African savannas. Particularly, to explore across a variety of tree species how species differences in canopy leaf traits and tree density affect light transmittance. I addressed this aim through the following narrower **objectives**.

To:

–Determine the relationship between light transmittance and (i) tree density and (ii) tree canopy cover.

–Determine whether the relationship between tree density and light transmittance differs across different tree species (Table 1.2).

–Investigate whether tree characteristics affect the amount of light transmittance by different tree species (Table 1.2).

2.2 Sampling methods

Please see *section 1.6* for information on how I laid out my sampling transects and sample plots using the modified PCQ method.

Table 2.1: Summary table for the methods and tools used to obtain the data variables used in this Chapter, two of which are calculated or extracted from other results or data.

Exp. variable	**Data type**	**Source**	**Instrument**	**Tools**
Mean PCQ distance (m)	Horizontal distance	Product of averaging four nearest neighbours	Using a 50 m measuring	Data forms, centre
Canopy cover (%)	Den.CanoCover Hem.CanoCover	Product of densiometer equation and product of GLA output	Computation devices and GLA software	Densiometer D600 Nikon™ Tripod
Hem. Light Transmittance (%)	%Light	distances at each PCQ plot Captured plot sky images and image analysis	material tape D600 Nikon™ camera, fisheye lens	maker Tripod, spirit level notes
D_{20} (m)	Index in meters	Extrapolated value, from the relationship between light and mean PCQ dist. for each tree species	Computation devices and the R-software	Linear Regression output and R-software
L_0 (%)	Index in percentage	Extracted from the regression relationship between light and mean PCQ distance	Computation devices and the R-software	Linear Regression output and R-software
Tree height (m)	Vertical geometric distance	Vertical height estimates of each tree sampled in the study	Ranging rod	Data forms and notes
Phenology	Nominal	Subjective classification	Personal observation and reference to literature	Notes and Palgrave (2002)
Leaf area Index (LAI)	Ratio	Calculated using the eversion formula	Measurements using a Ceptometer (LAI meter)	External sensor holder, notes
Leaf angle	Nominal	Subjective classification	Personal observation and literature	Notes Palgrave (2002)
Leaf type	Nominal	Subjective classification	Personal observation and literature	Notes Palgrave (2002)

D_{20} = Mean PCQ distances that result in 20% light transmittance, Exp. = experimental, L_0 = Light Transmittance at 0 m of mean PCQ distance, Cep. = Ceptometer, GLA = Gap Light Analyser software, Hem. = Hemispherical, PAR = Photosynthetically Active Radiation, PCQ = Point-Centred-Quarter method

2.2.1 Sampling the tree density gradient

The first step in collecting data on tree density was to layout a PCQ transect and sample mean PCQ distance as a proxy for tree density.

Since the distribution of trees is very variable, it is very difficult to estimate tree density using bound-plots[2] because a large sample size is required to estimate tree density and what is more, I wanted to sample tree density at a point[3] on a landscape (5×5 m plots were considered at Giant's Castle, Figure 1.2 MS 5).

Alternatives include plotless methods — where plots are without defined sizes. Plotless method use the mean of distances between trees and a point on a landscape *viz.* mean PCQ distance, to represent tree density, avoiding the large sample size requirement.

Accordingly, I used a modified Point-Centre-Quarter method (Mitchell & Colleges 2007). Modifications included measuring circumference at 0.2 m above ground to avoid buttress swellings, instead of diameter at breast height (DBH or D_{130}) and two perpendicular canopy spreads to capture the ellipse of the canopy along with its spread. Tree density was estimated from the mean of four distances measured in each of the four directions between the centre point of the sample plot and the four, or eight, closest tree individuals (*mean PCQ distance*), a variation from sampling strictly four closest tree individuals using the equation from Mitchell & Colleges (2007).

Equations 2.1 & 2.2: Used to calculate mean PCQ distance at a sample plot, which is the summation of the point-to-tree distances of the four or eight nearest trees to the center of the plot, divided by the total number of point-to-tree distances measured; with one or two point-to-tree distances measured at each quarter of a plot surveyed. Following Cottam *et al.*'s (1953) empirical evidence and Morisita's (1954) mathematical evidence, assuming a notation where :

n : total number of point-to-tree distances per plot (*observations/plots*)

i : the i^{th} point-to-tree distances observations at quarter $ji = 1$ *or* 2, equations 2.1 and 2.2 respectively.

$$\text{mean PCQ distance of one closest tree per quarter } \bar{r} = \frac{\sum_{i=1}^{4}}{4n} \tag{2.1}$$

$$\text{mean PCQ distance of two closest trees per quarter } \bar{r} = \frac{\sum_{i=1}^{8}}{8n} \tag{2.2}$$

[2]plots with defined boundaries
[3]within a space of a few meters

Together with mean PCQ distance from the centre point to nearest tree or two trees per quarter — subplot, I recorded the tree species names, height and stem circumference. Stem circumference and tree height were measured in order to calculate and quantify woody biomass estimates and stand age (which were used to run exploratory analysis *e.g.* to understand whether canopy cover and tree density had the same relationships with woody biomass as established literature as a means to assess credibility of my data; and not for use to estimate tree density or test hypotheses). The distance measurement methods (*e.g.* 5×5 m square plots and circular plot methods) usually require a number of sample plots to give an accurate measure of tree density for a landscape. However, a validation of tree density using data from the modified PCQ measurements against circular plot measurement was performed using data collected by Sally Archibald in 2012 from Fort Bragg in North Carolina, USA and showed a strong exponential decay relationship ($y = 2354.9^{-0.307x}; r^2 = 0.96$).

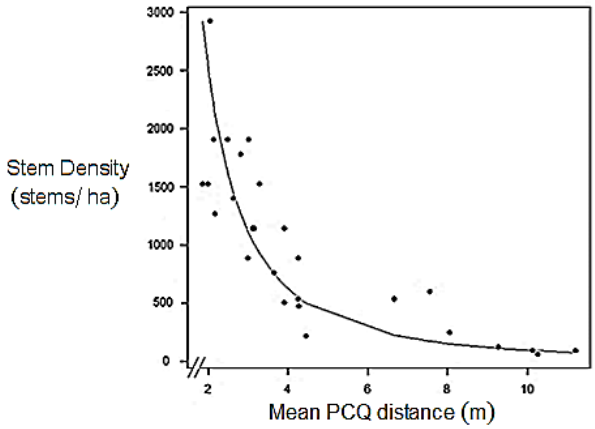


Figure 2.1: Relationship between mean PCQ distance (m) and stem density in stems/ha (from the circular plot of 10 - 20 m radius, one of the most accurate methods of measuring tree density) showing that mean PCQ distance is a reliable measure of tree density, because mean PCQ distance reasonably estimates actual counts of trees. A symmetric departure from a straight line, with a reverse J shape, a fit showing a distribution that approaches but never reaches both graphic axes, explainable with asymptotes, therefore the exponential assumption is tenable. The scale for the x-axes on the above plot has been cut off at 1.5 m in order for the start of the graph to be in line with the asymptotes at 2 m of mean PCQ distance. Density decreases exponentially with increase in mean distance, with small PCQ distances representing high stem densities. The line shows the fitted relationship (Density=1/ mean PCQ distance to the exponent negative two). The very high stem density values (> 2000 stems/ha) are unrealistic for a larger stand, but possible at the small sampling scale used. Data points • represent the point of interception between each mean PCQ distance value and value from circular plot method.

I therefore used the mean PCQ distance as a proxy of tree density for all my analyses. It must be borne in mind that the relationship between tree density and mean PCQ distance

is negatively exponential — few meters of change in mean PCQ distance represents a large change in tree density (trees/hectare).

2.2.2 Sampling light interception

Sampling tree canopy cover with a densiometer

Sampling tree canopy cover, I used a densiometer to measure canopy cover within the PCQ transect using a Spherical densiometer™ Model C (Werner 2009).

At the centre of each plot, a densiometer was placed on a tripod at 0.5 m above the ground. The densiometer was leveled on the tripod using an in-built spirit level. Using a permanent marker four black dots were marked equidistantly on each of the squares of the densiometer grid; in order the ensure that all plots were assed the same way.

During data collection, with the densiometer apparatus, the following two sets of values were recorded, (Figure 2.2):

- The number of dots not obstructing any reflection of the tree canopy within squares where at least one dot was obstructing some section of the canopy were enumerated and recorded.
- The number of 'squares' having all four dots free from canopy reflection (Figure 2.2)

The total number of uncovered dots was subtracted from the total number of dots, to obtain the number of dots covered. Using these data the percentage canopy cover or canopy openness were calculated following Shuett-Hames *et al.* (1999).

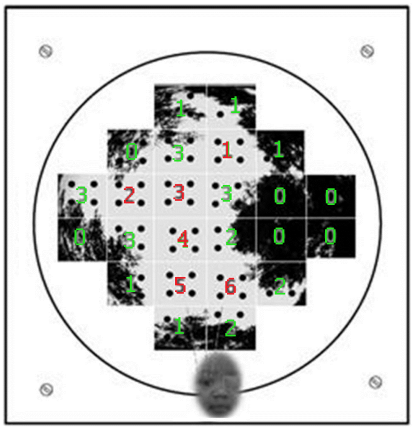


Figure 2.2: A spherical densiometer image showing uncovered squares (1 - 6 red — all four dots free of tree reflection) with all four dots being visible; all squares having a range from 0 - 3 have at least one covered dot (expressing the count of uncoverd dots — green). Schematic adapted from Shuett-Hames *et al.* (1999).

Sampling tree trait data

For each tree species at each site sampled, data on various vegetation traits were cross-referenced. Phenology leaf, leaf angle and leaf form were subjectively classified into dichotomous categories, following Palgrave (2002), (chapter one sections 1.6.2 Study species).

Phenology: was classified to deciduous and evergreen.

Leaf angle: was categorized into horizontal and vertical leaf angles.

Leaf type: was categorized into compound and simple leaves.

Leaf area index (LAI): Tree LAI is strongly related to the amount of light intercepted by tree canopies. Hence, it was included as one of the variables in the study. At each of the macro sites, monospecific stands of targeted tree species were sought, located and permanently marked with GPS co-ordinates.
Leaf area index is defined as one sided leaf area per unit of ground surface area. When measured at the scale of an individual plant it represents the investment in leaf area and light capture by the plant. The Ceptometer or AccuPAR™ or PAR/LAI meter (PAR = Photosynthetically Active Radiation) Model LP-80 manufactured by Decagon® Devices, Incorporated at Pullman, (the relatioship between PAR and LAI) is an automatic PAR measurement device that measures light/PAR and uses those light measurements together with some user-defined inputs to calculate LAI as an output using the inversions formula. Five individual measurements were averaged facing one direction, but the direction was changed five times under each tree canopy by moving around understorey shading and therefore each of the five directions had its own average of five measurements and this procedure was done for 18 to 237 trees. It is a valuable measurement in helping to assess canopy density and biomass.

At each of the monospecific stands of the different tree species, using the Ceptometer, light transmittance was measured directly. The unit of measurement in the research was an individual tree. The main targets were fully mature trees but given that it is extremely difficult to delineate cut-off of tree age in order to select mature trees only, hence the crude approach mentioned in the point above was adopted.

A target of twenty trees was measured at each monospecific stand, as far as possible. The data was collected systematically by circling around each sampled tree, taking five summary measurements of Photosynthetically Active Radiation (PAR) per tree. Each of the five summary measurements collected from each tree were aggregated at whole canopy level. This aggregation was done in order to reduce the variation in the light

measurements because the amount of light that passes a tree canopy can change very quickly and varies greatly within the same canopy.

The same steps as stated above were repeated for each of the species measured at each site or stand. All measurements that were collected from the same species were averaged as light transmittance of that tree species. This approach means that light transmittance that was measured with a Ceptometer was considered as a species average trait. Eventually each tree species had one average value of light transmittance that was obtained from a dataset with stacked data.

Sampling light transmittance data with a hemispherical camera

My target was 20 sample plots representing a range of tree densities at each site (using a wandering transect method). At each of the plots I recorded *i)* the light transmittance, *ii)* tree density and *iii)* canopy cover. Light transmittance was quantified using hemispherical photography. Sample size suggested is 6 - 10 photographs per stand (Canham *et al.* 1990; Easter & Spies 1994). Hemispherical photography was also used to quantify canopy cover (Beaudet & Messier 2002; Bellow & Nair 2003; Jain *et al.* 2004).

One photograph was taken at 0.4 m above each plot centre using a Nikon™ D 600 (5 mp) digital camera and fisheye converter (183^o view angle). Although literature suggests that hemispherical photography yields repeatable results (Englund *et al.* 2000; Hale and Edwards 2002), factors such as digital image size, compression, quality, and saturation can influence the analysis of digital fisheye photos (Englund *et al.* 2000; Frazer *et al.*2001; Inoue *et al.* 2004). To minimize these issues, the following camera settings were used as far as possible in line with recommendations from Frazer *et al.* (2001).

- –image quality: 1:4 mp
- –compression: JPG format
- –saturation: colour
- –image size: full (2560×1920 *pixels*)

Additionally, all sampling was done under uniformly overcast conditions when the solar disk was completely obscured, as far as possible. The camera was levelled with a spirit level and the fisheye lens oriented toward magnetic north using a compass prior to each shot. Percent visible sky (100% - 0% visible sky) from the hemispherical photographs was used to calculate tree canopy cover by using Gap Light Analyser™ software (GLA Version 2.0 by Simon Fraser University, Burnaby, British Columbia, and the Institute of Ecosystem Studies, Millbrook, New York).

Gap Light Analyser was also used to provide an indirect estimate of each plot's light transmittance. Hemispherical images or the skyward fish-eye images were firstly converted from JPG to bpm format and then uploaded into Gap Light Analyser software. All the images from each site (examples given in Figure 2.3) were analysed through Gap Light Analyser following the procedure for registering, recolouring, thresholding and analysis according to Frazer *et al.* (1999), and light data was obtained and tabulated in comma delimited text files.

For all analyses, the threshold pixel classification of 'sky' versus 'canopy' was set manually for every photo following guidelines outlined in the GLA user manual (Frazer *et al.* 1999). To minimize variance with threshold selection, one operator completed all analyses. Existing research suggests that the relationship between hemispherical photography and light may be influenced by photo analysis angle (Bellow & Nair 2003). To control for this influence I ensured that the images were analysed with northern bearing being always at the top of the images (12h00), because I ensured the the top of the camera was always facing north when the images were taken.

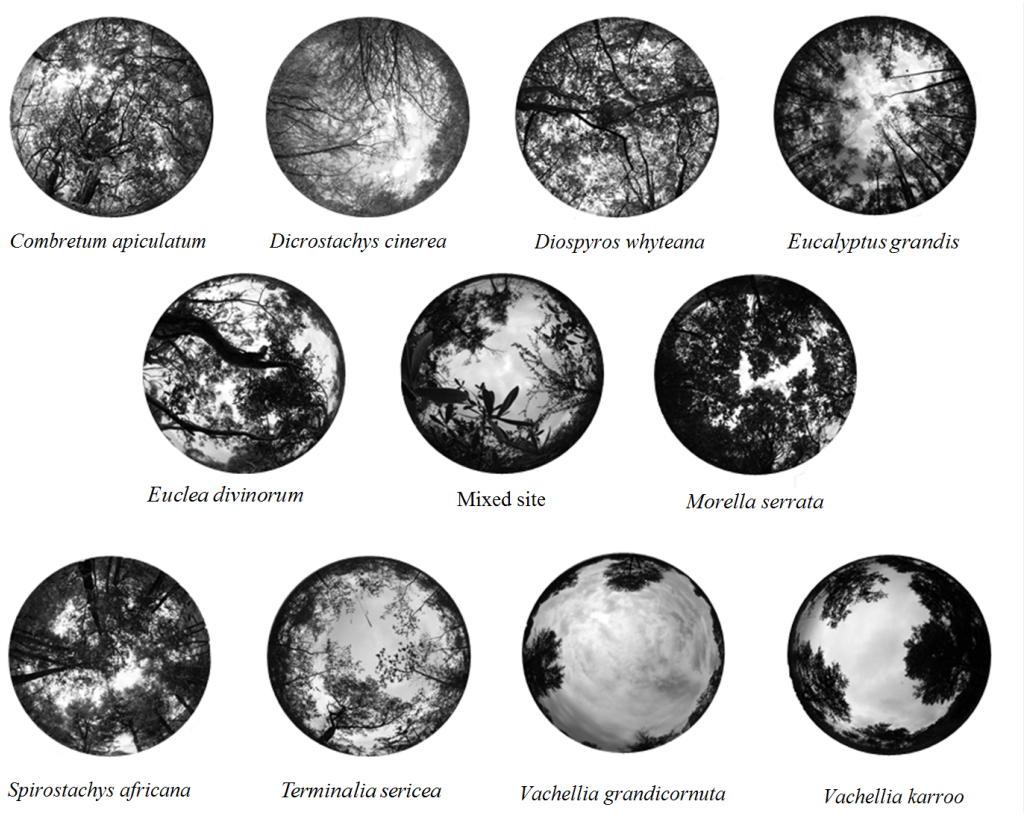


Figure 2.3: Hemispherical images showing typical differences in hemispherical images that were analysed for each of the tree species (sites) that were sampled in the study

2.3 Data analysis

Data were analysed to identify, describe, explore and present patterns graphically using `R` statistical software (`R` Development Core Team 2011, www.r-project.org, version 3.1) in order to answer my research questions. All analyses in this section were done using normally distributed data (mean PCQ distance: $W = 0.7423$, $P<0.0001$; Light transmittance: $W = 0.9713$, $P<0.01$; Hem. canopy cover: $W = 0.9778$, $P<0.01$; Den. canopy cover: $W = 0.8321$, $P<0.0001$, Shapiro-Wilk normality test). For variables with observations that had incomplete data pairs, or corresponding data for covariates due to missing data values; where interpolation was not applicable, the whole row of observations was deleted, this incompleteness is noted as 'missingness'[4] where applicable. I was interested in determining the answers to these following questions:

How do tree density and canopy cover affect light transmittance?: A test was performed to examine how tree density and canopy cover affect light transmittance. Data on tree density, canopy cover and understorey light of trees, were collected across 11 sites with different tree species by measuring paired mean PCQ distance in meters (PCQ method) canopy cover and light transmittance; 0 - 100% (hemispherical camera). Values from 156 plots were pooled. Sixty-five of the 156 plots also had other corresponding canopy cover data (densiometer), coupling some of the 156 canopy cover (%) values from hemispherical images. In order to understand how mean PCQ distance and canopy cover (x-variables) affect light transmittance (y-variable) I used quantile regression.

This method is appropriate because it allows plotting of data and permits fitting of specied, quantile regression lines that aid in extracting statistics on observed thresholds in empirical relationships from data, and as a result, respective coefcients can be assessed. In order to understand how mean PCQ distance (x-variable) affects tree canopy cover (y-variable) I used a scatter plot. This approach was appropriate because the intention was to assess the pattern of canopy cover data across the mean PCQ distance range (`graphics` package).

Does the relationship between trees and light transmittance differ amongst tree species?: Kernel density plots were used to assess the spread of the mean distance data. Density estimation is a smoothing operation. Inevitably there is a trade-off between bias in the estimate and the estimate's variability: large bandwidths will produce smooth estimates that may hide local features of the density; small bandwidths may introduce spurious bumps into the estimate. It was an appropriate approach because it allows precise features of the distribution of the data to be plotted. To test the hypothesis that

[4] cells with NAs in the dataset

the relationship between mean PCQ distance and light transmittance varies across tree species; linear regression models (Pinheiro *et al.* 2014) were fitted to the relationship between mean PCQ distance and light transmittance for each of the 11 tree species. This relationship is a negative exponential. Therefore, the purpose of these regressions was to assess and demonstrate differences in this relationship across species. The co-efficients of these linear regressions were used to compare differences in the relationship between mean PCQ distance and light transmittance across tree species. The light index and slope of each relationship from the 11 sites were extracted from the regression equation ($y = m\ x + c$). Index mean PCQ distance was extrapolated using the formula. The outputs were tabulated with the coefficients from the regression summaries. Thresholds in the relationships between light transmittance and tree density were explored using bar plots.

Can the differences in this relationship between tree species be explained using leaf and canopy traits?: Answering this question involved analysing dichotomous categories of phenology leaf angle, leaf type together with tree height and leaf area index (x-variables) across the light gradient and across light thresholds (y-variables) to determine whether there was a difference in the light transmitted between each pair of categories for each leaf trait and whether LAI and tree height affected light differently across tree species in a patterned way, as well as whether LAI as a key trait had any relationship with any other tree trait. The first stage of this analysis focused on dichotomous categories of phenology, leaf angle, leaf type and how these dichotomous categories differ across that light gradient and across the light transmittance thresholds (`t-test`) and data were presented graphically using bar plots. The second stage of the analysis focused on assessing how LAI compares across tree species and its relationship with leaf angle, patterns were assessd using a plot of group means (ANOVA, to test for statistically significant differences between goups, and post hoc test for identifying group-pairs were differences exist). The third stage involved assessing how LAI and tree height affect the light transmittance thresholds, patterns were assed using a scatter plots (Pearson's correlation, conducted using the `cor.test`, `stats` package (Becker *et al.* 1988).

2.4 Results

2.4.1 Effect of tree density and canopy cover on light transmittance

When all sites were combined, there was a weak positive relationship ($r^2 = 0.088$, $F_{1,155} = 15.03$, $P < 0.0001$, $SE = 20.92$) between light transmittance and tree density (Figure 2.4 *a)*, mean PCQ distances (m)). Although there were still many plots with high transmittance (>80%) at high tree densities, on average, light transmittance declines with increasing tree densities. There was a bottom limitation (Table 2.2) on light transmittance (5^{th} quantile regression fit), demonstrated by an increase in the minimum value of light transmittance with a decrease in tree density. Furthermore, maximum values of light transmittance never reached 100% with a maximum between 90 - 99%, at any point along the range of mean PCQ distances (95% quantile regression fit). In contrast, there is a much stronger ($r^2 = 0.426$, $F_{1,64} = 47.66$, $P < 0.00000$, $SE = 15.69$) relationship between tree canopy cover and the amount of light that is transmitted to the understorey of trees (Figure 2.4 *b)*, Canopy Cover (%)).

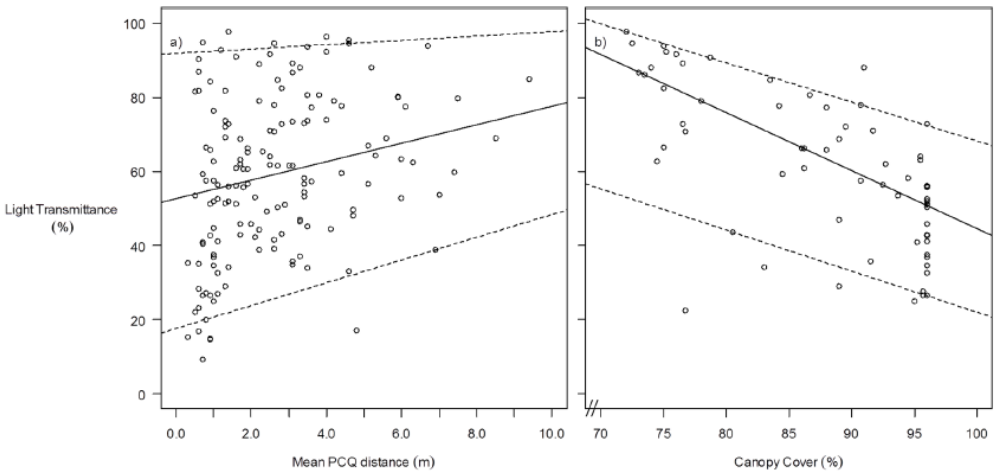


Figure 2.4: Scatter plot of the relationship between mean PCQ distance and %canopy cover against light transmittance. Line shows quantile regression fits (0.05,0.50,0.95), coefficients in Table 2.2. As mean PCQ distance increases light transmittance increases but with a huge variance, that is even greater at high tree densities.

Table 2.2: Coefficients for the relationships between main variables (light transmittance, mean PCQ distance, and tree canopy cover.)

Relationships	**Variables**		**CI**	**CI**
Lt *vs* mPCQd		Coefficients	Lower	Upper
y	Light transmittance	52.863	47.46	57.69
x	mean PCQ distance	2.054	1.51	3.95
Lt *vs* CanoCov				
y	Light transmittance	201.436	196.77	246.97
x	Canopy cover	-1.568	-2.145	-1.516

CanoCov = Canopy cover, CI = confidence interval, Lt = Light transmittance, mPCQd = mean PCQ distance,

2.4.2 Canopy cover and mean PCQ distance

About 4000 trees/ha which is equivalent mean PCQ distance of ~ 1.5 m (Figure 2.1), canopy cover begins to close-up completely (100%), while at mean PCQ distance of ~ 3.5 m which is equivalent to tree densities of ~ 750 trees/ha (Figure 2.1) a threshold is apparent (vertical dotted line, Figure 2.5), where open canopy cover closes-up quickly from a minimum cover of $\sim 20 - 30\%$ to above $\sim 70 - 80\%$ canopy cover with a change of less than ~ 0.5 m in mean PCQ distance (Figure 2.5).

Tree canopy cover that is above 90% rarely occurs when trees are sparse (between 0 trees/ha and ~ 750 trees/ha, equivalent to 3.5 m (Figure 2.1) and more in mean PCQ distance on avarage) but at greater than ~ 750 trees/ha, only canopy cover that is greater that 80% dominates. At a mean PCQ distance of 7.5 m tree canopies begin to cover $> 20\%$ of the sky area above a plot. Accordingly, beyond 7.5 m it is unlikely to obtain canopy cover that is greater than 80% instead canopy cover may be as low as 40%.

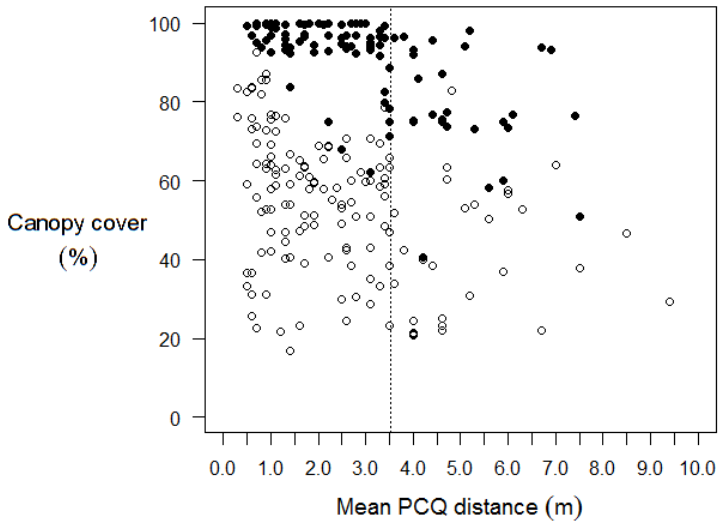


Figure 2.5: The closed circles (•) represent data points from mean PCQ distance and on canopy cover data as sampled directly with a densiometer ($r^2 = 0.385, F_{1,104} = 65.1, P < 0.0001, SE = 9.518$)(62 observations deleted due to missingness (absent data)). The open circles (∘) represent data points from mean PCQ distance and on canopy cover data as sampled directly with a hemispherical camera ($r^2 = 0.111$, $F_{1,144} = 17.98$, $P < 0.0001$, SE = 16.69).

2.4.3 Relationship between mean PCQ distance and light transmittance across sites

The mean PCQ distance range

As mentioned in the methods I intended to sample a range of different tree densities at each site (0 - 10/20 m). I mostly (5 out of 11 sites had sample range that was greater than 10) succeeded in sampling this range, but not for some sites (Mixed site, *Spirostachys africana, Diospyros whyteana*, Figure 2.6) where I had an under representation of intermediate to low tree density plots. This under representation made it difficult to fit significant relationships for some of these plots.

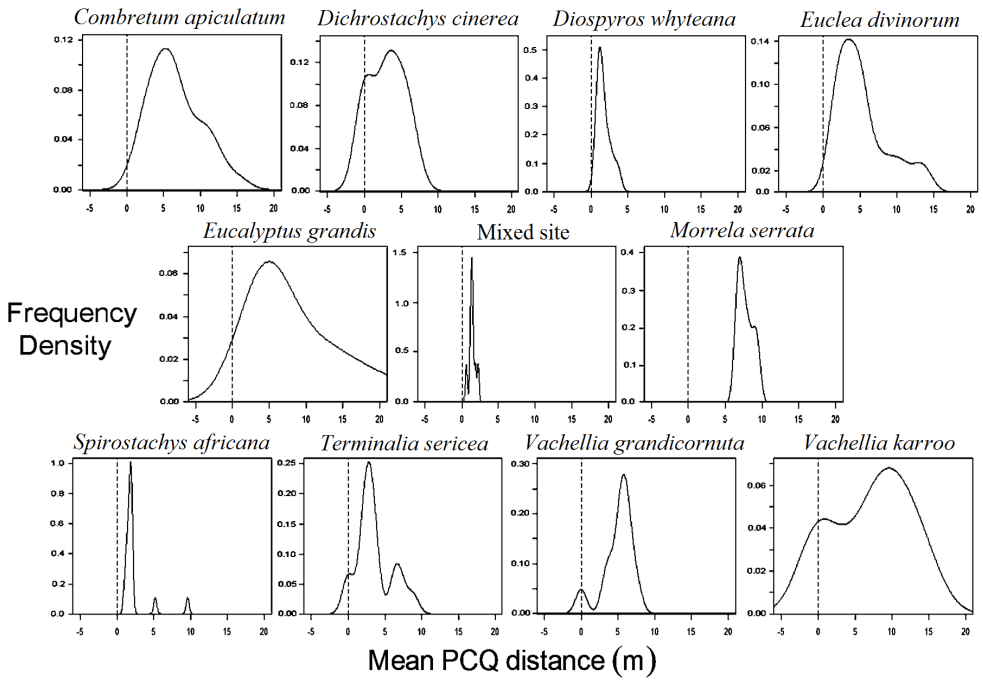


Figure 2.6: Kernel Density smoothing plots of mean PCQ distance values sampled directly from 11 sites with each site having a different monospecific stand of a tree species, showing the distribution of mean PCQ distance values across the range of mean PCQ distances covered. The graphs for the different sites have all been plotted on the same x-axes scale.

Mean PCQ distance and light transmittance across sites

When the data is no longer pooled but is grouped by tree species the relationship between tree density (mean PCQ distance) and light transmittance is much more obvious, but as expected, differed widely across tree species (Figure 2.7, Table 2.2). The regression coefficients showed that six of the 11 sampled tree species had an association between changes in tree density and light transmittance (r^2>20 %) with five of the six having a strong relationship (r^2>35%). Although light transmittance decreases with an increase in density for all species, the slope of the relationship ranged from 0.96 (*E. grandis*) to 14.33 (*M. serrata*).

Some species like *M. serrata* can cut out light to levels below 20% before 0 m in mean PCQ distance is reached — *i.e.* would be expected to exclude grass at low densities. The tree *M. serrata* is a forest species. The only savanna species that limits light to levels below 20% is *V. karroo*. Only five of these relationships are significant (Table 2.2), presumably, due to small sample size and limited range of distances sampled (*see Figure 2.6*). Some of the graphs indicate that the relationship is not necessarily linear — that

light transmittance decreases more steeply as PCQ distance decreases *e.g. M. serrata* and *E. divinorum*. However, due to limited sample size it was not possible to fit non-linear models so I used linear models for the rest of my analysis. There was no regression coefficient greater than 51%.

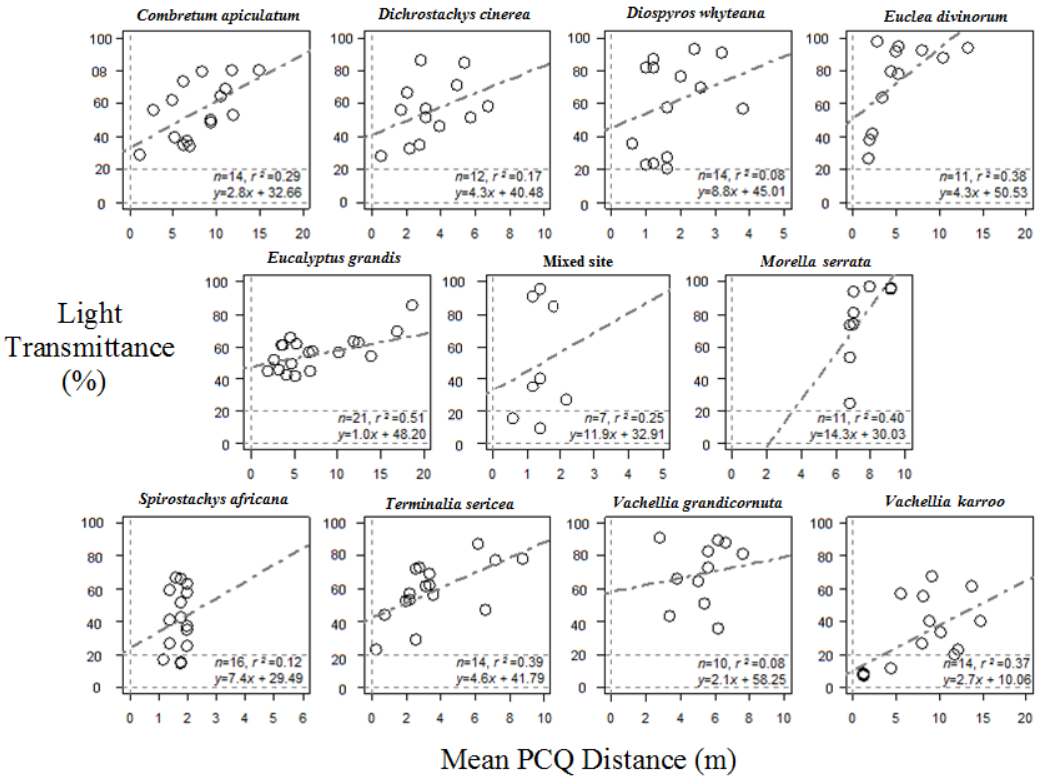


Figure 2.7: Light transmittance data collected with hemispherical camera plotted with mean PCQ distance (data collected with the Point-Centred-Quarter method). Significance and and coefficients are indicated in Table 2.3. Differences in the relationship between light transmittance (m) and mean PCQ distance (m) across tree species are apparent. These tree species differ in the slope of this relationship. Species with a steeper slope in this relationship cut out more light than species with a gentle slope of the regression line as mean PCQ distance decreases. The scale of the x-axes has been adjusted for each window to make data more visible. The mean PCQ distance of 3.5 m indicated is for comparative purposes and is a threshold mean distnace where canopy cover closes-up, Figure 2.5.

The $p-$values and r^2 show that six of the eleven regression coefficients sampled tree species had respective significantly positive relationship between increase in mean PCQ distance (decline in tree density) and increase in light transmittance at 95% confidence interval. D_{20} means that, to set light transmittance to 20% across all the tree species, mean PCQ distance would have to vary in order to achieve that (Table 2.3).

Species specific light transmittance thresholds

The p-values (Table 2.3) show that six of the eleven sampled tree species had a significantly positive relationship between increase in mean PCQ distance (*decline in tree density*) and increase isn light transmittance at 95% confidence interval.

Table 2.3: Tabulated summary statistics, on the relationships between mean PCQ distance and light transmittance across species. Species as genus and species names, regression formula and coefficient ($y = mx + c$ and r^2) respectively. Extracted values include the mean PCQ distance at which 20% light transmittance is reached (D_{20}, Table 2.4), an extrapolated value in meters, and L_0 the light transmittance when mean PCQ distance is at zero. The mean PCQ distance for each species (mPCQd±SD) averaged over all sites of each species sampled in the study. Only species with significant relationships on this table were used for further analyses.

Trees	$\boldsymbol{y = m\ x +}$	L_0	mPCQd	$\boldsymbol{r^2}$	***P***	D_{20}	***F***	**DF**
Combretum apiculatum	$y = 02.8x +$	32.66	3.36±1.69	0.29	.	-0.40	7.40	14
Dichrostachys cinerea	$y = 04.3x +$	40.48	2.13±0.78	0.17	ns	0.39	2.31	11
Diospyros whyteana	$y = 08.8x +$	45.01	0.87±0.45	0.08	ns	0.25	1.18	13
Euclea divinorum	$y = 04.3x +$	50.53	2.97±2.06	0.38	.	-0.31	6.20	10
Eucalyptus grandis	$y = 01.0x +$	48.20	5.44±4.93	0.51	***	-0.29	21.07	20
Mixed site	$y = 11.9x +$	32.91	0.70±0.23	0.25	ns	0.25	0.6	7
Morella serrata	$y = 14.3x + -30.03$		3.88±0.50	0.40	.	0.19	6.77	10
Spirostachys africana	$y = 07.4x +$	29.49	1.16±1.01	0.12	ns	0.43	2.11	15
Terminalia sericea	$y = 04.6x +$	41.79	2.03±1.09	0.39	*	-0.37	8.89	14
Vachellia grandicornuta	$y = 02.1x +$	58.25	2.60±0.69	0.08	ns	0.31	0.23	9
Vachellia karroo	$y = 02.7x +$	10.06	3.46±2.29	0.37	.	1.63	7.48	13

Significance code: [***] = 0.001, [**] = 0.01, [*] = 0.05, [.] = 0.05, [ns] = not significant, coef. = coefficient, stat. = statistic

Note that the values of L_0 (Table 2.3) vary across the sampled species. Light transmittance when mean PCQ distance is at zero (L_0%) refers to the extrapolated value of light that is transmitted by tree canopies when the modelled mean PCQ distance is at zero — when there are no spaces between stems of tree individuals. If mean PCQ distance is held constant at zero light transmittance would still vary across species. The L_0% values are theorietical and therefore are purely used to show differences between species.

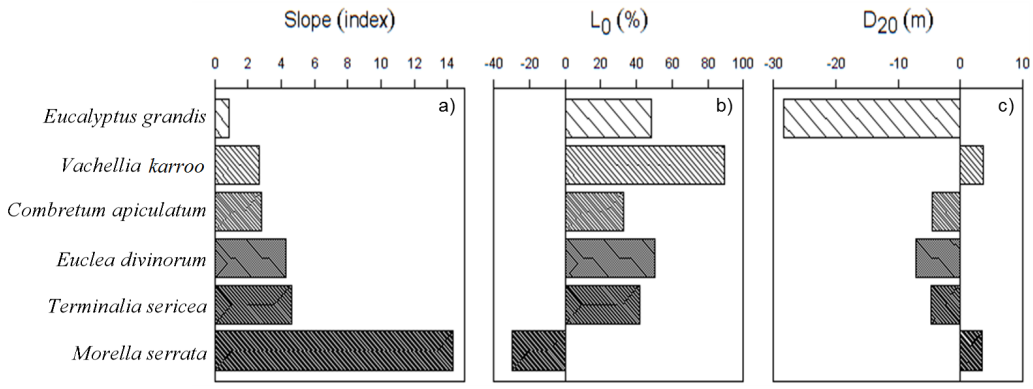


Figure 2.8: The three indices of difference in light transmittance across tree species showing the relationship between light transmittance and mean PCQ distance across species. D_{20} is an extrapolated value; L_0 and the slope have been extracted from the relationships between mean PCQ distance and light transmittance across species for which this relationship was significant.

Table 2.4: Matrix for cross comparisons of D_{20} across species, using the mean relative difference (MRD). If MRD is less than 0.05† we fail to reject the null hypothesis that tree species are not different in how tree species transmit light.

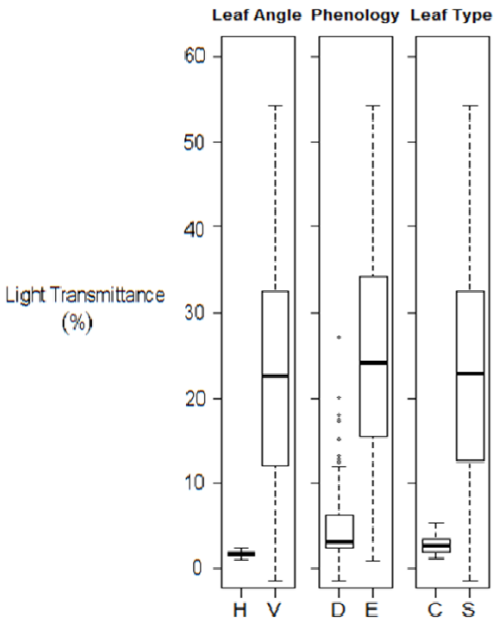
Index	**Species**	[1]**V.kar**	[2]**C.api**	[3]**E.dev**	[4]**T.ser**	**M.ser**
D_{20}	*Eucalyptus grandis*	1.130	1.160	0.748	0.832	1.123
D_{20}	[1] *Vachellia karroo*	—	2.228	2.928	2.286	0.049†
D_{20}	[2] *Combretum apiculatum*	—	—	0.5703	0.047†	1.773
D_{20}	[3] *Euclea divinorum*	—	—	—	0.332	1.492
D_{20}	[4] *Terminalia sericea*	—	—	—	—	1.738

The short hand of species column names is a convention of the first three letters of the genus and species names of the species in column two (Species) and the superscript numbers bear reference between columns and rows, *M.ser = Morella serrata*. Difference greater than 0.05 is significantly different †

2.4.4 Light transmittance and tree traits

Can phenology, leaf angle and leaf type explain variation in light transmittance across tree species?

There was greater light transmittance for evergreen than deciduous trees, likewise trees with vertically angled than horizontally angled leaves (Figure 2.9 and 2.10). Unexpectedly, leaf data did not support the hypothesis that compound-leafed trees are associated with high light transmittance relative to simple-leafed trees (Figure 2.10).



Trait	R^2	F	SE	P
Leaf Type	0.2083	89.96	2.86	<0.0001
Leaf Phenology	0.2737	128.9	12.31	<0.0001
Leaf Angle	0.1924	81.46	12.98	<0.0001

Figure 2.9: A comparison of light transmittance between deciduous (D) and evergreen (E) trees, trees with horizontally angled (H) and vertically angled (V) leaves as well as trees with compound leaves (C) against trees with simple leaves (S).

The slope ('m' in Table 2.3) represents the rate at which the light declines with density. The indices (Figure 2.10) of variation in the relationship between light transmittance and mean PCQ distance across tree species, D_{20} (m), L_0 (%) and the slope (index), did not vary significantly across tree trait categories. Although leaf type showed some response, the number of tree species in each of the categories could not allow a conclusive result. Leaf traits can explain variations in leaf area index.

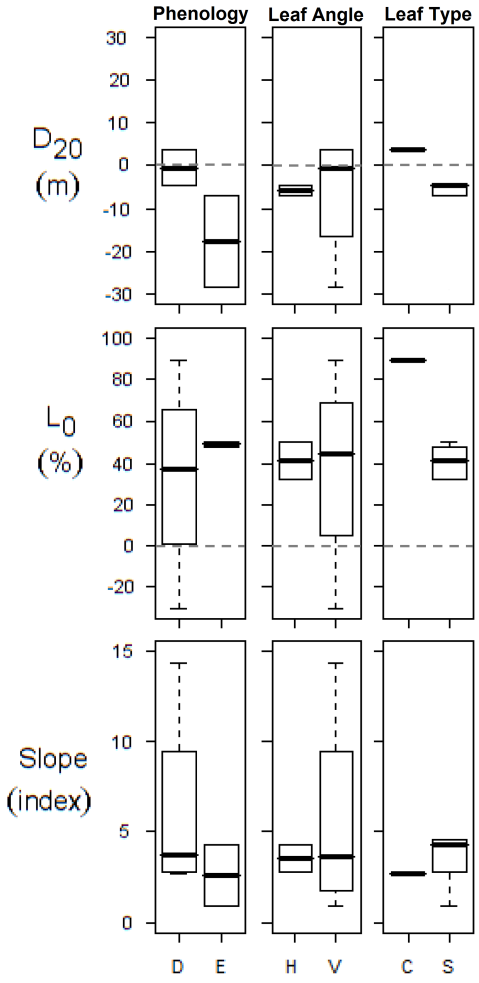


Figure 2.10: Tree species were subjectively allocated to leaf trait categories. D_{20} represents the tree density (PCQ distance) at which 20% of the light is transmitted. L_0 represents the x-intercept, the extrapolated light transmitted at a PCQ distance of zero. [D = Deciduous, E = Evergreen, H = Horizotal, V = Vertical, C = Compound, S = Simple.

Leaf area index explains species differences in light transmittance

Tree species were different in the mean ceptometer value of LAI (Appedix A.2 and A.3). LAI ranged from 0.05±0.013 g/m^2 (*T. sericea*) to 1.27±0.039 g/m^2 (*E. divinorum*); *V. grandicornuta* (1.12±0. 0.040 g/m^2), *T. sericea*, *S. africana* (0.08±0.007 g/m^2), *D. cinerea* (0.27±0.010 g/m^2)(Figure 2.11). Tree species with horizontal leaves (*E. divinorum, V. grandicornuta*) are associated with high LAI whereas tree species with vertically angled leaves (*D. cinerea, S. africana, T. sericea*) are associated with low LAI, Figure 2.11.

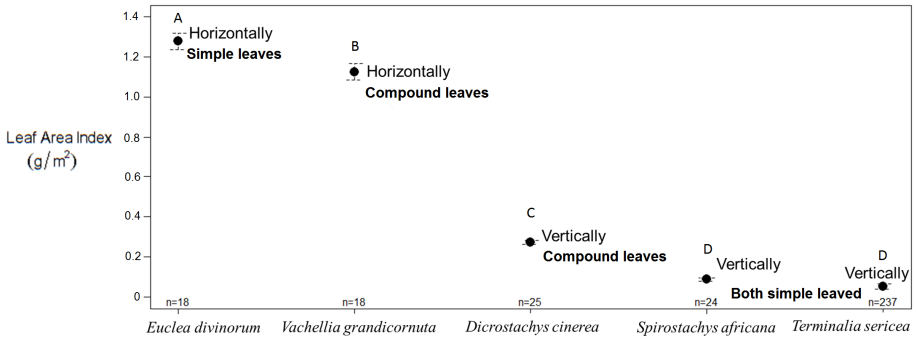


Figure 2.11: Tree species differences in the mean ceptometer value of leaf area index, error bars show standard error at 95% confidence interval. Tree species with horizontal leaves (*E. divinorum, V. grandicornuta*) are associated to high leaf area index whereas tree species with vertically angled leaves (*D. cinerea, S. africana, T. sericea*) are associated to low leaf area index.

Table 2.5: ANOVA for leaf area index (LAI) as a function of species and leaf angle, showing significant differences in LAI across species with different leaf angles)

	DF	**SS**	**MSS**	**F-value**	**P-value**
Tree Species	4	41.64	10.41	32002	< 0.0001
Residuals	317	0.1	0		

DF=degrees of freedom, SS = Sum of Squares, MSS = Mean Sum of Squares

Table 2.6: Tukey Honest Significant Differences (HSD) cross comparison of mean LAI across tree species. Stadard diviation in brackets)

Mean LAI	**Species in comparison**	**Diff.**	**Lwr.**	**Upr.**
Euclea divinorum	*Spirostachys africana* vs *Terminalia sericea*	0.034	0.024	0.045
1.276 (0.04)	*Dichrostachys cinerea* vs *Terminalia sericea*	0.219	0.209	0.229
Vachellia grandicornuta	*Vachellia grandicornuta* vs *Terminalia sericea*	1.069	1.057	1.081
1.123 (0.0406)	*Euclea divinorum* vs *Terminalia sericea*	1.222	1.209	1.234
Dichrostachys cinerea	*Dichrostachys cinerea* vs *Spirostachys africana*	0.185	0.171	0.199
0.273 (0.0104)	*Vachellia grandicornuta* vs *Spirostachys africana*	1.035	1.02	1.05
Spirostachys africana	*Euclea divinorum* vs *Spirostachys africana*	1.187	1.172	1.203
0.088 (0.0076)	*Vachellia grandicornuta* vs *Dichrostachys cinerea*	0.85	0.835	0.865
Terminalia sericea	*Euclea divinorum* vs *Dichrostachys cinerea*	1.002	0.987	1.018
0.054 (0.0137)	*Euclea divinorum* vs *Vachellia grandicornuta*	0.152	0.136	0.169

Diff. = mean difference, Lwr = Lower CI, Upr = Upper CI, Comparisons with a difference that is less than 0.05 are not significantly different.

LAI and tree height explain light transmittance differences

In order to test whether LAI and tree height could explain the variation in the indices of differences in the relationship between light transmittance across tree species, (D_{20} (m), L_0 (%) and Slope (index) in Figure 2.12; each of the indices was compared between categories of each of the two traits (LAI and tree height, Table 2.5).

Patterns observed across matrix plot, in Figure 2.12, indices and tree traits show that the relationship between tree traits and these indices can be explained better by tree height than LAI (Figure 2.12). D_{20} (m) and L_0 (%) increase with tree height, but the slope decreases with tree height (Table 2.5); therefore this result does not support my hypothesis that tall trees cut out more light because this result shows that it's shorter trees that do. However, since LAI may at times exert greater influence than the tree density, such that a tree expected to transmit more light based on mean PCQ density may end up transmitting less light than expected because LAI has further reduced the amount of light transmitted.D_{20} (m) and slope increase with LAI while L_0 (%) decreases with LAI (Table 2.5).

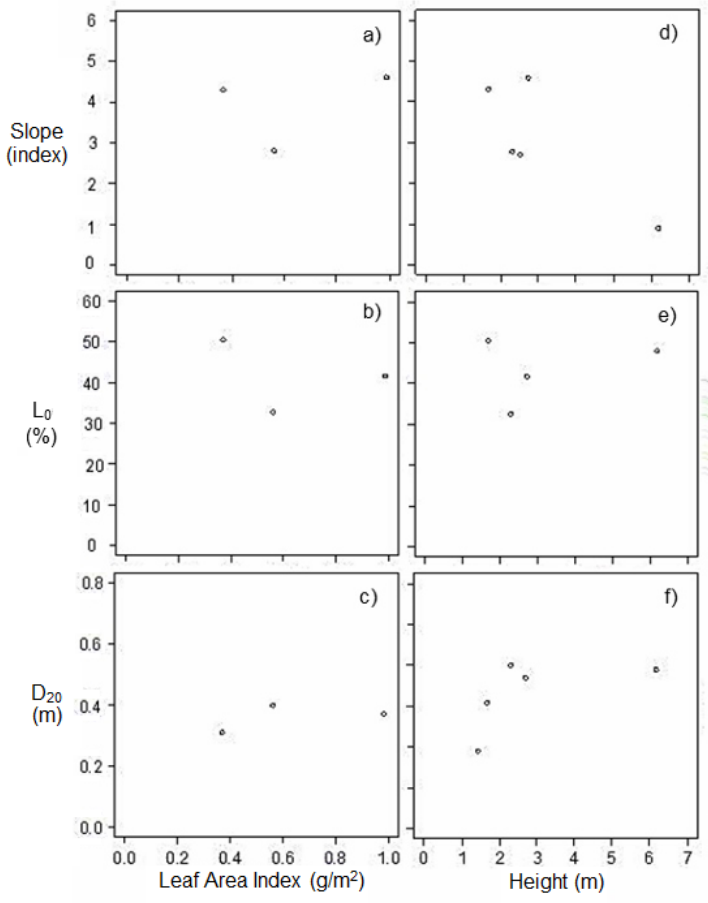


Figure 2.12: Matrix plot of the relationship of the three indices with (Slope, D_{20} and L_0) one leaf characteristic (LAI) and one tree architectural trait (tree height). LAI — leaf area index, L_0 % — the light transmittance when trees are at maximum density, D_{20} — the mean PCQ distance at which light transmittance of 20% is reached and slope — the steepness of the fitted regression model line in the relationship between mean PCQ distance and light transmittance.

Table 2.7: Tabulated summary statistics for ***Figure 2.12***, on the relationships between the drivers of light transmittance (leaf area index and tree height) against the indices of light transmittance (D_{20}, L_0 and slope).

***X* Var.**	***Y* Var.**	***Y* Coeff.**	***X* Coeff.**	***T*-statistic**	***P*-value**	**Corr.Coeff.**
	Slope	NA	NA	0.3885	0.7641	0.3621315 *a)*
LAI	D_{20}	NA	NA	0.9456	0.5178	0.6870497 *c)*
	L_0	NA	NA	-0.3088	0.8093	-0.2950865 *b)*
	L_0	-0.6757075	0.8940994	0.6308	0.5624	0.3008131 *e)*
Tree Height	Slope	-0.9464877	0.4351535	-1.4311	0.2257	-0.5819122 *d)*
	D_{20}	-0.9888081	-0.3157131	-4.0668	0.01526	0.8973539 *f)*

Letters link the results to Figure 2.12 (*a) b) c) d) e)*). The significance of these realtionships has been compromised by the small sample size

2.5 Discussion

2.5.1 Tree and canopy density on light limitation

From the relationship between light transmittance and mean PCQ distance (Figure 2.4 *a)*) with canopy cover (Figure 2.4 *b*), I realised that savanna trees become sparse as they grow larger. Thus, an increase in canopy cover; per individual tree, represents increase in stand age.

Where decrease in mean PCQ distance maybe less than an increase in tree canopy cover and therefore resulting in a decrease in light transmittance in savanna unlike in plantation forests species. For example in Britain; Hale *et al.* (2009), used data on basal area (m^2ha^{-1}) of stands of Stika spruce (*Picea sitchensis*) and Scots pine (*Pinus sylvestris*) against total light transmittance from hemispherical images. Presenting changes in stand structure as a global site factor (GSF), denser stands were observed as trees grew larger, and were associated with decline in light transmittance. Whereas, in savanna where some species self-thin as stands grow, the response of light transmittance may form an inverse exponential curve, where light decreases to a point beyond which light begins to increase again.

By inference therefore increase in basal area represents increase in stand age, because savanna trees can be expected to limit less light than forest species, which is in agreement with my hypothesis on species variation in the relationship between tree density and light, which I assess in the following section. The mathematical approach used to calculate stem density in the current study — based on Mitchell & Colleges (2007) and Mitchell (2015), was an exponential one. Hence, a straight linear model was a weak fit for describing the

shape of the relationship between light transmittance and mean PCQ distance. Consider that the different tree species included in the pooled data may have very different linear relationships, by varying leaf and architectural traits, making the collective non-linear. Since the main aim however, was not to precisely describe the shape of the relationship between light transmittance and mean PCQ distance, unlike Hale *et al.* (2009), straight linear models were fitted. Meanwhile, the aim was rather to assess the direction of the relationship — whether sunlight declines significantly with an increase in tree density.

There is a winding scatter with increase in tree density, from the collection of mean PCQ distances and light transmittance data that has been pooled across all tree species or locations; varying trait composition. This scattering suggests that tree species affect light transmittance differently with increase in tree density. Hence, in the next section we test this secondary hypothesis.

This observation also supports that, as savanna trees mature, they become more sparse — with the rate, alternative possibilities and consequence depending on the tree species[5]. Alternatively, trees may grow tall and closer together, resultantly reducing the mean space between tree stems to less than 2 m and eventually increasing canopy cover to higher than 80%. Beyond 80% canopy cover, light transmittance drops below 20% of full sunlight — the theoretical conservative light threshold for grass growth, supporting the hypothesis that 80% canopy cover results in 20% light transmittance (Figure 2.5). This observation represents the discovery of a threshold mean PCQ distance of 2 m ∼2500 trees/ha (Figure 2.1) which is the tree density representing 80% cover and the light threshold for grass growth (20% lgiht transmittance).

(Figure 2.1) Light transmittance declines with increasing canopy cover (Figure 2.4 *b)*). The sampled data is limited between 70 and 96% cover. This limitation could be due to the fact that the results of the densiometer method rely on a calculation, which, given that the apparatus was not designed using African savanna, maybe failing to accommodate the architecture and response of the life history of trees in the African savanna.

Nonetheless, 70% tree canopy cover may seem very far from 0% cover. However, thinking carefully, the theoretical threshold tree canopy cover beyond which fire does not spread is suggested to be 40% tree canopy cover (Archibald 2010; Scholes 2003). Therefore, relatively 70% is 30% from the hypothetical zero-growth threshold of 40% for tree canopy cover. Trees with a closed tree canopy can be expected to transmit less light (Figure 2.4). As more seedlings are recruited, canopy cover increases gradually closing inter-canopy

[5]The rate at which a stand of a trees species becomes dense given the rate at which it recruits and the alternative possibilities of how it gets dense and consequence; whether the stand ends up in forest or not, or even whether its management succeeds and all depends on the traits of the tree species

gaps, leading to less light transmittance to the understorey.

In addition, Figure 2.4 *a*) and *b*) reveal that the area occupied by stems and canopies increases as light decreases — with the inference borne in mind. The mean PCQ distances between 1.5 and 2 m, as well as canopy cover of 80% and light transmittance of 20%, are important results for this chapter because they are the key thresholds for grass growth and support my main hypothesis for this chapter. Together with the discovery of a strong threshold at 3.5 m mean PCQ distance (∼880 trees/ha, Figure 2.1) where canopies will start to cover substantial area of ground surface (Figure 2.5).

Existence of the 3.5 m threshold for canopy closure is a compelling observation because densiometer data corroborates hemispherical data that at 3.5 m mean PCQ distance canopy cover is more likely to be at its maximum (Figure 2.5). Also that, at 7.5 m of mean PCQ distance (∼225 trees/ha, Figure 2.1) canopy cover >40%, (where the closed circles start in Figure 2.5) is rare. Langan *et al.* (2015) showed that, in bi-stable ecosystems the emergent tree community trait suite differs markedly between forest and savanna biome states and highlight the same key variables outlined in this dissertation, as drivers of the variation in the growth environment for plants.

My result that tree height (Figure 2.12) and tree cover (Figure 2.4 & 2.5) can be implicated in the maintenance of savanna and thus its shift to forest supports my hypothesis that tree architecture and tree canopy cover play a role in the light transmittance driven local scale savanna dynamics, and is also supported by other published work including Langan *et al.* (2015) who showed that the emergence of the savanna biome could be attributed to markedly different ecosystem structural properties mainly height, tree cover and above ground biomass. In agreement, Langan *et al.* (2015) shows that change in grass biomass as an ecosystem structural property, given the fire feedback, plays a crucial role in the maintenance of savanna. While the current study further demonstrates how a grassy structure as a fundamental ecosystem structural property can get lost due to light limitation by trees, the greatest value of this observation is that it shows how savanna trees are more likely to reach the greatest densities that could quickly achieve maximum light limitation, by creating a predominantly closed canopy cover that may shade some grass species; even if the canopy nonetheless has some open inter-canopy pockets that let in 100% of the sunlight. Later in Chapter Five, I will test whether grass can grow below 20% light.

2.5.2 Stand structure and light measurement

During analysis, it was realised that the data for *Combretum apiculatum* was inadequately collected by the methodology. This inadequacy was because *Combretum apiculatum* communities had distinctly different canopy levels, a primary canopy, and a secondary canopy. This canopy stratification presented a challenge because an image captured from the centre of the plot captured both the primary and secondary canopies[6], while the measurements from the PCQ were actually sampling only the secondary canopy excluding the bigger trees, which were occupying the primary canopy and blocked out most of the light.

Conducting density measurements at different vertical heights and aggregating the traits of the secondary canopy trees to the primary canopy was a solution adopted for this challenge but its details are outside the scope of this research.The mean PCQ distances of 1.5 to 2 m, as well as canopy cover of 80% and light transmittance of 20% coincide. This result is important for this chapter because it shows the mean PCQ distance at which the threshold for canopy cover creates the threshold light transmittance. Light transmittance decreased with a decrease in mean PCQ distance showing a widening scatter as tree density increased. This widening scatter might be explained by data collected from a mix of tree species and sites, and as such, some leaf and architectural aspects of the architecture of the sampled tree species might be the source of variation. This scatter might suggest differentiation in how tree species affect light transmittance as tree species increase in tree density, even if they are increasing at the same rate.

2.5.3 Is mean PCQ distance a species characteristic?

Even with purposeful sampling, the full range of mean PCQ distances could not be sampled for all sites, because the search for sites had to be limited. After which the required density was considered unavailable in the 40 m search perimeter and a new site was sought. The range of mean PCQ distances exhibited by different tree species suggest that these savanna tree species can have mean PCQ distances that range from 0.5 to 20 m (Figure 2.6). This constancy in the range could suggest that these savanna trees may have characteristic densities, but this submission remains to be tested by sampling the same savanna species and a range of environments to ascertain the extent of variation across stands of the same tree species varied across locations.

These ranges of mean PCQ distance, can be an artefact of the sampling approach and as such merely show the ranges of mean PCQ distance values for the sampled sites, which

[6] a primary canopy is a layer of big canopies of tall trees, that has a coexisting short secondary layer of tree canopies that is much denser below it.

cannot be generalised. Nonetheless, the extent to which I managed to sample the range of possible mean PCQ distance could have been influenced by the abundance of each distance class of the possible distance classes along the mean PCQ distance range. Furthermore, it is noteworthy that even with sites where the range of mean PCQ distances was between 0.5 and 20 m was not covered their distributions approximated normality. Whether the mean PCQ range for each tree species would be the same across different sites of the same species remains to be tested.

After noting all of the above, it is worthy considering that the variation in the mean PCQ distance range across the sites, could suggest that these tree species differ in their characteristic clumping, such that species with narrow ranges transmit less light from those with wider ranges.

2.5.4 Differences in transmittance across tree species

Tree species transmit different light levels and therefore differ in their ability to encroach. This encroacher differencing is signified by differences the slope on the regression lines fitted for the relationship between light and tree density across sites (Figures 2.7 & 2.8 as well as Table 2.3). This encroacher differencing was also supported by differences in how quickly tree species reach 3.5 m mean distance, which is the mean distance at which canopy cover reaches 100% cover. The thresholds L_0 and D_{20} also showed that tree species differ in light penetration (Figures 2.7 & 2.8 as well as Table 2.3). A high value of D_{20} may mean a species can intercept light more effectively, *e.g. Vachellia karroo* . Which means that other species may intercept more light with minor increase in tree density or that in order to achieve 20% light, mean PCQ distance would have to be increased more for a species with a high value of D_{20} (Table 2.4) than a species that has a negative index of D_{20}, for example.

The relationship between mean PCQ distance and light is different across the 11 sampled tree species. Six out of 11 of these relationships are significant. Indices that show the variation in the relationship between mean PCQ distances and light transmittance (Figure 2.8) indicated that tree traits can explain the variation in the relationship across tree species and involving tree traits in the relatioship between mean PCQ distances and light transmittance.

2.5.5 Trait composition drives transmittance differences

There can be some close agreement between leaf angle and leaf area index (Figure 2.11). Trees with horizontal leaf angle tend to have higher leaf area index than trees with vertical

leaf angles. At a stand level, all the leaf trait categories differed significantly in light transmittance, with evergreen, horizontal, and compound leaves transmitting less light than deciduous, vertical, and simple-leaved trees. However, at the plot level, tree height emerged as a more important tree trait (Figure 2.12), with taller trees transmitting more light than shorter trees. In the following chapter I focus on the implications of differences in light transmission by trees on grass species composition, biomass and cover.

Leaf angle: The fact that trees with horizontal leaves transmit less light than trees that hold their leaves vertical as observed in this chapter, supports early observations on the effect of leaf angle on light such as found by Hikosaka & Hirose (1997). Subjectively categorising leaf angle overcame the difficulty of leaf angle measurement, which can be erroneous since leaves can change angles through the length of a day (Gilbert *et al.* 1979) and vary within a canopy (Björkman & Holmgren 1963).

In the contrary, Gilbert *et al.* (1979) defended their precision in leaf angle measurements by disputing that photo-inhabitation will generally pronounce the effects of leaf angle in two catagories proposed by Björkman & Holmgren (1963) and which the current study supports by motivating that trees change leaf angles within a day. Yet the varience of grouped leaf angles of Gilbert *et al.* (1979) was approximating the means in most cases (data from Gilbert *et al.* 1979) showing high within a canopy and within a species variation in leaf angle under high precision. This species variation in leaf angle is supported by personal observations using protractor measurements for leaf angle in savanna species.

Leaf type: Compound leafed trees may transmit less light than simple leaves; by scattering the sun's rays more thus increasing diffuse light and reducing direct sunlight, which is the radiation type that delivers light of 'high' quality — light that is within the PAR range of $\sim 400 - 700$ nm which is $\sim 40 - 80\%$ light transmittance (Lieffers *et al.* 1999).

Leaf area index: Trees with horizontally angled leaves tend to have high leaf area index and transmit less light (Figure 2.11). The relationship between leaf angle, LAI (Hikosaka & Hirose 1997) and light transmittance (Falster and Westoby 2003), is not a new finding, it has been attributed to variation between sun and shade leaves within canopies, for example as found by Mc Millen and Mc Clendon (1979). They showed how tree leaves use both strategies of horizontally and vertically angled leaves to prevent photo-inhibitation; horizontally angled sun leaves to create wider shades that protect shade leaves — which increases LAI, and vertically angled shade leaves to reduce sun capture — which decreases LAI.

Phenology: Trees that lose their leaves during the dry season transmit more light than evergreen trees, but only during periods of leaf fall. Generally, evergreen trees have more

direct light and can transmit more light than deciduous trees. Earlier studies (Hutchison & Matt 1977; Uemura 1994; Lieffers *et al.* 1999) have shown phenological differences as a driver of seasonal variation in canopy light transmittance, but the current study also shows the existence of between tree species with phenological differences within a wet season, that are contrary to intuition. Since change in climate (natural or human induced) alters phenology of natural vegetation (Villalba *et al.* 1998; Villalba *et al.* 2003), future climate change can be expected to alter the amount of light transmitted by trees. It was clear that leaf phenology and leaf type were stronger drivers of the differences in how trees intercept light. There was agreement between leaf area index and leaf angle with horizontal leaf angle predicting high leaf area index. The literature supports the outcome of this study that light transmittance decreases with an increase in leaf area index (Figure 2.12 *a), b), c)*). Kitajima *et al.* (2005) showed that light received by the ground decreases with an increase in LAI from analysis of maximum LAI and total light extinction.

Tree height: Taller trees were found to transmit more light than short trees (Figure 2.12 *d), e), f)*) and this can be explained by the observations of Kitajima *et al.* (2005), that taller trees generally have lower LAI than short trees.

2.6 Conclusion

The relationship between mean PCQ distance and light is different across the 11 sampled tree species. Six out of 11 of these relationships are statistically significant. Indices that show the variation in the relationship between mean PCQ distances and light transmittance indicated that tree traits explain the variation in the relationship between mean PCQ distance and light transmittance across tree species. There can be some close relationship between leaf angle and leaf area index. Trees with horizontal leaf angels tended to have a higher leaf area index than trees with vertical leaf angles.

At a stand level, all the leaf trait categories differed significantly in light transmittance, with evergreen, horizontal, and compound leaves transmitting less light than deciduous, vertical, and simple leaved trees. However, at a plot level, tree height emerged as a more important tree trait, with taller trees transmitting more light than short trees. In the following chapter, the implications of these differences in light transmission on grass biomass, grass cover and grass height are of focus. Tree canopy cover declined with a decline in tree density, although not all the time, showing conspicuous thresholds at tree densities of about 2 to 4 m and as well 6 to 8 m of mean PCQ distance. These thresholds exhibit some lagging in the response of tree canopy cover to changes in mean PCQ distance.

Nonetheless, clumping of trees or closing of tree canopies is still expected to occur less where woody vegetation is sparse, than where vegetation is dense. As such, areas that appear to be recruiting young cohorts of trees can be expected to have more closed canopies in the future. For the same reason, tree species that are able to grow in close proximity of each other are more likely to encroach and have a closed canopies.

Chapter 3

Effect of light transmittance on Grass Biomass, Cover, Height and Species Composition

3.1 Introduction

3.1.1 Grass productivity and light requirements

Light is a key resource for plants — it is light's energy that drives the photosynthetic pathway, allowing plants to convert CO_2 to energy and sugars, resulting in biomass accumulation. Therefore, grass biomass reflects primary production that is fuel for fire given available resources (Mutanga *et al.* 2004; Davis *et al.* 2002).

The positive relationship between photosynthetic rate and light availability varies for different plant types. The C4 grasses require more light than C3 grasses, because of their higher energy requirement (Sage 2004). However, within the C4 grasses there are shade specialists — species more tolerant of low light conditions, that preferentially grow and compete vigorously beneath tree canopies. Shade specialists have traits like high nitrogen content and specific leaf area that allow them to maintain a positive carbon (C) balance at low light levels (Lieffers *et al.* 1999; Falster & Westoby 2003). Further, characteristics that make a plant shade tolerant; leaves with a high specific leaf area and a low C:N ratio, might also reduce the flammability [1] (Ripley *et al.* 2010a).

[1] Used here as the quality of being easily ignited and ability of a plant to burn rapidly; a general trait that can be used in reference to grass species, *e.g.* Annual grass species are generally more friable than perennial species.

Turnover in grass composition is expected as trees become denser, decreasing light penetration and reducing grass biomass and cover. Accordingly, response of grass biomass to tree cover is convex — *i.e.* low tree cover has very little impact on grass biomass. As cover increases, a threshold is crossed where grass biomass declines rapidly (Scholes & Archer 1997). This decline in grass biomass could be due to greater root competition from trees, but grasses are known to be superior competitors for nutrients and water (Scholes & Walker 1993; February *et al.* 2013). A major driver of decline in grass biomass, cover and height is the reduction in light availability at ground surface (Fynn *et al.* 2011). Shade-tolerant forbs and C3 grass persist when light conditions deteriorate, but also have traits that lead to low grass biomass (Fynn *et al.* 2011).

Under tree canopies, where light is a major limiting resource for grass growth, certain plant traits can increase the ability of a grass species to survive and grow (Falster & Westoby 2003; Fynn *et al.* 2011; Montgomery & Chazdon, 2001) for example high Specific Leaf Area (SLA), high Nitrogen (N) content. However, these traits impact other aspects of a grass's life history — for example leaves with high N and high SLA are very palatable for grazers, but also decompose quickly — (high friability) and therefore would not support a high fuel load for fires. Sage (2004) suggested that there was a threshold of $\sim 20\%$ of light. This $\sim 20\%$ threshold implies that tree canopies, which cut out $> 80\%$ of light (in a South African savanna for the tree species sampled), should be able to exclude grass but this value has never been experimentally demonstrated.

Productive grasses that produce a lot of biomass during the growing season will be more flammable due to higher fuel loads. Similarly, grass that decomposes slowly, retaining a large amount of moribund biomass during the dry season is likely to be more flammable than grass that decomposes more quickly (Ripley *et al.* 2010b). The growth form of the grass could also affect flammability: grass that holds its leaves upright as aerated, large tussocks might have more biomass, while grass that grows horizontally would provide more continuous fuel bed. Finally, the rates at which grass dry out at the end of the growing season might also affect their flammability: grass that stays green for longer or grass that drys and decopose before the dry season would be less flammable.

Ripley *et al.* (2010b) linked these flammability traits of grasses to photosynthetic pathways and showed that C4 grasses are more flammable than their conspecific C3 counterparts. Recent publications (Ripley *et al.* 2010b; Lundgren *et al.* 2016) show that this flammability difference is strongly linked to evolutionary origin, and that photosynthetic pathway is less important than clade. Limited understanding of the effect of trees on light penetration and grass growth under tree canopies is a hinderance to

managing bush to achieve predetermined and prescribed states of biomass, cover and grass species composition.

The aim of this chapter was to study the relationships between the amount light that trees transmit to their understorey and types of trees (species and vegetation functional traits) [2] as well as the amount of understorey grass. I addressed this aim through the following narrower **objectives**.

To:

– Test if grass becomes limited at 20% light transmittance.

– Asses changes of grass species composition in relation to light availability.

– Investigate whether grass characteristics can explain changes in grass biomass and composition along a gradient of increasing light transmittance.

3.2 Sampling methods

3.2.1 Data used in this chapter (Table 3.1)

At the center of each PCQ plot a 0.5×0.5 m quadrat was placed and all the grass species within recorded, together with their height, cover and biomass; all grass variables were paired. Collecting the same data in each subplot or quarter i.e. four or five per plot (if one sample is also collected at the center) did not yield different results. All grass sampling (biomass, cover and height (Table 3.1)) was conducted within the sampling unit of 0.5×0.5 m quadrats, constructed with a 5 mm steel rod. The sampling was done once at each plot, the quadrat was placed directly over the centre point as determined by random numbers or arbitrary purposeful distancing. Therefore, collecting one sample (*one quadrat sample*) at the centre of the PCQ plot yielded similar data as collecting five or four samples per plot with less effort. However, where the plots were 5×5 m squares (Giant's Castle site) the four plots were placed 1 m apart diagonally across the plot.

[2]The light trasmittance data as referred to here and used in this chapter is the same light trasmittance data that were collected for testing the hypotheses between trees and light, in Chapter Two

Table 3.1: Data sets used in this chapter, together with their sources, instruments and tools used to collect the emperical data.

Eco. variable	**Exp. Variable**	**Source**	**Instrument & Tools**
Light	%Light	Captured sky images of plots and GLA image analysis	D600 Nikon™ camera, Tripod, Spirit level, Fish-eye lens, GLA software
Grass Growth	Grass Height	Empirical observation	Notes, 1 m ruler, data sheets
Grass Connectivity	%Grass Cover	Empirical observation	Notes, data forms, Domin adaptation of the Braun-Blanquet cover scale
Grass Production	Grass Biomass	Empirical observation Destructive sampling	Black garbage bags, sickle, brown paper bags, 500 g scale
Species Composition	Species Names	Grass ID	Grass ID books, identification keys, specimens, magnifying glass

†ID = IDentification, GLA = Gap Light Analyzer, Exp. = Experimental, Eco. = Ecological

3.2.2 Sampling grass data

Placement of the quadrats used for grass sampling: In Chapter 1 Section 1.6 I discussed the study sites and sampling design where I explained that for my research question I needed to measure grass variables at the exact locations I measured light transmittance and tree density. Quadrats (0.5×0.5 m quadrat) were placed at the center of each PCQ plot sampled.

Sampling grass cover (%) in quadrats: Grass cover was estimated as the percentage of the quadrat that was covered by live grass only, recording percentage crown cover out of 100% (the whole quadrat).

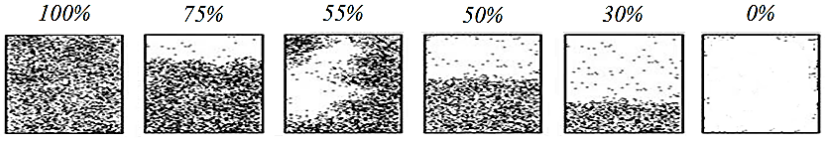


Figure 3.1: Example of recorded percentage grass cover in quadrats. Each square represents a quadrat viewed from above.

Sampling grass species dominance and composition in quadrats: The three most dominant grasses, based on their dry weight ranking ('tMannetje & Haydock 1963) were recorded in each 0.5×0.5 m quadrat.

Sampling grass Height (m): One value for mean grass height (also called "grass table height") in each quadrat was estimated using a measuring stick (improvision for a 2 m folding ruler). Since grass plants are not of uniform height, the relative height of grass within each 0.5 m quadrat was estimated and recorded in meters (Figure 3.2).

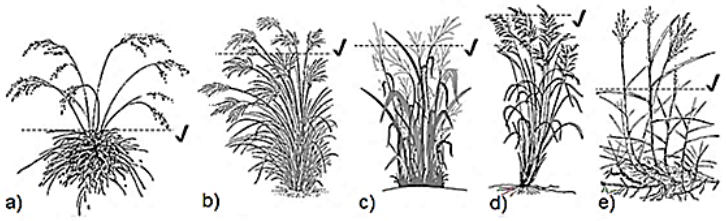


Figure 3.2: Diagram showing where grass height measurements were taken *a)* densely tufted grass with leaves concentrated at base, sending up only a few peduncles that carry closed drooping inflorescence *b)* Densely tufted grass leaves elongate slightly vertically and send up a moderately dense peduncle cohort open inflorescence. *c)* Mixed grass tufts with weakly tufted grass with broad leaves, late flowering with an early flowering grass, with short leaves that are concentrated at base. Only peduncles of the early flowering grass were considered. *d)* A weakly tufted and loosely-leaved grass with a vertically uniform foliage. *e)* A creeper that is more horizontally distributed.

Sampling grass biomass (g/m^2): All live plant material rooted within 0.5×0.5 m quadrants was cut at ground level, and together with undecomposed litter, collected and packed in 8l brown paper bags. Paper bags were marked with plot and site identification numbers — first three letters of the site's name and sequential quadrat numbers and plot. In the laboratory[3] grass was separated from, tree leaves, sticks and herbs in each brown paper bag. Grass biomass samples were oven dried for 42 to 64 hours at 60 to 70 ℃ (self regulating 10 ℃ flucuation). Large samples tended to maintain ostensible evidence of moisture after 42 hours when felt by hand and were as a result retained in the oven for another 12 hours before being re-examined for signs of moisture which if were present the sample was retained in the oven until the sampled showed no signs of moisture on examination, before reweighing.

Grass biomass values used for analysis were the mass of grass minus the weight of the brown paper bag. All grass data (grass biomass, cover and height) for each of the 169 plots from the 11 sites had corresponding light transmittance values.

Data on leaf length and leaf width of grass species were obtained from van Oudtshoorn (2012) and tabulated, against light transmittance values together with corresponding grass clades and photosynthetic pathway groupings according to the Grass Phylogeny Working Group II (2012).

[3]Grass samples that could not be dried at field sites were transported to the Council for Scientific and Industrial Research (CSIR) laboratory in Pretoria for drying and weighing by the author.

3.3 Data analysis

Exploring how grass biomass and cover change along a gradient of increasing tree cover: I assessed the relationship between grass biomass and light transmittance — *using pooled data for both variables* using linear regression models (`R`'s `lm` & `aov` functions `stats` package), and extracted the middle 80% interquantile range by fitting the 10^{th} and 90^{th} quantiles (`quantreg` package).

To assess variation in optimum light conditions of grass species: I made use of the presence data for my mean optimum analyses *i.e.* the records of plots where a grass species was recorded. In order to assess the light levels favoured by each species, I therefore extracted the median, the 75^{th}, and 25^{th} quantiles as well as the minimum and the maximum illustrating the confidence intervals of average light levels that were present in all the plots where each of the 16 most abundant grass species was recorded, to fit box and whiskers for each grass species.

Ascertaining the relationship between grass clades, grass characteristics, photosynthetic pathway groups and light conditions: I tabulated the 16 most abundant grass species into the grass clades and photosynthetic pathway groups following the grass portal ($http://grassportal.shef.ac.uk:8080/grassportal/$) and the ecological index method (van Oudtshoorn 2012). The regression coefficient least squares method was used by fitting a linear model to assess the proportion of the variance in light transmittance that accounted for changes in leaf width and length, to understand how these two key leaf characteristics change with increase in light transmittance.

3.4 Results

3.4.1 Relationship between grass biomass, cover and light transmittance

There was a decline in grass biomass (r^2=0.17, $F_{1,12}$ P =<0.0001) and cover (r^2=0.12, $F_{1,12}$=17.12, P <0.0001) with a decline in light transmittance (Figure 3.3 *a)* and *b)*). For both cover and biomass, the mean 10^{th} and 90^{th} quantiles increased with light transmittance, although more steeply for grass biomass than cover. Grass cover also had larger residuals than grass biomass. Both grass biomass and grass cover showed a negative relationship with light transmittance, but the evidence for a threshold response is stronger for grass cover than for grass biomass. Plots with less than <20% light transmittance still did have some grass — but never more than 100 g/m^2

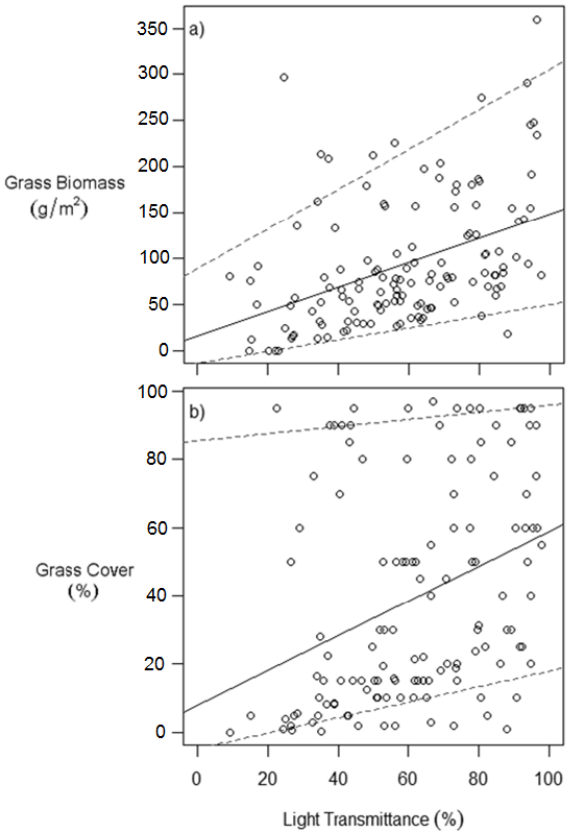


Figure 3.3: Relationship between light transmittance plotted against two of the grass variables grass biomass and grass cover. The black solid lines represents the modelled linear relationship between *b)* mean grass cover or *a)* mean grass biomass and mean light transmittance. The two dotted lines = 10th and the 90th quartile respectively.

3.4.2 Response of grass species composition to light transmittance

Non-grassy vegetation (sedges and herbs) was split to both sides of 80% light. Cyperaceae *spp.* had optimum light levels above 80% while herbaceous species generally had optimum light levels below 80% although the range was wide. Five grass species and sedges (Figure 3.4) had mean optimum light levels above 80% light (*Sporobolus africanus, Urochloa mosambicensis, Eragrostis curvula, Alloteropsis semialata* and *Tristachya leucothrix*) while the optimum was between 60 and 80% light for another six of the grass species sampled (*Melinis repens, Themeda triandra, Digitaria eriantha, Eragrostis plana, Brachiaria nigropedata* and *Enteropogon macrostachyus*) and below 80% light transmittance for others (*Panicum maximum, Hyparrhenia hirta*). Two species had an interquantile range that spanned below 40% light (*Brachiaria nigropedata* and *Panicum maximum*) while *Eragrostis curvula* had its entire interquantile range above 80% light (Appedix B.2). Overall there was a significant difference in light preference amongst grass species ($\chi^2 = 76.228$, $DF = 38$, $P = 0.00023$, Kruskal-Wallis rank sum test).

Only *Brachiaria nigropedata* had optimum light below 80% but had a positively skewed mean. Therefore, these grass species can be classified into three categories 1) species whose median values are always above 80%; 2) species whose median values are below 80% but distributions still skewed towards high light (*Eragrostis plana, Digitaria eriantha, Themeda triandra*); and 3), species whose distributions are below 80% light.

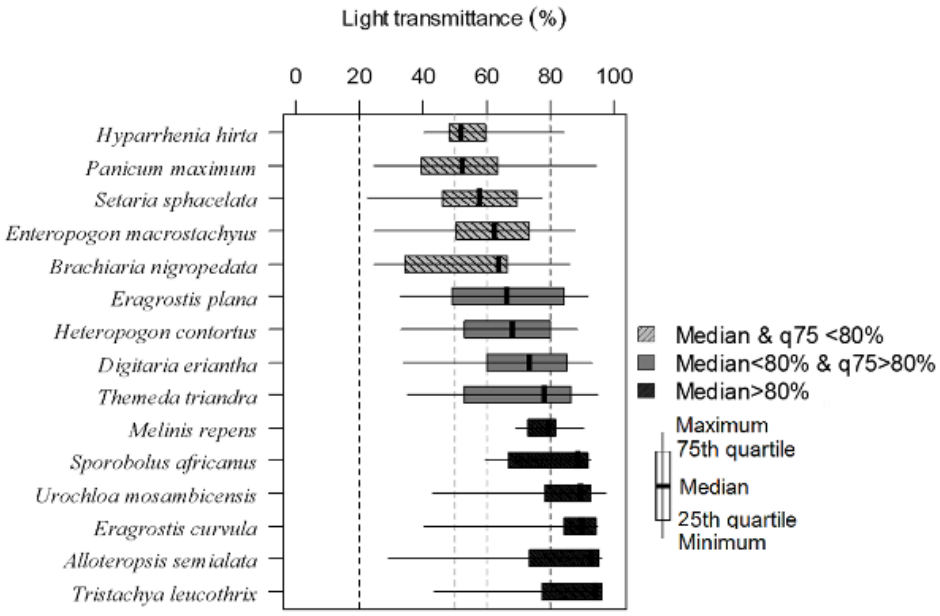


Figure 3.4: Distribution of grass species along the light transmittance range, with the median light level for each of the 16 most abundant grass species in the study indicated by the bold line that is inside each of the horizontal boxes, the size of each horizontal box is determined by the interquartile range (75^{th} and 25^{th} quartiles) which delineates the middle 90% of the values of the light transmittance data about the mean. The horizontal lines that extend through the horizontal boxes show the range of each species (maximum to minimum light) under which each of the grasses were encountered.

3.4.3 The relationship between light and grass traits

The different grass species were classified according to different phylogenetic orders and according to physiological and ecological differences in order to assess if there is a classification that can be associated to the order in which grass species preferred light. Photosynthetic pathways and anatomic groups did not show any association to variation in light preference. Leaf length increased (r^2=0.21, SE=154.4) and leaf width declined (r^2=-0.24, SE=1.221) with increasing light transmittance (Figure 3.6). In sampled grass communities the maximum grass width ranged between 1 and 20 mm, while leaf length ranged between 150 and 800 mm.

Based on the difference between the r^2 values; the relationship between leaf length and light was not as strong as the relationship between light transmittance and leaf widths, but since this difference is very small and the p-values have a difference of 1, we can accept the relationship between light transmittance and leaf length based on its ecological significance. Minimum leaf width is reached around 40% light transmittance. While the maximum leaf length was only reached once the light transmittance has reached levels

above 90%. Decreaser species prefer lower light conditions than increaser species do (Figure 3.4 & 3.5). Grass species with open leaves prefer lower light conditions than grass species with folded leaves (Figure 3.5). Climax species prefer lower light conditions than subclimax species but pioneer species prefer more light than both species categories (Figure 3.4 & 3.5).

Grass species that prefer lower light conditions are more likely to have open leaves, high grazing value and be climax species in communities where they occur. The relationship of leaf width and light transmittance (Figure 3.5) is stronger ($F_{1,15}$=4.823, P<0.05) than the relationship between leaf length and light transmittance ($F_{1,15}$=4.048, P=0.06).

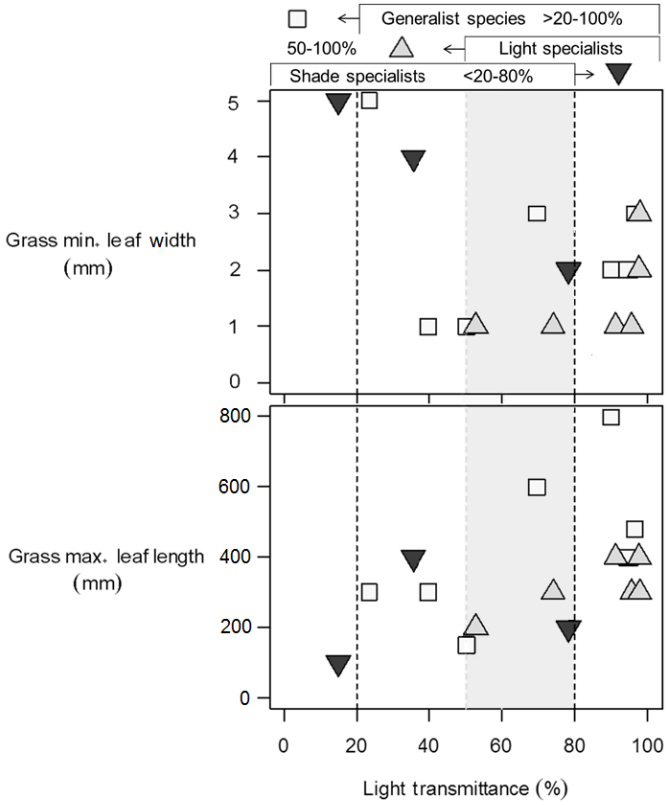


Figure 3.5: Relationship between light transmittance and grass leaf length and width. Increase in leaf length and decline in leaf width along a gradient of increasing light transmittance. Each data point represents a species from each of the grass species listed in figure 3.4. Values for each species are averaged value from many individuals of the same species.

3.5 Discussion

3.5.1 Grass growth and light

My results indicate that an increase in woody canopy cover — through decreasing light transmittance; can have an impact on the biomass, cover and species composition of grass in the understorey. Despite large variability in grass biomass, both biomass and cover declined as light availability declined, but the pattern was stronger for cover than for biomass and much weaker for grass height. The reason for the weaker pattern for grass biomass is that there were plots that had very high grass biomass values at low light transmittance levels, which created high residuals that weakened the positive response of grass to light *e.g.* when a quadrat lands over a large tuft a large value of grass biomass gets recorded.

Fuel loads below 200 g/m^2 tend not to carry fire (Govender *et al.* 2006, Schultz 1988, Thonicke *et al.* 2001, Trollope 1984). Moreover, theory predicts that fires should stop spreading when less than 40% of the landscape is flammable (Turner *et al.* 1989, Archibald 2010). Maximum grass biomass drops below 200 g/m^2 at around 20 - 30% light transmittance, and it is at this value that maximum grass cover also drops below 60%. The light transmittance of 20% is likely to be a critical threshold for fire spread. Accordingly, since grassy cover clearly drops below 40% at light transmittance levels below 20% — percolation theory predicts that fires should struggle to spread below 40% cover (Turner *et al.* 1989, Weber 1991, Archibald *et al.* 2012). My data showed that some grasses can grow below 20% light. This finding agrees with Winter *et al.* (1982) who showed that *Microstegium vimineum* was a shade adapted C4 plant that can grow under 5% of full sunlight, although Barden (1987) later showed a 17% reduction in *M. vimineum* growth to be associated with 5% full sun.

However, Hoffmann *et al.* (2012) demonstrate that it is not only fuel load that prevents penetration of surface fires into closed canopies. The fuel moisture content and weather conditions are also likely to change, — where less wind and moist fuels reduce fire spread probability (Trollope & Potgieter 1985, Rothermel 1983). Although I did not consider meteorological data, I would expect higher fuel moisture, high N and low SLA in areas where light transmittance is low. As light transmittance decreases to 40%, grass species like *Panicum maximum* and *Brachiaria nigropedata* dominate, and these grasses have characteristics such as high N and high SLA; characteristics that lead to moist fuel or fuel that decompose quickly before other grass species in their immediate habitat locality dry-up; that, as a result, would smother fire.

Therefore, my data supports the assumption that 20 – 30% light transmittance does represent a threshold where grassy fuel properties change to ones that no longer promote fire although grass is present below this threshold. From Chapter 2 it is clear that the tree density at which this amount of light is transmitted varies greatly between different tree species. Ludwig *et al.* (2004) also noted that the productivity of the herbaceous layer is higher under large trees than under small trees.

Tree species like *V. karroo*, *M. serrata* and *C. apiculatum*, limit a lot more light than tree species like *T. sericea* or *V. grandicornuta*. Although it should be mentioned that because of canopy gaps grass species that preferentially grow under high light may occur because canopy gaps let in lots of light. Much stronger relationships with light were found for grass cover than for height (insignificant result not presented), both of which showed a strong threshold response at around 20% light transmittance as predicted by the literature (Sage 2004). The thresholds for biomass data are not as explicit as cover and height data, and it could be because forbs were excluded.

3.5.2 Response of grass species to light

The grasses sampled at my study sites varied widely in their preferred light levels. The variation in the relationship between grass biomass and light transmittance across sites suggested that a different factor is creating variation at site level.

As a result, grass species that are growing at each of the sites are different along the light range of each site (Figure 3.5), as expected. Species with wider leaves, low nitrogen content and low ratio of wet to dry leaves were mostly Category 1 species (Figure 3.5), while species with high ratio of wet to dry leaves, high nitrogen content (*as previously mentioned*) and high ratio of wet to dry leaves were mostly Category 3 species (Figure 3.5). The *Andropogonoid* family predominantly fell into Category 1 (Figure 3.5) while Category 2 was dominated by the panicoid family (Figure 3.5 & Appedix B.2).

More C3 grass species fell into Category 3 than two and one which were dominated by C4 grass species. Forbs and *Oplismenus hirtilis*, which are C3 species, do better at lower light as expected from the literature (Ehleringer *et al.* 1997). In addition, all *Andropogonoids* seem to favour high light as expected from the literature (Bond 2008). Species that have the same characteristics could be from the same clade or family (Appendix B.1) because these species evolved from the same lineage (Clark *et al.* 1995). What this lineage relationship means for fire is that, a switch in grass species that results in a switch from andropogonoids to panicods or C4 to C3 grass species also corresponds with a switch to less flammable species. This result supports one of the functional-based mechanisms

predicting that competition for light can lead to diversity loss (Yang *et al.* 2015).

The high variance in the relationship between light transmittance and grass biomass was possibly due to differences in characteristics of grass species growing at different sites. Some of the selected sites were grazed, although site selection did not avoid termites no infestations were noted.

The soil was sampled at each of the plots and personal observations confirmed that the soil was not very variable along each transect while the turnover in grass species composition showed rapid changes. There were rapid changes in grass species composition along the various transects sampled associated with changes in light transmittance.

The high variance in the relationship between light transmittance and grass biomass may be caused by variation in grass species that are growing at the different sites. When the composition of grass species on a landscape changes because the amount of light that reaches the understorey has changed; the potential of the landscape to produce biomass can also change. Since different grass species prefer different levels of light for optimum growth, and each grass species is assisted by its leaves to persist at its optimum light range (Tilman *et al.* 1997, Ludwig *et al.* 2004, Fynn *et al.* 2011).

When light levels change, to persist under shade grass species have adopted wider leaves; while narrow, long leaves will prevent overheating yet provide enough surface area to achieve high photosynthetic activity under full sun. In each case (under shade or full sun) grass species without leaves that allow effective light capture under a given light level, will be replaced by species that can use available light levels effectively; imposing a differencing on the composition of grass characteristics that are responsible for light capture, like grass leaf width and leaf length of a landscape, as incompetent grasses become rare. As the proportion of grass species that can maximise light capture under shade by having broader leaves increases, indirectly a landscape's biomass production declines and *vice versa* when the proportion of species that can minimise photo-inhabitation in full sun dominate.

In this view of biomass, light interaction, soil conditions at different sites, variation in defoliation by large herbivores and termites, are not disregarded as possible sources of variation. These confounders do not demerit this view. Where selected sites exhibited signs of defoliation; defoliation was assessed and soil samples collected, as done in this research. Moreover, although site selection did not set out to avoid termites, none were noted. Moreover, although not analysed, soil samples were collected using a soil auger and personal observations and notes on soil colour, texture, depth and organic matter were made. Therefore, I submit that the variation in grass species composition under tree canopies is more likely to be due to light than soil moisture and nutrients.

We can see (Figure 3.5) that some grass species occupy a wide range of light conditions (20 – 100% light transmittance) and as such I term these grasses 'generalist species'. These generalist species include forbs and *Urochloa mosambicensis*. Although not true generalists, *Panicum maximum* and *Seteria sphacelata* can occur under a wider range of light transmittance conditions. Grass that is adapted to low light conditions (< 20%) comprise very few species (5); whereas, the majority of grass species (10) find optimal light conditions between 50 – 80% light transmittance (all grass species sampled, grey-shaded area in Figuer 3.5). This optimum light level is supported by published work (Man & Lieffers 1997). At high levels of light (> 80%) grass with high standing biomass dominates (Fynn *et al.* 2011).

Fynn *et al.* (2011) also support that grass traits drive the response of grass species to light but highlight that traits have a weak explanatory power to describe the interaction between effects from light response and effect form competition across species unless traits that relate to light capture such as leaf length and leaf width are incorporated as these leaf traits show strong competitive responses, to light and competition across grass species.

Since grass that grows in the shade has wider leaves, this widening of leaves could suggest that shade grass prioritises maximising light capture by increasing leaf area. Similarly, the grass that grows in the light could be limiting light capture by limiting leaf surface — to avoid photo-inhabitation. However, because the leaves of grass that grows under full sun are also longer in addition to being narrow, this narrowing of leaves could suggest that grass species that grow in full sun can still have a considerably large leaf area but one that does not maiximise light capture.

Shade tolerance would not be rewarding when nutrients are limiting. The current study shows how shade tolerance relates to increasing leaf area. By producing wider leaves, through investing less dry matter per unit area of leaf surface thus spreading leaf material wider, genera like the *Panicum*, can maximise light capture and grow at low light levels. But for grass that grows full sun, like *Andropogonoids*, investing limited resources (water and nutrient) on capturing an abundant resource (sunlight) would be un-rewarding.

Areas with potential to become forest will quickly gain precursors of woody plants, like ferns and forbs, and eventually become populated by woody plants quicker in over and under utilised landscapes.

It is noteworthy that *Hyparrhenia hirta* and *Eragrostis chloromela* were recorded under mean light conditions much lower than would be expected; these grass species usually grow under full sun (personal observations). In addition, it is now known that grass of the same species can have different responses to light when growing in different environments

e.g. Themeda triandra in the Eastern Cape grasslands around Tsolo and Maclear and areas of the Drakensberg alpine is a short and small-tufted; yet *Themeda triandra* from the Limpopo, Mpumalanga and Gauteng provinces tends to be taller with larger tufts (personal observation).

Ludwig *et al.* (2004) oppose this light hypothesis, asserting that changes in grass species composition when trees increase in density are caused by changes in soil nutrients rather than changes in soil moisture or light availability. However the authors do not infer their conclusion from analyses of light and soil moisture content data, although these variables are confounders in their experiment, instead they use association of changes in soil nutrients and species composition alone.

Even though under canopy environments; under bush and large trees, a different suite of grass species from outside tree canopies fundamentally suggests that light and moisture are also evolved.

Moreover in my research grass biomass at some sites was higher outside of tree canopies than on plots that are under tree canopies (Appendix B.3) this differencing in production across sites caused high variability of grass biomass data when pooled across sites. Ludwig *et al.* (2004). As in the current study, Ludwig *et al.* (2004) found a similar response for the genus *Vachellia* (previously *Acacia*). As at my *Eucalyptus grandis*, *Vachellia karroo*, *Combretum apiculatum* and *Euclea divinorum* sites, Ludwig *et al.* (2004) noted that, under large trees and the *Euclea divinorum* species, grass species such as *Cynodon* and *Panicum* species dominate probably mainly due to high soil nutrient concentration, because these grass species typically occur on fertile soils.

However, literature does not fully support that grass species that do not occur under tree canopies are avoiding nutrients. Furthermore, literature does not adequately dismiss that light is a primary driver of variation in grass species composition that filters outside all grass species that do not have shade tolerant traits (personal observations).

3.6 Conclusion

I used grass cover, biomass and height to assess if grass becomes limited at 20% light transmittance. The relationship between grass biomass and light transmittance showed large variance. Plots of the relationship between light transmittance and two drivers of grass biomass, grass cover and height showed the grass cover could explain the changes in grass biomass better than grass height.

In addition, between 80% and 100% light levels, grass reaches its maximum mean biomass

and beyond 30% to 40% light, grass biomass starts to level off. This suggests that grass species that preferentially grow under high light condition consistently produces high grass biomass. Since the quantity of biomass that each of the grasses produce is different, this differencing suggests that a change in grass compositons will result in a change of grass biomass.

The most important result of this chapter is that grass species respond differently to different light transmittance levels and this differencing in light response is due to the characteristics that each possess, resulting in some species having better tolerance of shade than others species.

In the assesment and quantification of changes of grass species composition in relation to light availability, grass species that were found along the gradients of light transmittance varied in response to light. These grass species showed three general patterns: species that preferentially grow under low light, those that preferentially grow under intermediate light and those that preferentially grow under high light.

Light transmittance of 60% is thus proposed as the optimum light level for grass growth. The light transmittance between 30% and 70% appears to be optimal light for most grass species in the South African savanna. This optimal light can be observed from the high number of grass species that thrive at the 30 – 70% light range, as well as the decline in the variance of grass biomass data in this light transmittance range.

I conclude that an increase in shade conditions may change species composition from grass species with narrow long leaves that are specialised to survive in full sun to grass species with wide short leaves that are specialised to survive in low light conditions. The rate of decline in grass biomass depends on the response of grass species to light. Response of grass to light is driven by the response of grass traits to light. A decline in sunlight at the understorey of trees reduces grass biomass, cover and height, showing a threshold response.

Chapter 4

Conclusion and Synthesis

Throughout this dissertation, I show how bush encroachment is a critical challenge which global projections indicate will increase into the future due to concerted changes in rainfall and fire frequency as well as increasing atmospheric CO_2 that is associated climate change. Elevated CO_2 is predicted to increasingly be the main driver that is tipping the tree-grass balance in savannas in favour of woody vegetation, an action that exacerbates bush encroachment even in frequently burned open savannas.

Changes in response to CO_2 may result in major biome shifts in favour of savanna over forest or the opposite way. For example, recent work suggests shifts of the Amazon rain forest to savanna due to risk of severe drying (Phillips *et al.* 2009), or similar opposite examples of encroachment from around the world (Loehle *et al.* 1996, Bowman *et al.* 2001, Favier *et al.* 2004, Goetze *et al.* 2006, Mitchard *et al.* 2009). To understand this shift in biomes better we need to understand the threshold dynamics of the system, and in particular, the tree densities at which important functional changes occur — like the loss of the grass layer, or switches to different grass functional types, which I addressed in this dissertation.

In the body of this dissertation I further demonstrate why investigating the distribution and coexistence of trees and grass is a formidable intellectual challenge. Particularly, because savanna vegetation is defined by dynamic interactions, among drivers of tree cover and grass cover. I substantiate that understanding whether different tree species transmit different levels of light, and whether different light levels support different grass species can explain how the other side of the fire feedback works, [1] a pespective which is least represented in literature, but yet closes knowledge and scientific gaps besides having socioeconomic implications[2]. I broadly hypothesized that trees can limit fire, by limiting

[1] the side on how trees limit fire as opposed to how fire limits trees
[2] Used here to refer to social as well as economic implications

the amount of light that reaches the ground, thus, retarding grass biomass and cover, and therefore fire. I then address this hypothesis in two chapters.

First I assessed how different tree species limit light at different densities (Chapter 2), and then I investigated how grass characteristics respond to decreasing light availability, and explored the light tolerance thresholds of different grass species (Chapter 2).

A key finding of Chapter 2 was that there was a 10% decline in light transmittance for every 3.8 m decline in mean PCQ distance (750 tree/ha) and every 7% increase in tree canopy cover average, but this relationship is non-linear. I identified a mean PCQ distance of 3.5 to 4 m, equivalent to tree density of 1500 to 800 trees per hectare as the threshold where light becomes limiting in general. Only when trees become very dense ($> 90\%$ tree cover or PCQ distances < 1.5 m) did light transmittance drop below 20%. However, because of the differences in their architectural and leaf level characteristics, these relationships were different across the 11 tree species that I studied, with slopes ranging from -30.02 to 89.39.

Phenology, leaf angle and tree height appeared to be the most important traits controlling this variability. Several tree species, with fine leaves held at vertical angles, never reduced light below 20%. In general tall species transmitted more light than short species, and vertically angled leaves transmitted more light than horizontal leaves, and simple leaved species transmitted more light than compound leaves.

It was surprising to discover that gaps within a canopy can override all the traits that confer low light transmittance, and enable high light transmittance. Thus leaf clumping is an important characteristic. I explored the impacts of these findings on the grassy understorey in Chapter 3. Grass biomass declined with decreasing light transmittance but no clear thresholds were apparent from my data. In contrast, there is a threshold of 30% light transmittance below which grass cover is reduced to close to zero. I identified three different groups of grasses: those that require high light and are never found at $< 80\%$ transmittance; those which require low light and are never found at $> 80\%$ light transmittance; and, species which bridge this range. However, no grass species persisted well below 30% transmittance. A key finding was that grass that specialises in growing in shade also carries characteristics that do not support high grass biomass production and cover.

Trees species that limit more light have a fewer number of understorey grass species that can be nested under their canopies than tree species that allow more light; creating variation in understorey grass species composition across tree species. Understory

(*the page number is centered for the first page of this chapter.*)

vegetation differs across all the sampled tree species. A key synthesis of these two chapters is that species that preferentially grow in the shade that dominate the understorey of trees that limit a lot of light generally have characteristics that may negatively affect fire spread.

Synthesising the results from these two chapters, it appears that the theoretical prediction that tropical grasses (mostly C4) should not persist below 20% transmittance is upheld — and my data suggest that 30% transmittance is perhaps a more appropriate threshold. Moreover, as these shade-tolerant species are not likely to be very flammable, the threshold where fire would be prevented from spreading might be higher than what biomass and cover suggest — although it was beyond the study scope to test this hypothesis[3]. Once tree canopies are thick enough to cut out 70% *i.e.* 100 – 30% light then, runaway bush encroachment/conversion to forest is likely; as the positive feedbacks with a grassy understorey keeping tree seedlings down will no longer be evident.

Using data from Chapter 2 I can determine where the threshold where grass stops growing is for the tree species that I studied. It varies from $\sim$ 5000 trees per ha to $\sim$ 3000 trees per ha. *Eucalyptus grandis*, *Vachellia grandicornuta*, and *Terminalia sericea* never reach densities that cut out more than 30% light (Figuer 2.7). Some grass species like those from the *Cynodon* genus seem to be least affected by the allelopathy of the *Eucalyptus grandis* species. However, *Vachellia karroo, Euclea divinorum*, and *Spyrostachys africana* often achieve densities which would prevent a grassy understorey.

4.1 Applications of this work and implications

This dissertation therefore provides a framework to assess which are likely to be the most problematic bush encroaching species (*Vachellia karroo* rather than *Terminalia sericea* for example) and allows managers to focus their attentions on the species which are more likely to result in system switches, and on the tree densities which are most at risk of switching.

This work also has implications for understanding differences at continental scales in the location of the forest-savanna boundary: savannas in Africa and Australia have very different dominant tree species, and my work indicates that *Eucalyptus* (an Australian species) transmits far more light than most African species. This high light transmittance might help to explain why savannas dominate over forests in high-rainfall savannas in Australia, whereas the opposite is true in Africa (Lehmann *et al.* 2011). For example,

[3]Testing this hypothsis would need the same tree species to be sampled across different sites and those sites would have to be similar in grass species composition

mean PCQ distance can be used to test recommendations for thinning before implementation of recommendations. Using results from this work it is possible for management to understand the species of grass that are likely to be encouraged by different levels of thinning or increase in woody plant cover, for specific tree species.

For mixed stands, the information on which traits result in increased light interception can be used to infer the relationships between tree density and grass growth.

Mean PCQ distance can be used to test recommendations for thinning before recommendations can be implemented. Using results from this work it is possible for management to understand the kinds of grass that are likely to be encouraged by different levels of thinning or increase in woody plant cover, for specific tree species. For mixed stands, known algometric relationships between various variables and light can be multiplied by the relative abundance of the respective tree species at a site in order to aggregate the effect of the differences on light transmittance and develop precise interventions in mixed stands.

Given that the impact of canopy cover in limiting light transmittance and changing grass composition, biomass, and cover is so important it is recommended that canopy cover must be incorporated in most long term monitoring because it can be an early warning proxy for changes in primary production and fire regimes, especially in savanna management. Given the difference noted in the grass species in the understorey of different tree species, the successional changes at stands of different tree species cannot be expected to follow the same pattern. It is therefore recommended that site-specific approaches and interventions are necessary when managing bush encroachments.

4.2 Key challenges

Mixed modelling could have been an approach that could have accommodated the noisy nature of grass biomass data but it was also beyond the study scope. A challenge during this research was availability of grass flammability data. This challenge limited the result from providing a clear account of the impact of grass traits on fire occurrence and spread.

4.3 Further research

Therefore, future research on these flammability traits is recommended. This research would include lighting fires to test if flames would burn into canopies of different tree species in order to understand if the grass species that are growing under the different tree

species are able to carry high enough fire flames or whether the fire would burn at all under tree canopies.

Another potential research that could be derived from my study, on the section that tests whether mean PCQ distance is a tree species trait is work that includes repetitive purposeful sampling of mean PCQ distance (on different stands of the same species) and an assessment using an adjusted approach of preparing mean PCQ distance data and using data imputation to cover the whole range of possible mean PCQ distance values sampled directly and improve the distributions of mean PCQ distance data. Furthermore, this would test whether indeed some species have narrow ranges despite efforts to make them similar.

Appendix A

Poaceae subfamilies, tribes & photosytheticpathways

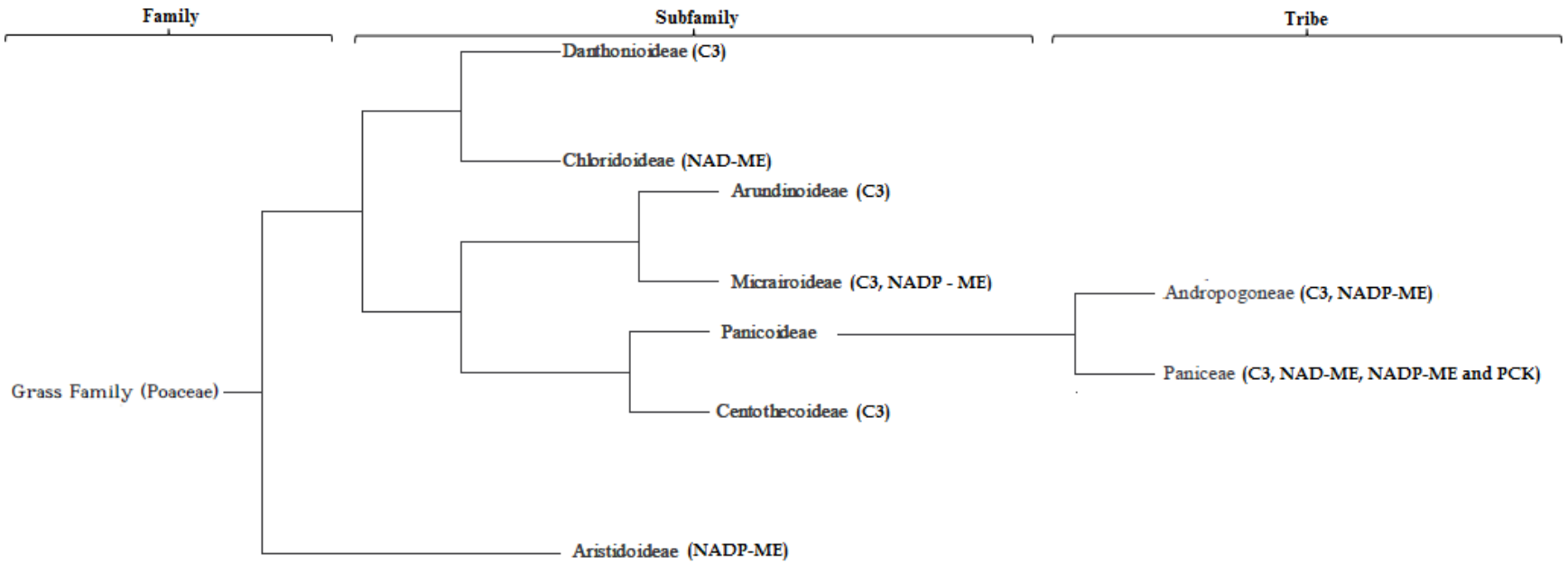


Figure A.1: The representation of photosytheticpathway evolution in grasses (sensu Grass Phylogeny Working Group 2001) across the PACMAD (*Panicoideae, Arundinoideae, Chloridoideae, Micrairoideae, Aristidoideae* and *Danthonioideae*) clades (Sanchez-Ken *et al.* 2007, Ripely *et al.* 2010b).

Appendix B

Response of grass species along the light gradient

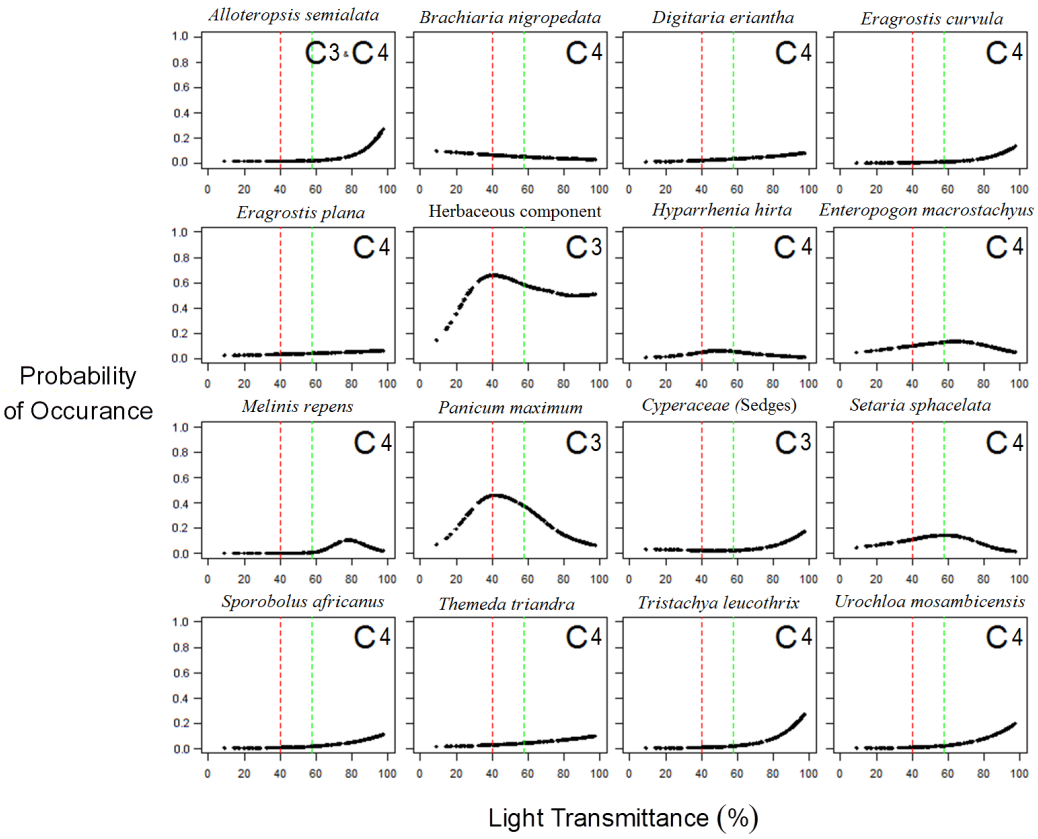


Figure B.1: Panel plot, showing the probability of occurrence of grass species – that were present in at least five plots in the whole study, along the light transmittance gradient. Light transmittance was measured with a hemispherical camera and image analysis. Probability of occurrence was derived from a logistic model of presence/absence data *vs* light transmittance. Grass species have peak probability of occurrence at different positions along the gradient of light transmittance. The lines indicates the points of modelled intersection between each probability of average light transmittance value (%) at each plot and corresponding paired value of probability of occurrence as calculated from presence absence data.

Appendix C

Response of grass biomass along the light gradient

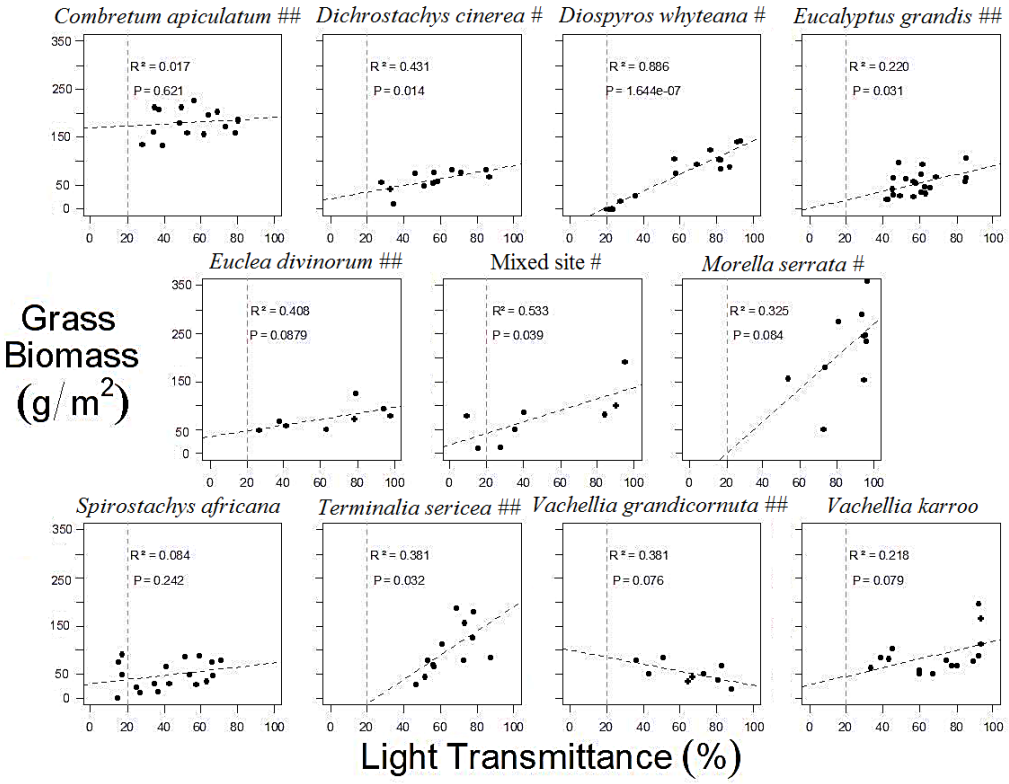


Figure C.1: The sites with the symbol # are sites where there were some signs of light grazing from game but no domestic livestock while sites with the symbols ## are sites where there was a fence structure built to completely exclude grazing. The dotted vertical lines represent the 20% light transmittance threshold below which grass biomass is expected not to occur. Grass biomass was obtained by weighing grass that was harvested from within 0.5×0.5 m quadrats after drying it. The light transmittance data was obtained from analysing hemispherical images. The symbol (•) represent data points where light transmittance values (%) for each plots corresponds with paired values of grass biomass (g/m^2) at each of the seampled plots.

Chapter 5

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