

Thicket Expansion in a *Vachellia karroo*- Dominated Landscape and its Effect on Herbaceous Communities

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Where leaders learn

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ABSTRACT

Grass and forb species found in savannas are highly diverse, contributing to the structure and function of the savanna system. Where mean annual rainfall is seasonal and high enough to support closed canopy vegetation such as forests or thickets, savannas can exist as an alternative stable state maintained by disturbances such as fire and browsing. Biotic and abiotic processes act on savanna and forest (or thicket) systems maintaining both their tree and herbaceous cover at levels that ensure their persistence in those states. Studies have shown that many semi-arid rangelands in South Africa have undergone a rapid increase in tree cover (of both native and non-native species) over the past several decades. This process of increasing tree cover in semi-arid savannas, termed bush encroachment, results in a biome shift, changing landscapes that were once grasslands with few trees to ones dominated by broad-leaved trees with fewer sun-adapted forbs and grasses.

The aim of this study was to investigate the impact of changing woody cover and its associated changes in tree composition, tree canopy structure, light dynamics in the understory and herbaceous community composition on Endwell farm in the Eastern Cape. Canopy cover changes between the years 1949 and 2019 were analysed at 51 sites on the farm and related to historical rainfall patterns. There had been a general increase in tree cover over the past several decades on the farm, and many sites showed a change from open (0-15%) in 1949 to low (16-35%), moderate (36-50%) and high (51-100%) canopy cover in 2019. In earlier years most sites had a canopy cover below 50%, and the higher canopy cover values (> 65 %) occurred in more recent decades. Canopy cover of ~ 50% was found to be rare in each decade. This suggests that ~50% canopy cover maybe a transient, unstable state. The period with the highest rate of canopy cover increase was 2002-2013, and this increase coincided with a high mean annual rainfall 10 years prior to 2002 and a high mean annual rainfall in most years between the 2002-2013 period. The period between 2002 and 2013 also had the highest number of sites transitioning from lower to higher tree canopy cover classes, indicating that rainfall may have been a factor driving bush encroachment during the past several decades.

An increase in canopy cover (a decrease in light transmittance) was accompanied by changes in woody species composition during thicket formation. The low canopy cover (high light transmittance) sites were dominated by *Vachellia karroo* and *Scutia myrtina* trees, while high tree cover sites had fewer *V. karroo* and *S. myrtina* trees and were rather characterised by an abundance of thicket tree species. Species proportion, NMDS and dendrogram plots indicated that sites with a light transmittance range between 50-100 % had similar tree species

compositions, different from sites with light transmittances <50 %. An increase in tree density was strongly correlated to an increase in canopy cover (from 2019 satellite imagery), density of trees > 3m, maximum height reached by trees, diversity of trees, total canopy volume, total canopy area and leaf area index (LAI), and a decrease in light transmittance. A structural equation model (SEM) was used to explore the relationships between canopy characteristics (maximum canopy area, canopy volume, tree diversity, density of trees, density of trees >3m, individual trees and maximum canopy height), aerial canopy cover in 2019, and light transmittance. The model explained 73 % of the variation in light transmittance, mostly via the direct effect of canopy characteristics. Canopy characteristics had a strong influence on both aerial cover in 2019 and directly on light transmittance, but canopy cover in 2019 had a weak influence on light transmittance.

The herbaceous layer was rich and dominated by C₄ grasses such as *Eragrostis plana*, *Sporobolus fimbriatus*, *Themeda triandra* and *Digitaria eriantha*) and forbs including *Hibiscus aethiopicus*, *Helichrysum dregeanum*, *Helichrysum nudifolium* and *Gerbera viridifolia* at low canopy cover sites with high light transmittance. In contrast, high tree cover sites had fewer herbaceous species in general. Grass and forb species characteristic of these sites high canopy cover sites were *Panicum maximum*, *Loudetia flavida*, *Pellaea viridis* and *Cyperus* spp. Different sites with low light transmittance (< 50 %) had similar herbaceous species composition. Basal cover, richness, abundance and diversity of herbaceous plants decreased significantly with an increase in tree density, density of trees >3 m, canopy volume, canopy area, canopy cover, LAI, and increased significantly with increasing light transmittance. Most grasses had their highest densities at LAI < 0.5, which was estimated to correspond to ~75% light transmittance and ~38% canopy cover and then started to decline thereafter. Herbaceous species basal cover was also highest at LAI < 0.5. An SEM model indicated that herbaceous diversity, basal cover and richness responded both to light availability and to the structure of the woody vegetation directly ($R^2 = 0.53$). While the effect of light transmittance on herbaceous communities was strong (0.41), there was little difference between the effect of light transmittance and canopy characteristics (-0.35) on herbaceous communities.

Two possible threshold points, relating to two types of transitions in vegetation structure, could be deduced from this study. The first threshold occurred at canopy cover ~ 40% (LAI < ~ 0.5, light transmittance ~ 75%), at which point many of the common herbaceous species, including the dominant C₄ grasses, began to decline in abundance while the composition

remained characteristic of the savanna state. A canopy cover of less than ~ 40% at a site provides a suitable state for a high abundance of grass and forb species which help maintain an open system by facilitating fires. The second threshold marked a compositional shift between savanna and closed-canopy vegetation states. Savanna species (trees, grasses and forbs) dominated at high light transmittances (>50%) and were significantly reduced at low light transmittances (< 50%), indicating a possible species composition threshold at ~50% light transmittance at which a savanna state switches to a thicket (LAI ~ 1 and canopy cover ~70%). This point indicated the point where there was a significant difference in both tree and herbaceous plant compositions, with a marked reduction in the occurrence of C₄ grasses at light transmittance < 50%. Fire is suppressed when the C₄ grass layer is lost, and further thicket encroachment will take place causing complete canopy closure. Land managers in this system should start becoming concerned about a reduction in grass biomass when canopy cover reaches about 40% and would have to reduce tree cover before the threshold of 50 % light transmittance (70% canopy cover from aerial photos) is reached to maintain a savanna system.

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DECLARATION

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



MARINA KHOZA

I certify that the above statement is correct.



Prof. S. VETTER

Supervisor

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Chapter 1

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1.1. Literature review

1.1.1. The state of open ecosystems

Savannas and grasslands are open ecosystems that exist throughout the tropics, in all continents, and encompass a wide diversity of both abiotic and biotic characteristics, floristic composition, and vegetation history (Solbrig, 1996; Bond & Parr, 2010; Veldman, 2016). Savannas are often described as ancient ecosystems that have a continuous layer of graminoids (grasses and grass-like plants) which dominate the herbaceous stratum, forbs and a discontinuous layer of trees or shrubs (Scholes & Archer, 1997; House *et al.*, 2003; Bond & Parr, 2010; Veldman *et al.*, 2015b; Veldman, 2016). Grasslands and savannas take up 20% of the earth's terrestrial surfaces (Scholes & Archer, 1997), contributing to the world's economic, environmental, and cultural value (Parr *et al.*, 2014). Trees in these environments are usually fire tolerant and vary in density from overly scattered individuals to closed woodlands (House *et al.*, 2003; Sankaran *et al.*, 2005). Tree cover in savannas can change rapidly over a few years in response to rainfall or drought events, herbivory, fire (Roques *et al.*, 2001; Bond, 2008; Midgley *et al.*, 2010) and rising CO₂ levels (Bond & Midgley, 2000; Bond *et al.*, 2003; Kgope *et al.*, 2010; Buitenwerf *et al.*, 2012). In some arid regions (with mean annual precipitation (MAP) < ~ 650 mm) that do not experience frequent fires; climate or herbivory may be responsible for their persistence (Sankaran *et al.*, 2005; Bond, 2008; Hirota *et al.*, 2011; Staver *et al.*, 2011a, 2011b). Although savannas appear deprived of trees, they have existed for millions of years, accommodating a large number of animal and plant species that are not seen in any other biome (Ratnam *et al.*, 2011; Veldman, 2016).

1.1.2. Savannas and forests/thickets as alternative stable states

More than one possible vegetation state is presented by the alternative stable theory for a given set of environmental conditions. States are controlled by positive and negative feedbacks in the form of climate conditions, fires and other factors that are known to

contribute to maintaining each vegetation state (Staver *et al.*, 2011a). The understanding of tropical forests or thickets and savannas in mosaics was first explained using the successional state theory (Thomas & Palmer, 2007; Bond & Parr, 2010). The assumption was that these open landscapes suitable for grasses to grow were a result of human disturbance and that natural grasslands would only occur when climate and soils excluded forest trees. This held that successional grasslands would transform back to forests unless disturbances such as fire and herbivory acted against them (Bond & Parr, 2010). The successional concept cannot explain early successional vegetation that has existed for millions of years (Bond & Parr, 2010).

Recently, forests have been invading grasslands, rather than grasslands invading forests (e.g., Delegue *et al.*, 2001; Burbridge *et al.*, 2004). This suggests that both savannas and forests can displace each other if environmental conditions change to suit either state. The state will persist when positive feedbacks promote the necessary environmental conditions to maintain it, while impeding the other from developing (Bond & Parr, 2010). Savanna tree species grow slowly and are limited by their intolerance of shade when recruiting in forests (Azihou *et al.*, 2013), but forest seedlings struggle with the drier soils and microclimate in the open savanna habitat. Soils in forest floors are moister and closed canopies limit grassy fuel loads and thus prevent fire (Hofmann *et al.*, 2009) from occurring.

It is now widely understood that savannas and forests are alternative stable states where more than one stable state is possible for a set of environmental conditions (Scheffer & Carpenter, 2003; Warman & Moles, 2009). Whether tree cover responds smoothly to environmental stresses or shows sharp transitions between binary stable states at tipping points is not fully understood. The fact that frequency distributions of woody cover at large scales show clear peaks, suggests that intermediate woody cover represents a transient and unstable state separating more stable states (Hirota *et al.*, 2011, Staver *et al.*, 2011).

The process of bush encroachment may occur through the formation of bush clumps which increase in number and size over time (O'Connor & Chamane, 2012). This process begins with a founder species establishing and facilitating the establishment of other species (Barnes & Archer, 1996; Dean *et al.*, 1999). The founding species encroach, changing the environmental conditions at a site (Jamison-Daniels, 2021). This encroachment process initiated by founding species results in a state that is no longer conducive for savanna species to establish. Few studies documenting bush encroachment clearly distinguish between woody thickening because of an increase in savanna tree species, leaving the C₄ grass layer

intact, and an increase in broad-leaved trees that result in a complete biome shift where the grasses are shaded out (Archer, 1995; Parr *et al.*, 2012). Thicket expansion refers to the process where the thicket expands into the savanna, causing the savanna to switch into a thicket (Parr *et al.*, 2012). This process is usually irreversible and unlikely to revert to a savanna as it prevents fire spread (Archibald *et al.*, 2010). Savanna thickening is reversible because savanna tree species increase while leaving the C₄ grass layer intact.

1.1.3. Determinants of tree cover change in savannas

Forests replace savannas in regions where the annual rainfall exceeds ~ 1500 mm (Cole, 1986; Lewis, 2006) and the length and intensity of seasonal drought is minimal (Lehman *et al.*, 2011). There are other regions in the world with sufficient annual rainfall for forests to grow, which are dominated by grasslands instead, shrublands, savannas, and open woodlands (Swaine *et al.*, 1992; Moreira, 2000; Russell-Smith *et al.*, 2003; Bond, 2019). Frequent fires reduce tree density of woody savanna (Higgins *et al.*, 2000; Bond *et al.*, 2008) and hinder the recruitment of forest juvenile trees (Hoffmann *et al.*, 2003; Hoffmann *et al.*, 2012a, 2012b). Without fire, woody recruitment is possible, and seedlings can mature quickly, increasing tree cover. Increased woody cover has feedbacks on fire intensity and frequency as well. Studies indicate that the threshold point of fire prevalence in savannas is 40% tree canopy cover. Above this point, fire can no longer spread, thus representing a threshold above which tree cover rapidly closes (Archibald *et al.*, 2009; Staver *et al.*, 2011a).

In mesic regions, with mean annual precipitation > 800 mm, there are many observations of forests expanding into savanna after long-term fire suppression (Bowman *et al.*, 2001; Durigan & Ratter, 2006; Pinheiro *et al.*, 2010). Fires can occur annually in regions with high rainfall, where the grasses grow quickly (Higgins *et al.*, 2000; Roques *et al.*, 2001). Cardoso *et al.* (2018) study in Lope National Park in Gabon showed that the composition and flammability of the grass layer was influenced by fire within the savanna before reaching the fire suppression threshold, and grasses were impacted by tree canopy cover, which was also influenced by the behaviour of fire. Hennenberg *et al.* (2006) also show that a decline in grass biomass marks the point at which fire stops in a forest-savanna boundary.

Insufficient nutrient stocks can also limit tree density (Bond, 2010). Locally, edaphic factors such as shallow, sandy, or flooded soils may make some sites incapable of becoming forests during fire suppression. In semi-arid savannas, climate alone may play a key role in preventing the development of a closed forest canopy (Sankaran *et al.*, 2005; Good & Caylor,

2011). For some arid South African savannas, the successful establishment of acacia seedlings is proposed to occur during above-average rainfall years. Woody encroachment is exacerbated by periods of above average rainfall after a drought season (Aucamp *et al.*, 1983; O'Connor & Crow, 1999; February *et al.*, 2013).

Changes in herbivory activity are thought to be contributors in the transformation of many woodlands to grassland (Laws, 1970; Dublin *et al.*, 1990; Van de Vijver *et al.*, 1999). It is the continuous grass layer that fuels fires, which in turn keep the landscape open and enhances grass productivity by killing trees. Fire and browsers are both found in areas with low tree covers and much reduced beyond the critical tree cover threshold, and they both have an impact on tree cover (Staal *et al.*, 2018). Different functional groups of herbivore impact tree cover differently. In semi-arid savannas, browsing of saplings and young tree seedlings can suppress tree cover (Staver & Bond, 2014). Grazing herbivores, especially large ones, have the potential to change landscapes through their trampling and foraging activities (Bond & Loffell, 2001; Birkett, 2002). Livestock is the dominant form of herbivory in the tropics (Oesterheld *et al.*, 1992; Hempson *et al.*, 2015). Livestock is even dominant in areas where indigenous herbivores are present. Herbivores may deplete the grass layer, reducing fires and thus facilitate tree seedling recruitment.

In some African savannas, herbivory or fire may not explain the observed continent-wide change in woody structure (Devine *et al.*, 2017). In a review of global and local drivers of woody encroachment, CO₂ enrichment was proposed to be driving woody encroachment using a two-system conceptual model in arid vs mesic grassy biomes (Devine *et al.*, 2017). In arid savannas, which are water-limited, increasing CO₂ results in increased water efficiency (Polley *et al.*, 2003; Eamus & Palmer, 2007; Kgope *et al.*, 2010), which promotes additional tree growth. In mesic savannas, where woody plants are limited by disturbances such as herbivory and fire, woody encroachment is proposed to be a result of increased carbon allocation to rootstocks which aid in tree recovery after a disturbance allowing trees to reach reproductive maturity (Bond & Midgley, 2000; Buitenwerf *et al.*, 2012).

1.1.4. The conservation of natural savannas and grasslands

Grassland conservation has been overshadowed by forest conservation for many reasons, one of them being that forests have higher carbon stocks aboveground and below ground (Abreu *et al.*, 2017; Silva, 2017; Duarte-Guardia *et al.*, 2019) and society generally viewing forests as having higher aesthetic value (Bond & Parr, 2010; Overbeck *et al.*, 2013). Furthermore,

savannas were long considered as successional vegetation states, which were potential vegetation for a forest (Bond & Parr, 2010; Veldman *et al.*, 2015a). This suggested that they were not ecosystems in need of conservation, but rather a target for forest restoration.

One of the greatest threats to the ecological functioning of savannas is their conversion to forests or closed woodlands either by an invasion of native trees or non-native invasive trees or afforestation (Bond, 1996; Bond, 2019). Bush encroachment has been recognised as one of the top three rangeland problems across 25% of magisterial districts in South Africa (Hoffman *et al.*, 1999). The conversion of grasslands into woodlands is detrimental to livestock production as well as biodiversity (Mugasi *et al.*, 2000; Anadon *et al.*, 2014). The need to plant more trees and create carbon sinks gives little opportunity for savannas to be acknowledged as biomes of high value (Veldman, 2016; Zaloumis & Bond, 2016). The high levels of biodiversity and endemism that are characteristic of savannas with a long history of evolution should be taken into consideration when investigating the impacts of increasing tree cover in savannas (Brannstrom *et al.*, 2008; Abreu *et al.*, 2017). Bush encroachment thus threatens the high levels of biodiversity and endemism in the herbaceous layer of open ecosystems.

1.1.5. The role of forb and grass species in maintaining the savanna system

The classical description of savannas as vegetation types consisting of a continuous grass layer, with a discontinuous tree layer, pays little attention to the forb layer. Forbs, which are a plant form that includes any non-graminoid herbaceous vascular plant, may dominate or co-dominate in some grasslands and savannas (Peterson *et al.*, 2007), comprising a considerable and distinct component of the herbaceous layer (Siebert & Dreber, 2019). In South Africa, rangeland research is conventionally driven by agriculture rather than conservation concerns, and therefore, management decisions are often based on dominant grass species (Uys, 2006; Trollope *et al.*, 2014). Enhanced forb species diversity is also regarded to be a sign of a degraded system -medium to intensely grazed (Van Coller, 2014). They are therefore perceived negatively when they dominate the grass component which is an important source of forage stability in savannas (O'Connor, 2015). Consequently, the biology and function of the forb component in these systems is has been neglected (Uys, 2006; Siebert & Scogings, 2015). Forbs constitute the largest component of herbaceous species richness in grassland and savanna ecosystems (Pokorny *et al.*, 2004; Scott- Bond & Parr, 2010; Koerner *et al.*, 2014; Shaw & Morris, 2015; Zaloumis & Bond, 2016), although

this changes along gradients of increasing tree cover (Dreber *et al.*, 2018) and grazing intensity (Hanke *et al.*, 2014). In addition, the interaction between grasses and forb species is poorly understood because most studies on the competitive interactions between plant life forms are centred around the understanding of tree-grass interactions (Siebert & Dreber, 2019). Although research on forb species in savanna systems is limited, studies aimed at conserving savannas and grasslands focusing on the cover and composition of herbaceous species can still be conducted. Conservation studies could be focused on managing forb species response to disturbances as they contribute to herbaceous species diversity in savanna ecosystems; while reserve management studies may still require management interventions should forb abundance increase at the expense of perennial grass productivity (Siebert & Dreber, 2019).

When assessing whether a regime shift has taken place in a savanna or grassland system, one would study the composition of forbs and grasses in the system as herbaceous communities have an indicator potential for regime shifts responding to land use habitat destruction and climate change (Zerbo *et al.*, 2018). Coiffait-Gombault *et al.* (2012) suggest that a combination of short-lived and long-lived perennial forbs and grasses are good indicators of old-growth savannas, especially in grasslands of the arid tropics and temperate steppes. Annual, biennial, and short-lived perennial species are the ones that colonise sites that have experienced disturbance (Mack & Thompson, 1982). They become an important component of dynamic, old growth savannas (Veldman *et al.*, 2015b). The abundance of annuals indicates severe degradation associated with altered disturbance regimes, biological invasions and a decrease in native plant populations (Mack & Thompson, 1982).

The influence of forb species in the maintenance of grasslands and savannas as alternative stable states is rarely mentioned. Due to their functional traits and abundant biomass, grasses rather than forbs are the main creators of more intense fires that suppress tree establishment and are thus likely to have a greater impact on the distribution of open ecosystems (Wragg *et al.*, 2018).

1.1.6. The effect of trees on the herbaceous layer

Trees may suppress the growth of grasses and other herbaceous plants through direct competition for water, light and nutrients resulting from overlapping root profiles and canopy shading (Scholes & Archer, 1997; Ludwig *et al.*, 2004). At the same time, trees may facilitate herbaceous production through the improvement of the biophysical or biogeochemical

conditions for growth (Dohn *et al.*, 2012). Trees may also improve soil water availability through their roots (hydraulic lift) or through decreasing sub-canopy evapotranspiration. Lowered soil temperatures also reduce water stress for the herbaceous community (Jarvel & O'Connor, 1999; Ludwig *et al.*, 2004).

There exists a threshold point between savanna and closed canopy systems at which tree canopy cover sufficiently excludes heliophilic C₄ grasses and creates a moist and less windy microclimate (Hoffman *et al.*, 2012b). This critical point has been demonstrated to exist in specific sites, and its role in conjunction with that of fire is complex (Lloyd & Veenendaal, 2016). Below the threshold point, C₄ grasses dominate, and will burn during the dry seasons (Bond & Van Wilgen, 1996a; Charles-Dominique *et al.*, 2018), top-killing trees that are caught in the flame zone, and thus maintain the open canopy environment. Above the tree cover threshold, fire sensitive forest or thicket species can establish while the recruitment of savanna tree species is suppressed by a lack of light, resulting in the formation of a closed canopy thicket or forest.

The relationship between grass production and the quantity of trees in mixed tree-grass ecosystems is shown to be convex (Scholes, 2003; Scholes, 2004). This means that the grass will be productive for the initial increase in tree cover than it does for subsequent increases in tree cover (Scholes & Archer, 1997). In some cases, the grass production remains unaffected during the first initial increase in tree basal area and is affected above a certain level of tree basal area (Scholes, 2003). The convex relationship between tree cover and grass production is thus important for land managers seeking to manage forage production for grazers in savannas.

The relationship between increased tree cover and abundance and diversity of forbs has been less well studied, despite its implication for biodiversity conservation. Understorey vegetation has been shown to vary along light gradients associated with varying tree canopy cover in savannas and woodlands (Scholes & Archer 1997; Leach & Givnish, 1999). Grasses and many forbs are mostly abundant in open or partially shaded patches. The way in which herbaceous plant abundance and species composition interact is still poorly understood (Ludwig *et al.*, 2001). There are reports suggesting that legume biomass decreases beneath tree canopies (Gea-Izquierdo *et al.*, 2009) and that herbaceous species richness is lower underneath crowns (Marañón, 1986). However, forb species have been found to take advantage of improved soil conditions in subcanopy habitats than grasses, because they are more shade tolerant (Singh *et al.*, 2004).

A major driver of biodiversity loss in savannas has been shown to be size-asymmetric competition for light (Borer *et al.*, 2014; DeMalach *et al.*, 2017). In a shrub/grass mixture, complete canopy cover of one species over another will lead to unequal competition for light. There will be consequences for the species that are experiencing excessive shading. In addition, above ground competition for light is more prominent in forests than in sparse shrub communities (Martens *et al.*, 1997). However, this changes when sparsely treed communities experience an increase in tree cover. Overstory characteristics vary along vegetation gradients and as a result produce complex patterns in understory light because tree height, tree architecture can change with increases in woody plant cover (Padien & Lajtha, 1992). Overstory characteristics such as spatial pattern, height, and cover of woody plants determine the patterns of understory light (Martens *et al.*, 2000). Additionally, the branching level of trees, angle, type of leaves and the density of leaves are tree characteristics that influence the amount of light available in the understory (Lieffers *et al.*, 1999; Montgomery & Chazdon, 2001; Archibald & Bond, 2003). A short tree, for example will cast more shade in the understory than a taller tree with the same canopy diameter and trees with leaves hanging vertically downwards will cast less shade than trees with their leaves opened horizontally (Lieffers *et al.*, 1999; Montgomery & Chazdon, 2001; Archibald & Bond, 2003).

1.1.7. Bush encroachment in the Eastern Cape

The occurrence of livestock farming in many semi-arid grasslands and savannas has led to bush encroachment and a reduction in their carrying capacity (Archer *et al.*, 1988; Asner *et al.*, 2003; Buitenwerf *et al.*, 2012). An increase in tree density results in a noticeable change in species composition and nutritional value of grasses. A study in the Kei Road-Komga area in the Eastern Cape has shown that a substantial amount of bush encroachment had taken place in the Eastern Cape between 1949 and 1999 (O'Connor & Crow, 1999; Puttick *et al.*, 2014; Skowno, 2018). Valleys in this region had been transformed from open savanna to more closed woodlands, leading to the loss of open grasslands. The encroachment in the Kei Road area is a result of *Vachellia karroo* invasion, where there is a pattern of increased recruitment with increased rainfall after prolonged seasons of drought (O'Connor & Crow, 1999; Skowno, 2018). *Vachellia karroo* seedlings survive with the increase in soil moisture and have an advantage over the grass communities (O'Connor, 1995). There are also other environmental causes for changes in the Eastern Cape. Heavy grazing by livestock during

droughts, gives rise to woody invasion because of reduced fires and competition (O'Connor & Crow, 1999; Lechmere-Oertel, 2003). The increase in woody biomass in the Kei Road-Komga region and many other areas within the Eastern Cape has resulted in the abundance of mono-specific woodlands of *V. karroo*, which have impacted the herbaceous layer production (O'Connor & Crow, 1999; Puttick *et al.*, 2014).

The proliferation of *V. karroo* in the Bisho Thornveld savannas of the Eastern Cape often facilitates the entry of other woody species which may increase the effect of tree competition on the herbaceous layer (O'Connor & Chamane, 2012). Understanding the rate at which the encroachment and facilitation processes take place is beneficial to landowners who want to maintain a high diversity state of the herbaceous layer. The importance of knowing whether there are critical thresholds that affect herbaceous production (forage productivity, richness, diversity, etc.) and lead to fire exclusion (thus limiting management options for reducing woody cover) is important. If such thresholds exist, it will be necessary to determine where they occur and to be aware of the management options for turning things around. Furthermore, investigating the processes that lead to a switch in vegetation structure from an open to a closed system is likely the key to solving the bush encroachment issue in these systems.

1.2. Research aims and thesis overview

This study was carried out in the Eastern Cape Province (Smaldeel region) where savanna and thicket are found forming boundaries with each other. The overall aim of this study was to reconstruct the extent and rate of canopy cover change at selected sites across Endwell farm and to investigate how the process of bush encroachment has led to altered tree stand characteristics, light environment and herbaceous layer composition and cover over the past seven decades. This study investigated historical increases in tree cover at 51 sites on the farm and the corresponding changes in canopy structure that could be linked to the abundance, diversity, and richness of herbaceous species.

The specific aims, research questions and hypotheses are detailed in the overview of the remaining thesis chapters below.

1.2.1. Using historical aerial photographs to determine woody cover change

Chapter 2 describes the methods used to quantify tree cover and how sites were selected based on historical evidence of increasing and decreasing tree cover. Changes in woody tree cover in 51 sites were analyzed using historical aerial photographs from 1949 to 2019. This was done to identify common trajectories of woody cover increase and I predicted that canopy cover in 2019 (used as a measure of woody encroachment in later chapters) would be a reasonable proxy for encroachment history. I also used frequency distributions of canopy cover at each of the plots at different time points to identify possible stable vs more transient states of canopy cover. Based on the observation by Staver *et al.* (2011) I expected canopy cover to be stable at low and high values with intermediate canopy cover representing an unstable, transient state. Lastly, I related canopy cover change over different time periods to rainfall variation to see if there was evidence of drought or high rainfall periods having led to widespread woody cover increase.

1.2.2. Impact of tree cover increase on light dynamics in the understory

The second aim of the research, presented in Chapter 3, was to relate current woody cover to changes in the composition and structure of the woody vegetation, and how these in turn affected light transmission and leaf area index (LAI). Based on the analyses of woody cover change, the current state of woody cover was assumed to represent a stage in thicket expansion, with higher percent aerial woody cover corresponding to more advanced stages of encroachment and thicket formation processes. I aimed to address the following questions: (1) what is the woody composition, % cover and light transmittance associated with different stages of encroachment? (2) Is there evidence that higher woody cover in 2019 represents a more advanced stage of the thicket encroachment process (as documented by O'Connor & Chamane, 2012; Jamison-Daniels *et al.*, 2020)? And (3), what is the relationship between present-day canopy cover and LAI/light transmission? I also sought to determine whether there was evidence for threshold points (in canopy cover, light transmittance, and LAI) marked by changes in the tree species composition. I hypothesized that sites with high tree cover would have a denser and taller structure and higher tree diversity with an increasing representation of thicket precursor species. These characteristics would result in lower light transmittance in the understory.

1.2.3. Impact of woody cover increase on the herbaceous layer

In Chapter 4, the changes in the diversity and richness of herbaceous species in response to increasing tree cover and the resultant changes in canopy dynamics were investigated. The tree cover characteristics that affected light transmittance and LAI were predicted to influence herbaceous species composition. An increase in tree cover was expected to result in a decline in herbaceous species basal cover, diversity, and richness. Furthermore, this work aimed to identify whether there was evidence for thresholds of woody cover and light transmittance that led to abrupt changes in the abundance and composition of herbaceous species, consistent with the theory on alternative stable states.

The final thesis chapter (Chapter 5) discusses the findings of the study and their implications for land management in semi-arid savanna regions.

Chapter 2

Historical Woody Cover Changes at Selected Sites on Endwell Farm

2.1. Introduction

2.1.1. Changes in vegetation structure in the Eastern Cape

Models including both bottom-up (climate) and top-down (herbivory and fire) factors have been used to explain tree and grass coexistence and the response of savanna systems to disturbance and climate change (Higgins *et al.*, 2000; House *et al.*, 2003; Sankaran *et al.*, 2004). Savanna systems are complex and require multi-dimensional models focusing on more than one cause for increasing tree densities in the landscape (Kgosikoma & Mogotsi, 2013). There are environmental conditions and anthropogenic practices that tip the grass-tree balance in savanna systems which result in an increase in trees. In the Eastern Cape, land is used for agriculture, mainly pastoralism and some cropland cultivation (Graw *et al.*, 2017). There have been many agricultural management changes in the past decades which may have impacted the rates of woody increases in savannas (Kakembo, 2001). Bush encroachment remains a major concern for land and conservation managers since it leads to a reduction of grazing capacity of rangelands (de Klerk, 2004; Espach, 2006).

Rates of *V. karroo* encroachment into grasslands have been rapid in the Eastern Cape (O'Connor & Crow, 1999). Most bush encroachment in the Fort Beaufort commonage area happened in the early 1990s and the same pattern was observed in neighbouring commercial farms (Puttick *et al.*, 2014). *Vachellia karroo* lives for up to 40 years and can be seen in the earliest photographs from 1937 (O'Connor & Crow, 1999). *Scutia myrtina* has also been reported to establish as a solitary individual, but to occur more commonly under the canopies of established *V. karroo* in the Eastern Cape's grasslands (O'Connor & Chamane, 2012).

2.1.2. The interplay between rainfall and bush encroachment

In a semi-arid region, encroachment is thought to be influenced by moisture availability, which impacts woody plant establishment and recruitment (Higgins *et al.*, 2000; O'Connor

et al., 2014; Devine *et al.*, 2017). Some of the factors that resulted in the increase of vegetation cover in the Eastern Cape were the wetter period experienced in the region during the 1970s, the change from continuous to rotational grazing, and a decrease in fire frequency in the grassland systems (Puttick *et al.*, 2014). Different approaches have been taken to examine the impact of rainfall and soil moisture on bush encroachment. Wiegand *et al.* (2005) found that the conversion of an open patch of land to a closed patch was initiated by the spatial and temporal rainfall events that allowed acacia trees to germinate and establish. Increased moisture availability has also been found to increase seedling establishment of *Vachellia karroo* and that the establishment of *V. karroo* trees is likely to occur in certain years of suitable rainfall (above 500 mm) in drier regions (O'Connor, 1995a). The influence of rainfall on bush encroachment was observed to be stronger at the drier savanna site than in the mesic savanna site in the Eastern Cape (Skowno, 2018). In semi-arid savannas, encroachment of bush is usually a response to annual and inter-annual moisture variabilities (Briske *et al.*, 2003; Angassa & Oba, 2007). The intensification of bush encroachment is often associated with consecutive above average-rainfall years, which occur after a period of drought (Aucamp *et al.*, 1983; O'Connor & Crow, 1999).

The factors contributing to bush encroachment are complex and probably vary for each savanna system. Some studies support the hypothesis that tree density variation is caused by demographic bottlenecks in seedling recruitment and sapling release (Hoffman, 1999; Higgins *et al.*, 2000; Prior *et al.*, 2010). Many savanna trees, including acacias, reproduce rapidly after exceeding a particular height (termed “escape height” from fire). They can also remain below the escape height, and only resprout when they experience disturbances (Wakeling *et al.*, 2011). The growth rates of saplings are therefore important for predicting tree cover changes. The average time it takes for *V. karroo* to reach an escape height of 3 m is 13 years, after which they start to reproduce profusely, resulting in more sapling recruitment (Wakeling *et al.*, 2011). *Vachellia karroo* can also persist for a long time within the fire trap, until it grows fast enough between intervals of no fire (Bond & Van Wilgen, 1996b; Higgins *et al.*, 2000). Over long fire-free periods, when rainfall conditions are suitable for the recruitment of trees, the savanna system will therefore experience an increase in tree cover (Wakeling *et al.*, 2011).

In the Smaldeel region of the Eastern Cape Province, where this study was conducted, savanna and thicket patches exist within the same area. Semi-arid ecosystems such as the

ones in the Smaldeel area may transform into irreversible states over time, where changes in tree cover can result in vegetation regime shifts (Westoby *et al.*, 1989).

2.1.3. Aims and Hypotheses

The overall aim of this chapter was to examine changes in percentage woody canopy cover in various sites at Endwell farm over the past seven decades (1949- 2019) with the aid of historical aerial photographs, and to relate canopy cover changes with temporal rainfall variation. Tree cover was expected to generally increase over the years as shown in other studies in the Eastern Cape Province (O'Connor & Crow, 1999; O'Connor *et al.*, 2014, Skowno, 2018). While the initiation and rate of woody encroachment was expected to vary spatially. I expected that once woody cover at a site had increased above ~ 40 % (the fire suppression threshold), it would continue to progress. I estimated percent canopy cover at different time points from aerial photographs and used these percentage canopy cover values to identify canopy cover classes. This would allow for the grouping of sites by their percent canopy cover into classes: open, low, moderate, and high. The existence of transient stages would be inferred from certain canopy cover percentages being more common (and hence longer lasting/more stable) while others would be rare and presumably more transient. I determined whether different sites experienced similar rates of canopy cover increase despite different initiation times and linked the patterns observed to other studies suggesting that encroachment follows a predictable sequence (O'Connor & Chamane, 2012, Jamison-Daniels *et al.*, 2021). Assuming a relatively predictable sequence of thicket clump formation, sites with higher canopy cover would therefore also represent sites with a longer history of encroachment. If this was the case, canopy cover classes derived from the most recent available imagery (Google Earth, 2019) would represent progressive stages of encroachment that could be used for further analyses, which are reported in Chapters 3 and 4.

Finally, this chapter aimed to investigate whether rainfall patterns (periods of below- and above-average rainfall) could be linked with canopy cover increases. Periods of higher mean annual precipitation were expected to result in higher rates of tree cover increases, following the theory that trees establish better during high rainfall periods in semi-arid regions (Higgins *et al.*, 2000; O'Connor *et al.*, 2014; Devine *et al.*, 2017). Periods of above-rainfall years preceded by periods of below average mean annual rainfall were also expected to result in higher rates of percent canopy cover increases (Aucamp *et al.*, 1983; O'Connor & Crow, 1999, Skowno, 2018).

2.2. Study site

Endwell farm is situated in the Amathole district in the Eastern Cape province of South Africa (Figure 2.1). The farm lies in the Smaldeel region, which spans approximately 130 km west from Somerset west to Fort Beaufort. It falls within the latitudes and longitudes: -32°44'56.4"S and 26°27'41.6"E. The area lies at ~659 m above sea level. The main research site was located on the western, flatter and low-lying parts of the farm that have been reported to have experienced woody encroachment in the past and recent decades.

The study area was situated on gently to steeply undulating areas at the base of steeper mountains. Study plots were selected to fall on flat or gently sloping terrain to ensure topographic homogeneity. The predominant soil form in the area is Glenrosa and Mispah (Teague *et al.*, 1981). There is low water availability for plants because of the shallow topsoils. Most of the soils are derived from shale and sandstones of the Beaufort and Ecca series. The high silt and fine sands in the shale and sandstone result in very poor infiltration capacities (Henseley, 1980).

The climate at Endwell farm is semi-arid with warm, wet summers and cold, dry winters with occasional frost. The annual rainfall on the farm between 1924 and 2019 was 722 mm. Most rain is recorded during the months of October to March (Figure 2.2). The bulk of the rainfall in the Smaldeel region comes in a relatively few, heavy rainfall events (Teague *et al.*, 1981). There are instances of low-intensity rainfall; they usually last for two to three days (Marais, 1979). Periods of rain are also interrupted with intra-season droughts, and during this time, topsoil moisture is dropped below wilting point (Teague *et al.*, 1981). The temperature ranges between 4°C in July to 38°C in February.

The site falls within the Bisho Thornveld vegetation type (Mucina & Rutherford, 2006), which consists of a mosaic of grassland, succulent thicket, and Acacia thornveld dominated by *V. karroo*. Other common woody species include *Scutia myrtina*, *Ehretia rigida*, *Grewia occidentalis*, *Diospyros dichrophylla* and *Olea europaea* subsp. *africana* (Mucina & Rutherford, 2006). The grass layer is dominated by *Themeda triandra*, *Digitaria eriantha*, *Sporobolus fimbriatus* and *Cymbopogon plurinodis*. Under selective grazing, the grassland breaks down to a taller, more tufted *Digitaria eriantha* – *Sporobolus fimbriatus* stage, which facilitates *V. karroo* invasion (Teague *et al.*, 1981). At the study site, the vegetation ranged

from open grassland with scattered trees to dense broadleaf thicket. Different stages of woody encroachment can be observed at the site, including grassland with dense establishing *V. karroo* and the formation of thicket clumps, similar to the sequence described by O'Connor & Chamane (2012).

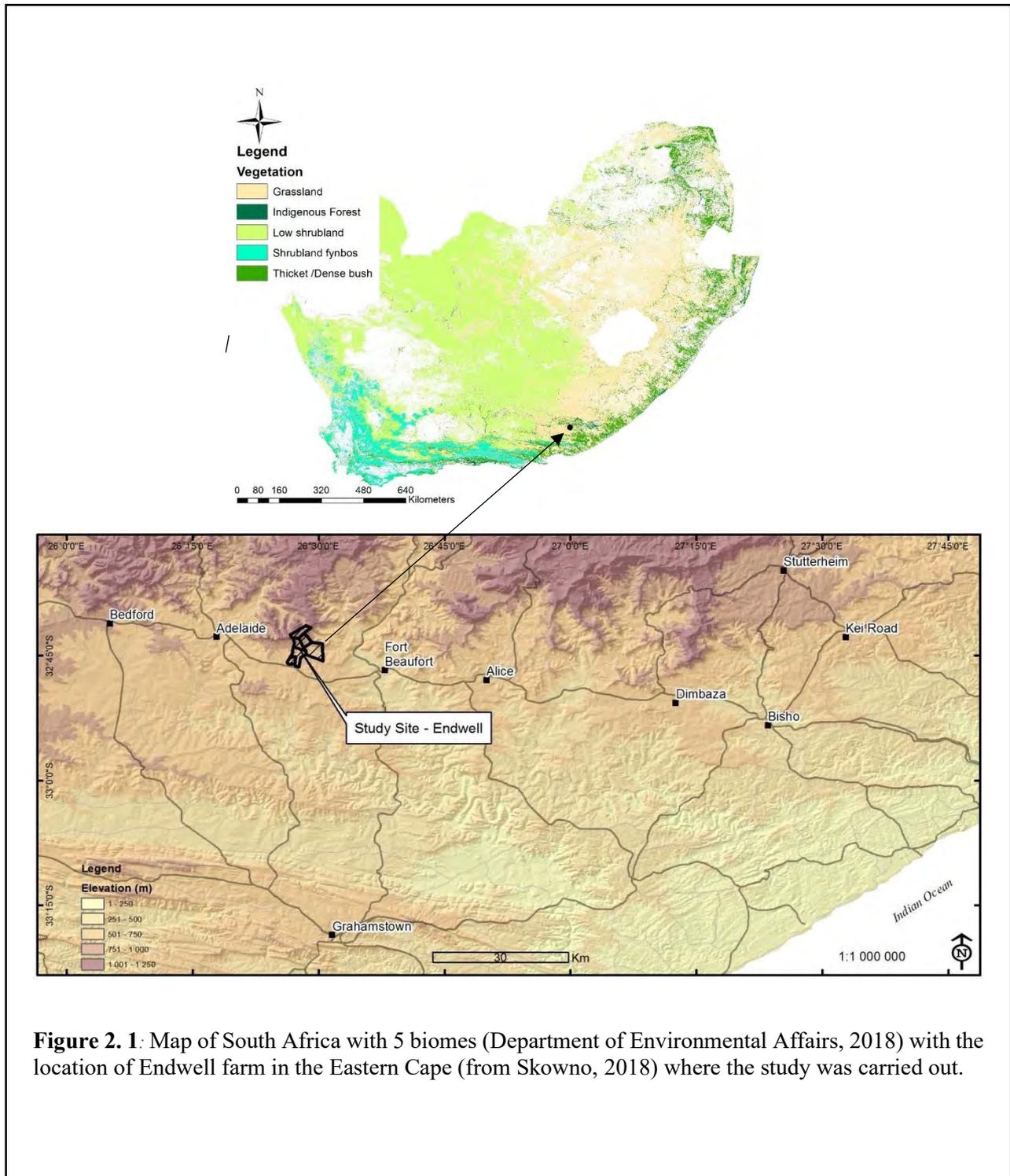


Figure 2. 1: Map of South Africa with 5 biomes (Department of Environmental Affairs, 2018) with the location of Endwell farm in the Eastern Cape (from Skowno, 2018) where the study was carried out.

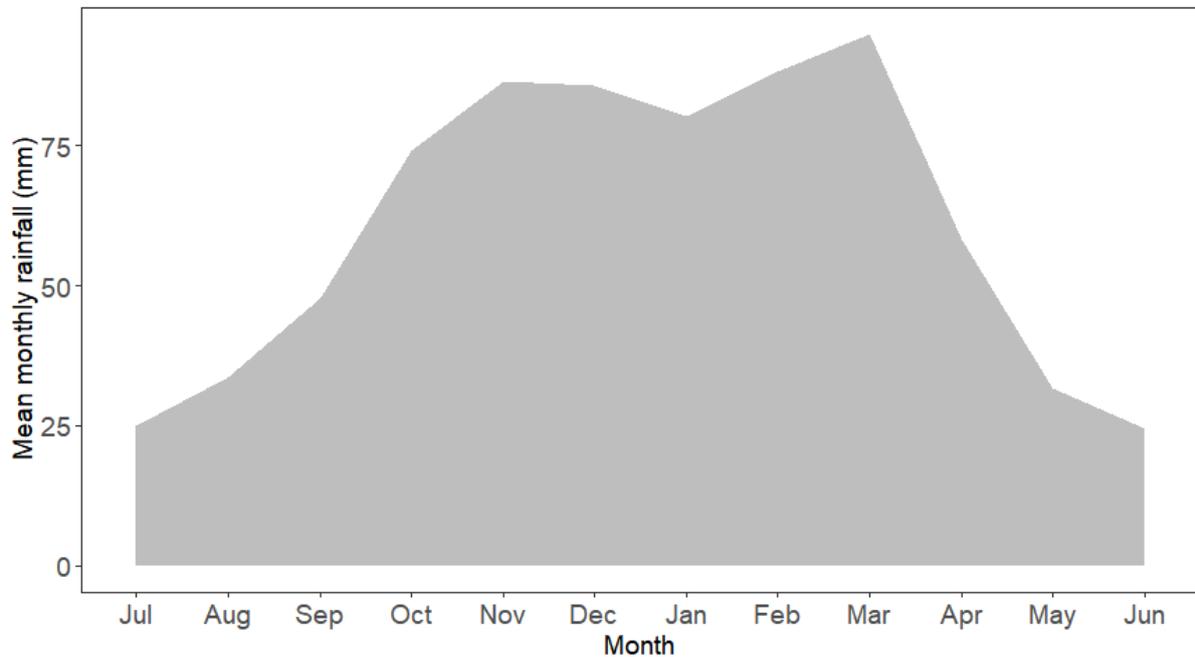


Figure 2. 2: Mean monthly rainfall at Endwell averaged between the years 1924-2019. Mean annual rainfall over the period 1927 to 2019 was 722 mm.

2.3. Methods

2.3.1. Preparing historical photographs for canopy cover analysis

Scanned high-resolution black and white aerial photographs were downloaded from Rhodes University's Geography online resources platform. The photographs dated back to 1949 and the most recent photographs were from the year 2013. The aerial photographs together with 2019 imagery from Google Earth were used to analyse woody cover change over a period of seven decades. The National Geo-Spatial Information (NGI) is responsible for historical aerial photography between 1926- 2008. The photographs were at different scales and improved in quality in the more recent years (2002 and 2013). It was important to analyse the photographs at a scale that enabled distinctions between the woody and grassy component. The focus of this chapter was to quantify tree cover, and the scale was set at a resolution to enable the classification of trees. Other studies that used aerial photography to classify tree cover were Bowman *et al.* (2001) and Wigley *et al.* (2010).

Table 2. 1:Aerial photographs obtained used for the study.

Date	Job and scale	Format
1949	231(1: 30 000)	Digital (JPG)
1968	544 (1: 40 000)	Digital (JPG)
1985	498 /222(1: 30 000)	Digital (JPG)
	498/ 406 (1: 30 000)	Digital (JPG)
2013	998 (1: 30 000)	Digital (JPG)
2019	(-)	Satellite imagery (Google Earth, 2019)

The photographs were downloaded onto ArcGIS 10 (ARC/INFO software by Environmental Systems Research Institute, Redlands, CA, 2010) and georeferenced to the Transverse Mercator WGS 27. The photographs were orientated to their true position through the selection of ground control points, which were dams, rivers and any other feature that was fixed and easy to identify. In most cases, dams, and road intersections were used as reference points. The photographs were mosaicked to form one continuous photograph, covering the study area. The mosaic was clipped to the study area. The visual appearance of the photograph was improved through colour and brightness changes (GIS ArcMap 10.6.1). Photographs that appeared blurry were enhanced by image dodging (to manipulate exposure), saturation and sharpening. The study area was highlighted and sites with a uniform vegetation cover forming an area large enough to fit into a 150 x 150 m (22,500 m²) frame were marked (Figure 2.3). Fifty-one sites in total were selected to represent a gradient of increasing canopy cover in 2019 and varying canopy cover histories. The canopy cover in 2019 represented the vegetation state of the sites at the time of sampling, and it was the most recent satellite imagery available. The vegetation cover in 2019 was also used to classify sites in the categories: open, low, moderate, high (see Table 2.2). The challenge was getting an equal number of sites in each category.

2.3.2. Analysing changes in canopy cover from 1949 to 2019

Aerial photography was used to assess vegetation cover in the years 1949, 1968, 1985, 2002 and 2013. I used a method similar to that of Wigley *et al.* (2010), which employs a lattice with

points at each site to determine plant cover. The manual classifications were performed using GIS ArcMap 10.6.1. A fishnet of 150 m× 150 m was applied to each site. There were 225 points, which were positioned in the middle of the squares within the 150 m × 150 m fishnet (Figure 2.3). The vegetation at each point was classified as tree or grass. The total number of points “touching” trees was counted (four times for reliability) and then used to calculate % tree cover. The total cover in each year was then determined by the total number of points falling on trees as a proportion of the total number of points. Figure 2.3 uses photographs from 1985 and 2013 to show how canopy cover was calculated at one site.

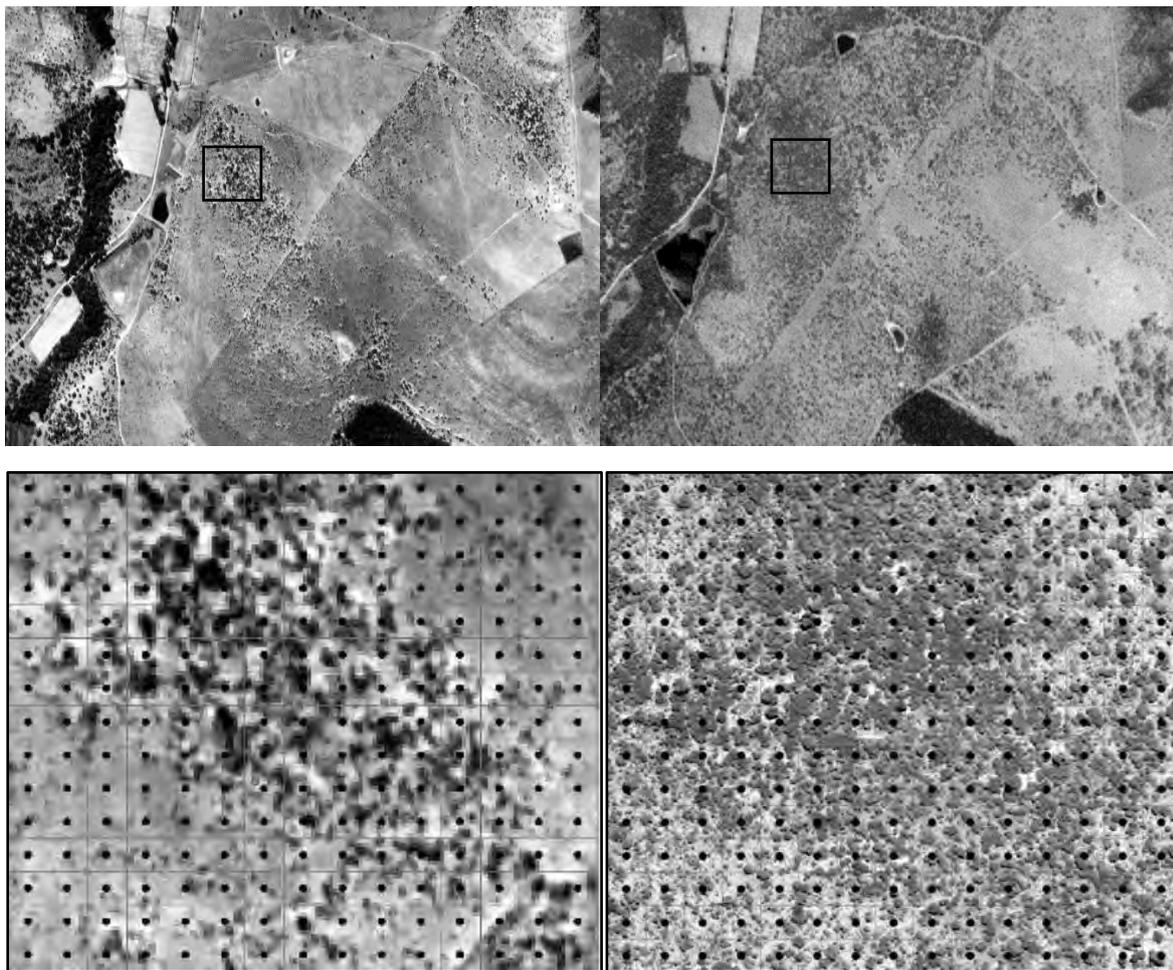


Figure 2. 3: Photographs illustrating how aerial canopy cover (%) was calculated at 51 sites. Showing one old aerial photograph from 1980 (left) and a photograph from 2013 (right). Black dots that fall on the trees are counted for each photograph at each of the 51 sites.

2.4. Data analyses

2.4.1. Analyses of canopy cover change

A Kernel density plot was used to estimate an unknown probability density of canopy cover over the years (%) using the package *ggridges* (R Development Core Team, 2019). Kernel density is a smoothed version of a histogram which estimates a probability density function based on a finite data set. Kernel density plots for each year (1949, 1968, 1985, 2002, 2013, 2019), with the total canopy cover, were then plotted using the ridgeline visualisation. This was used to determine common vegetation cover percentages over the seven decades.

The sites were classified according to four canopy cover classes: (open, low, moderate, and high) using their aerial canopy cover at each year (Table 2.2). There were limits to the number of sites to be included in the high canopy cover class because bush encroachment on the selected slope was at its advanced stage in small and fewer clumps on the farm. To ensure sufficient replication in each canopy cover class, I classified sites with a canopy cover > 50% as “high”, which was also the definition given by Puttick *et al.* (2014) for “closed woodland”. A heatmap was generated using the R package *ggplot2* to indicate the frequency of canopy class transitions (open-open, open- low, etc) between the decades.

Table 2. 2: Canopy cover classes: open, low, moderate, and high

State	Percentage
Open	0% -15%
Low	16%-30%
Moderate	31%-50%
High	51 %-100%

There were five periods between successive aerial photographs and the 2019 Google map image (Table 2.1)- with the interval between aerial photographic missions ranging from 7 to 19 years. Percentage canopy cover and rate of canopy cover increase (% y⁻¹) was estimated at the different sites for each year. The rate was calculated as change in canopy cover percentage per year.

$\frac{T2-T1}{Y2-Y1}$, here T1 and T2 represent tree cover between subsequent years. Y1 and Y2 is the corresponding years.

2.4.2. Historical rainfall analyses

To link rainfall patterns to canopy cover changes, the total rainfall for each year from 1949 until 2019 was calculated, together with the annual rainfall deviations from the mean. The dominant tree species on the farm is *V. karroo* and it takes an average of 13 years for it to reach 3 m. Small trees may not be visible in aerial photographs, and I therefore chose a period of ten years to represent the time a recruitment phase would take place in the farm, where trees would grow to a height > 3m (given that no disturbances arise). The average rainfall measured 10 years prior to a period was calculated and related to canopy cover changes during the period. The mean annual rainfall (mm) for each period was determined for all the years between the years successive aerial photographs were taken. For example, the mean annual rainfall between 1949 and 1968 was averaged (including the mean annual rainfall recorded in 1949 and 1968). To calculate the mean annual rainfall 10 years prior to the period between 1949 and 1968, the mean annual rainfall between 1939 and 1948 was calculated (including the annual rainfall recorded in 1939 and 1948).

The Foley's index (Foley, 1957) for 1,2,3-year cumulative rainfall deficit was used to measure the shortage of rainfall, as the difference between the observation and the long-term monthly averages. The index measures cumulative rainfall surplus or deficit normalised with reference to the mean annual rainfall precipitation. It is calculated as:

Foley's index = (actual rainfall for a period - expected rainfall for the same period)/expected annual rainfall), where expected rainfall is the long-term MAP.

2.5. Results

2.5.1. Historical tree cover changes from aerial photographs

A pattern of increasing canopy cover was observed in most of the sites, and the number of open sites decreased from 1949 to 2019 (Figure 2.4, Figure 2.5 and Figure 2.6). Aerial photographs taken in 1949 showed that 88 % of the sites were in the open (0-15% cover) class. There were no sites with high (51-100%) tree cover and only two sites had moderate tree cover (31-50 %) in 1949. An increase in vegetation cover was evident in the subsequent years. Most of the sites showed the greatest increase in canopy cover increase from 2002 to 2013. In the period between 1949 and 1968, three sites had moderate (30-50%) canopy cover.

More sites that were previously classed as open transitioned to the low cover class in the period from 1968 to 1985, while five remained open. Three sites transitioned to the high cover class (51-100%) in the period from 1968 to 1985. The number of sites in the high tree cover class (51-100%) increased with each time interval and only a slight decline was observed from 2013 to 2019. It is evident from Figure 2.5 that some sites were cleared.

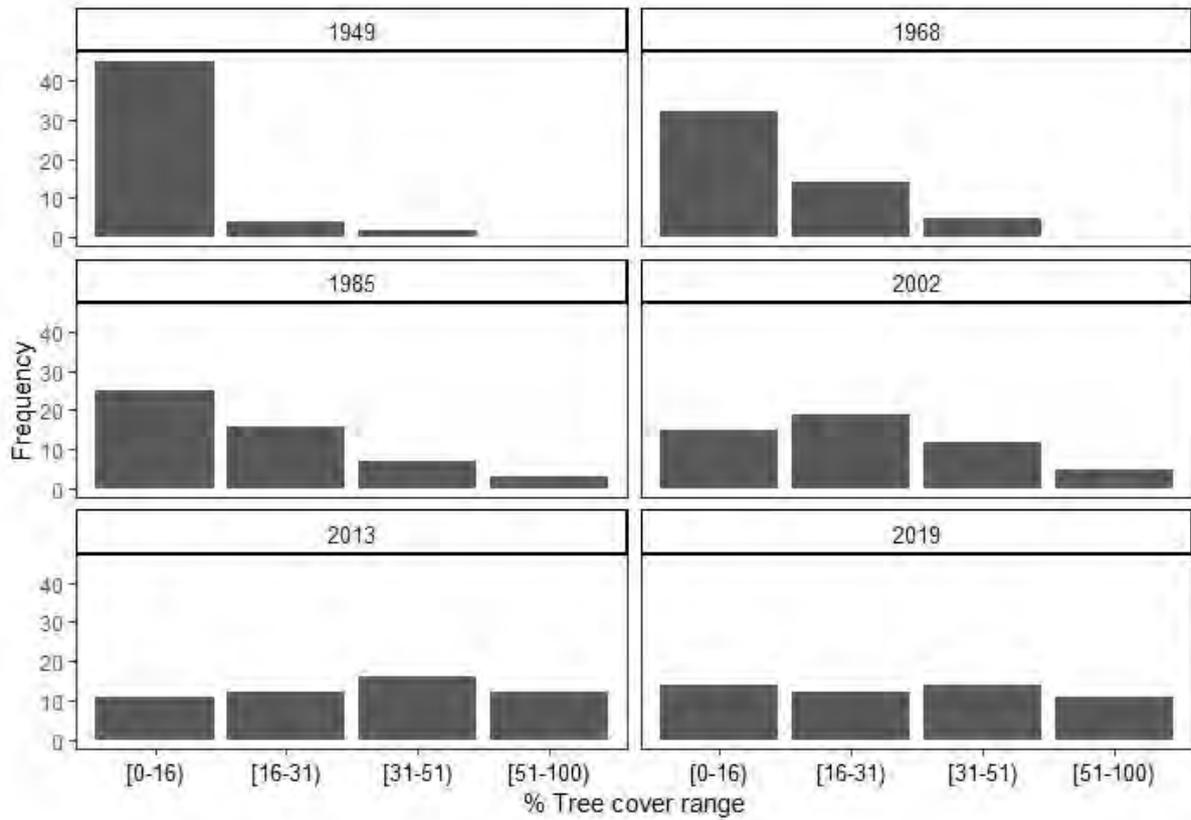
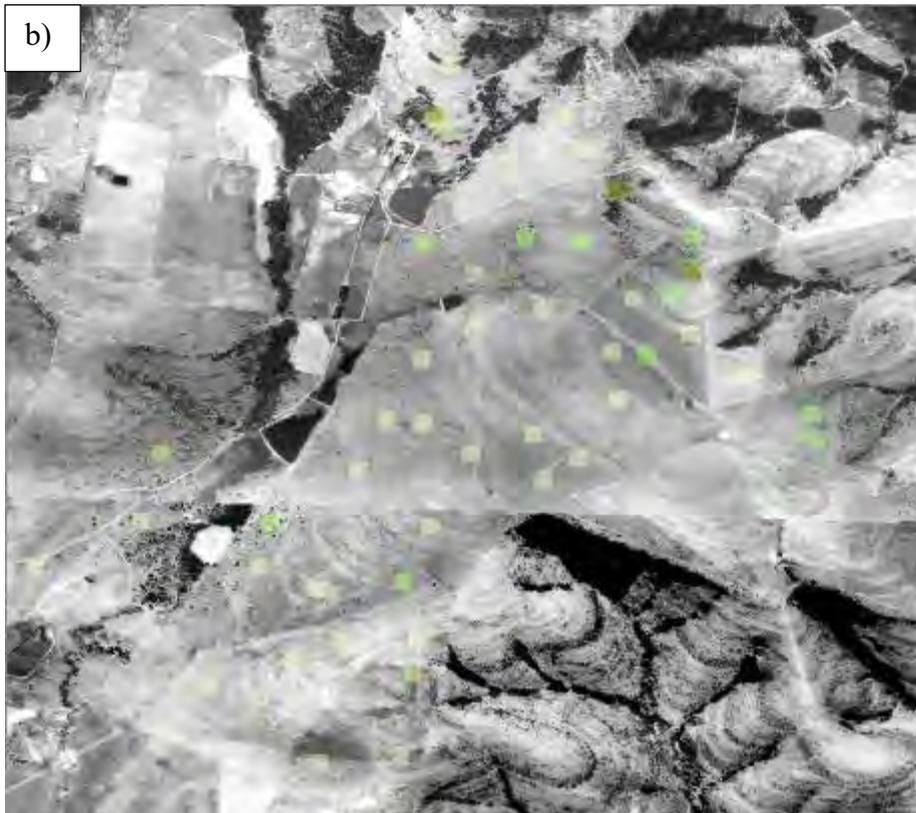
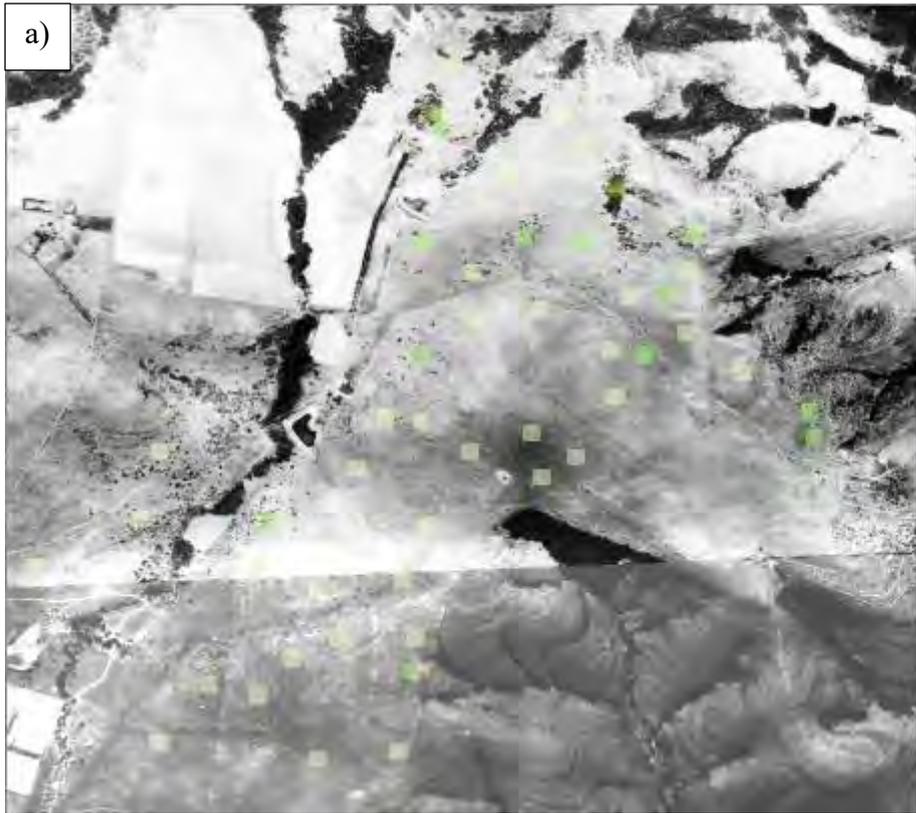
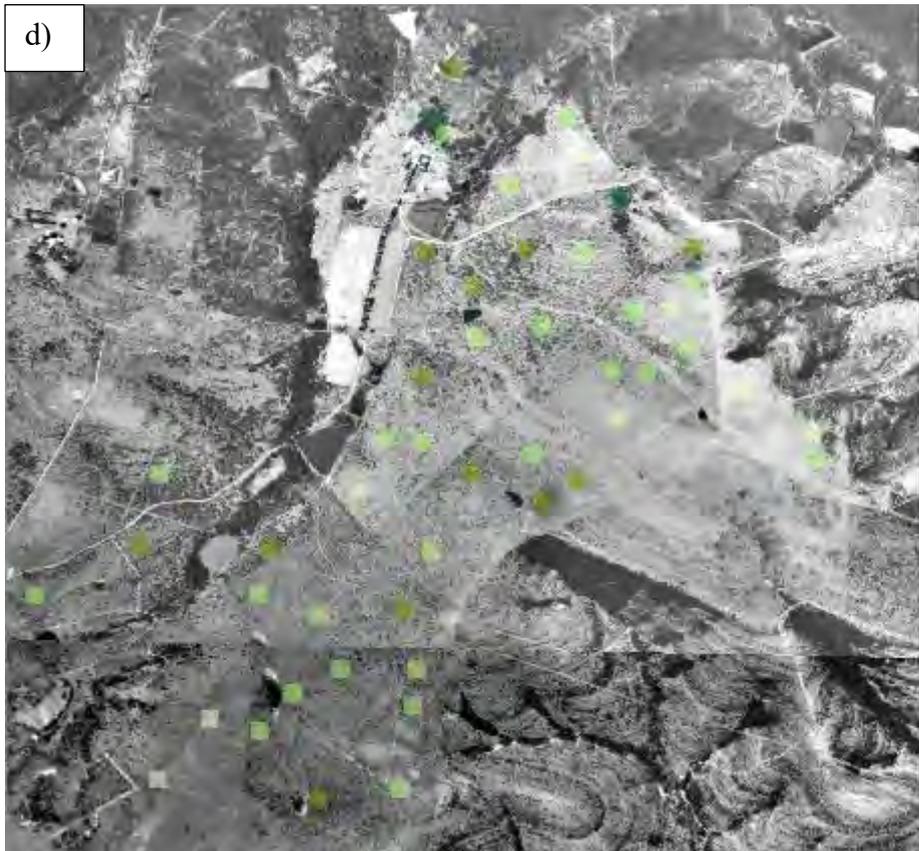
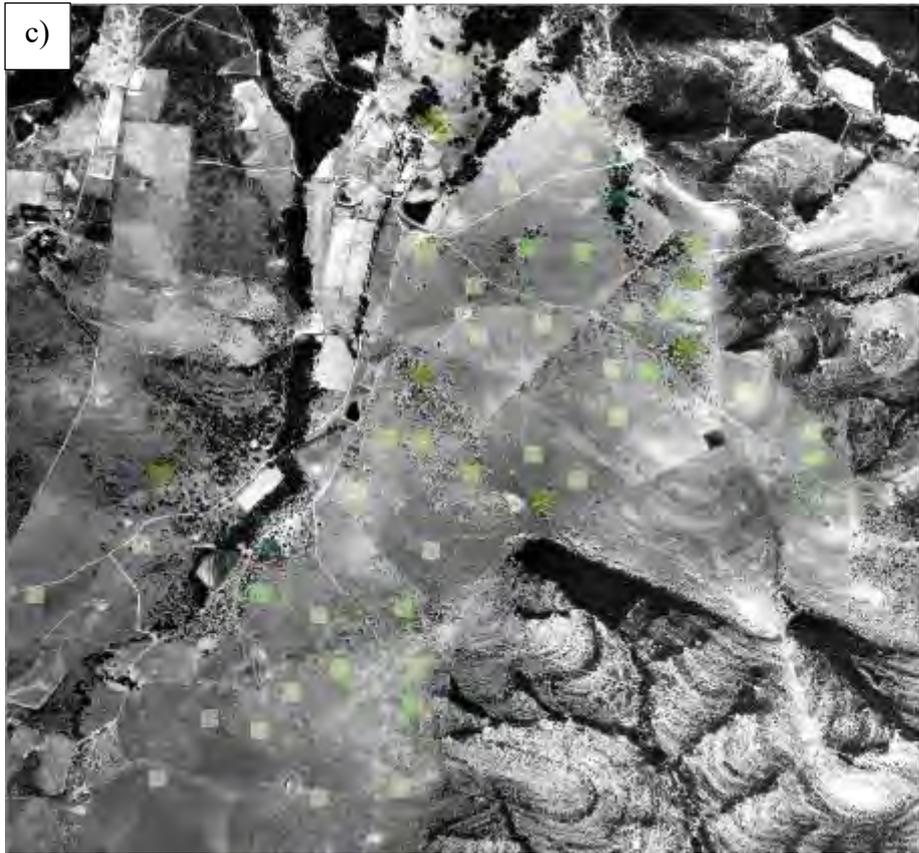


Figure 2. 4: Histogram showing the number of sites in each canopy cover class.





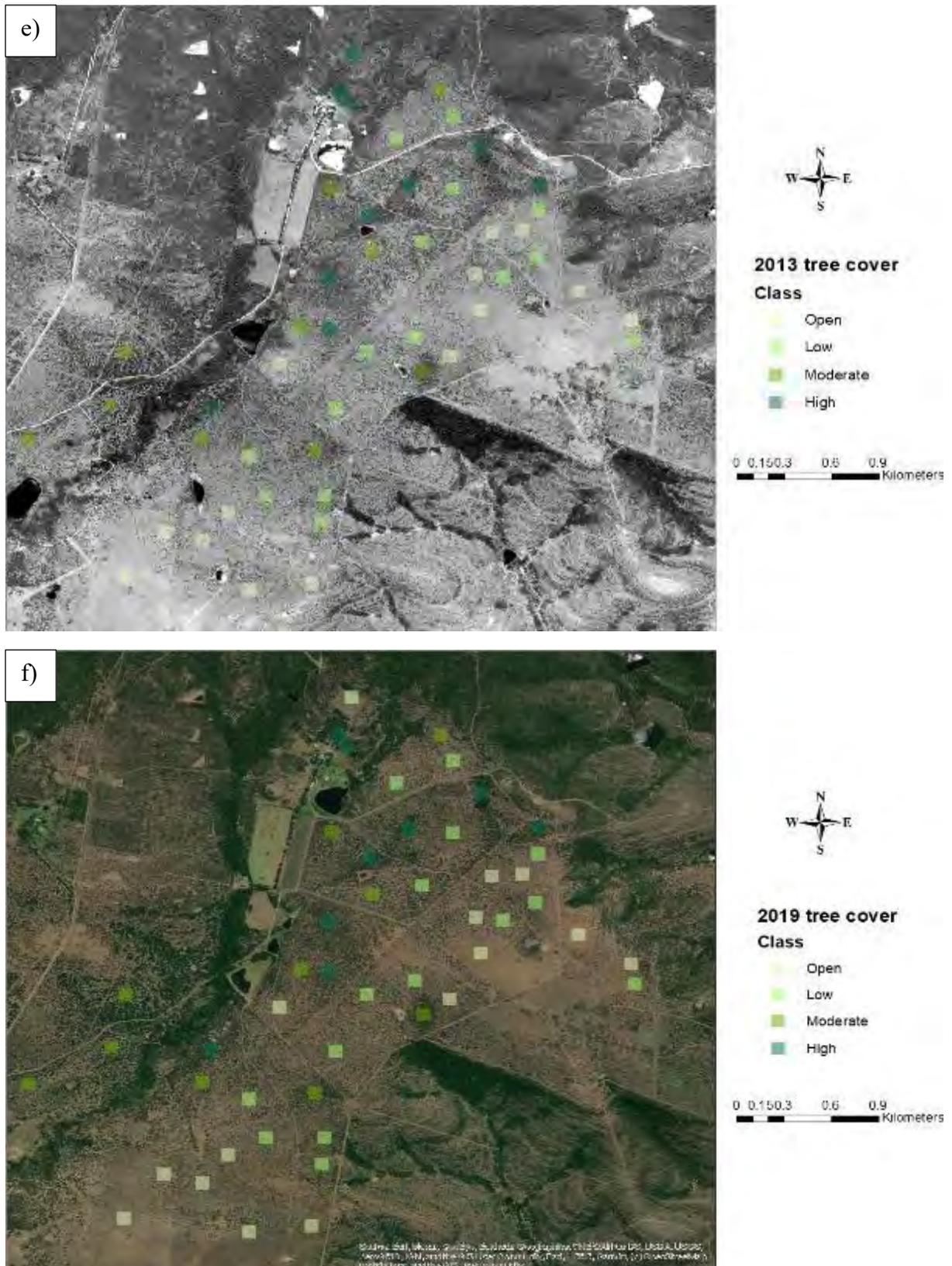


Figure 2. 5 a)-f): Aerial photographs of a section of Endwell farm where the study sites are colour coded to indicate their canopy cover classes open (0-15%), low (16-30%), moderate (31-50 %) and high (51- 100%). The photographs are showing the vegetation during the years: a) 1949, b)1968, c)1985, d)2002, e)2013, f) 2019.

Once woody cover change started, it generally progressed steadily over the subsequent time intervals. While canopy cover change was heterogeneous, overall, there was evidence that it took several decades for a site to go from low to high canopy cover. The exception was the period from 2002 to 2013 where some sites showed a dramatic increase in canopy cover. All sites with high canopy cover took at least 17 years (2002-2019) to get that high from a low baseline, but some have been at high cover for several decades, these will be the sites that have the most distinct woody composition as shown in Chapter 3. The low canopy cover sites showed a gradual canopy cover increase, while sites that were high in 2019 had a sharp increase between 1949 and 2019. There was a site in the low canopy cover class that had a sharp increase in tree cover, and then decreased sharply to 0% canopy cover. The rate of canopy cover change was thus different for all the sites, with most of the sites beginning at the same canopy cover (% 0) and ending at varied tree cover states in 2019. There were some sites that declined in canopy cover between the years, and these sites showed a distinct trajectory from the other sites in their designated 2019 canopy cover classes.

Frequency distributions of woody canopy cover over time (Figure 2.7) show that the highest peak in 1949 was between 0-5 % tree cover. The peak shifted to the right (from points a) to b) in Figure 2.7) in the subsequent years as canopy cover increased at most sites. A single dominant peak at low tree cover was observed in the years 1949, 1968, and 1985. The distribution of canopy cover was dominated by lower canopy cover values in earlier years (1985-2002), with most of the sites being below 40%. A greater spread of canopy cover was observed in 2013 and 2019, with an emergence of a distinctly bimodal (or trimodal) distribution from 2013. with the lower cover sites also appearing to have two peaks. The years 2013 and 2019 had a similar distribution of % canopy cover, indicating slight changes in canopy cover between those years. Across all years, canopy cover of ~ 50 % is uncommon (Figure 2.7, point e). While none of the sites had canopy cover >50 % until 1985.

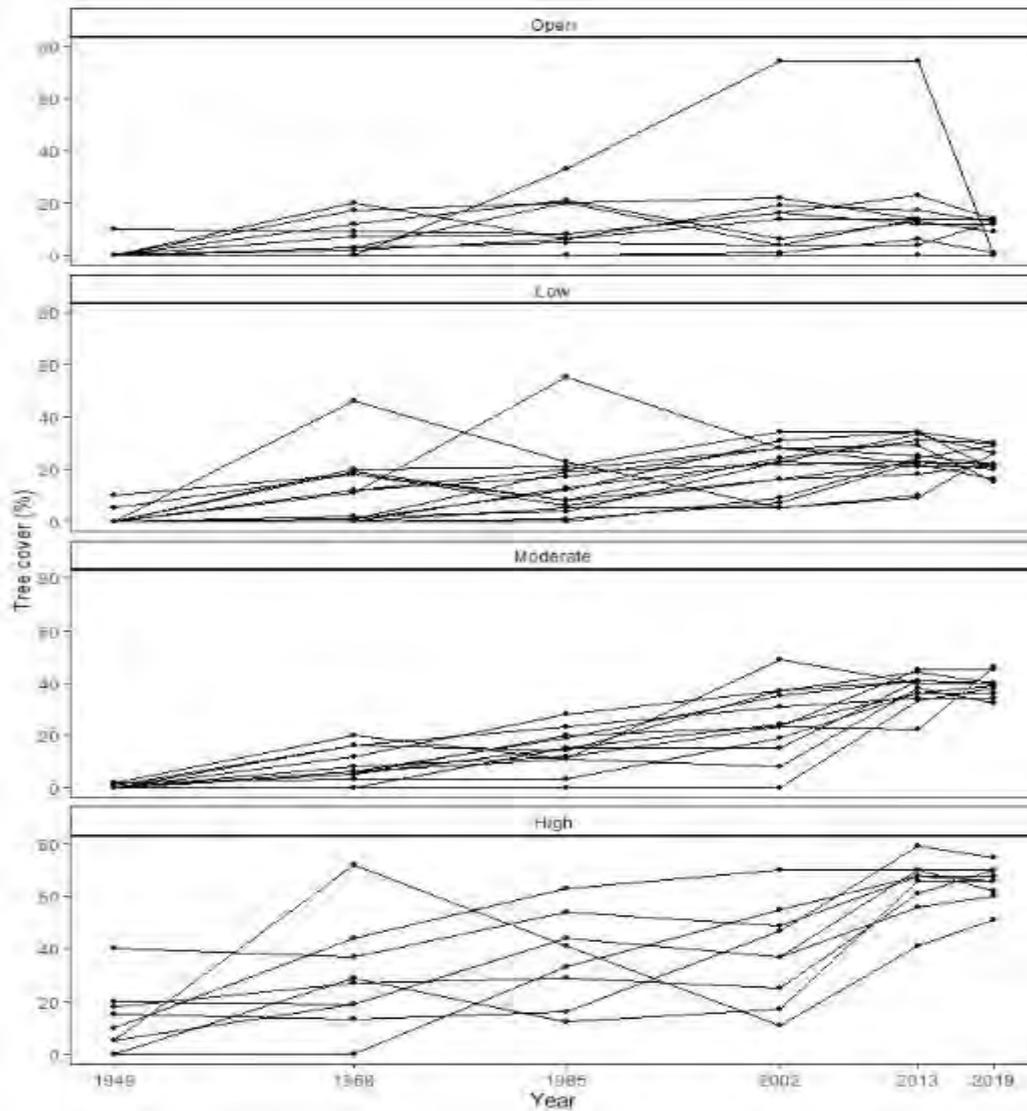


Figure 2. 6: Percentage canopy cover change estimated from aerial photography for the years 1949, 1968, 1985, 2002, 2013 and 2019 (from google imagery). There was a total of 51 sites (indicated by the lines). Each panel shows the trajectory of groups of sites that were in the same canopy cover class in 2019. Canopy cover classes are: (Open (1-15%), Low (16-30%), Moderate (31-50%), High (51-100%) according to 2019 aerial canopy cover. One of the sites was cleared in the open cover class graph, and it followed a different trajectory over the years.

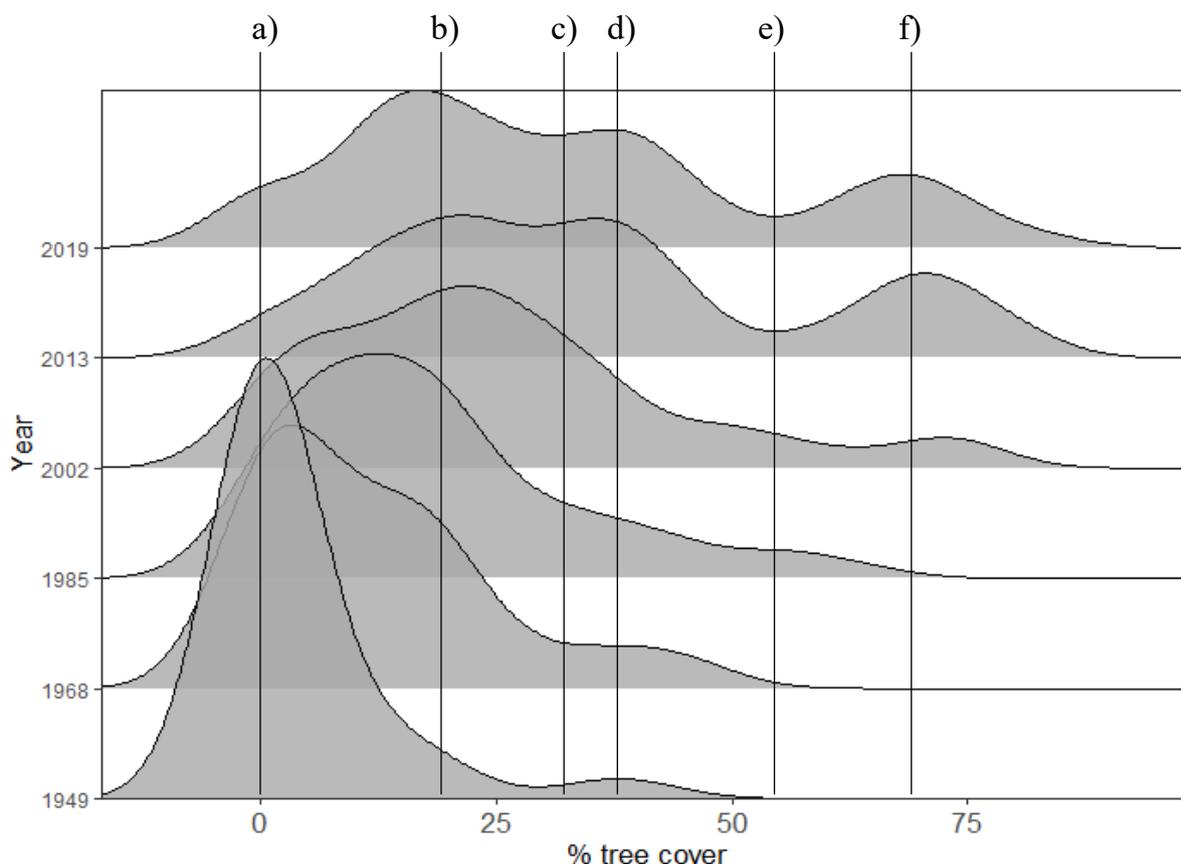


Figure 2. 7: Density plots as ridges for aerial percent canopy cover estimated in 1949, 1968, 1985, 2002, 2013 and 2019. Vertical lines on the graph indicate a) a peak (open state) in earlier years, b) peak at ~ 20% canopy cover in earlier years c) rare canopy cover state at ~ 30%, d) peak at 40% canopy cover (fire suppression threshold), e) 50% rare canopy cover and f) peak at 70% canopy cover at more recent years.

2.5.2. Tree cover transitions between years

There was a general decrease in the “open-open” transition and an increase in sites transitioning into “low”, “moderate”, and “high” sites over the decades (Figure 2.8). The most common transition from 1949 to 1968 was “open-open” followed by the “low-low” transition. There were 32 sites that remained open from 1949 to 1968, and 12 that remained at a low tree cover state. The most common transitions from 1968 to 1985 were similar to the period from 1949 to 1968. There were 24 sites that remained open from 1985 to 2002, seven sites had changed from open to low and 10 sites remained low. There was a notable change in the common transitions between 1985 and 2013. Only 9 sites had remained open from 1985 to 2002 and 15 open sites had shifted to a low tree cover state. There were more

sites changing from lower tree cover states to moderate or high tree cover state between 1985 and 2019. There were 6 sites that had changed from a low to a moderate tree cover state between 1985 and 2002. The period between 2002 and 2013 had the highest number of sites transitioning from a moderate to a high tree cover state and this was also the period with the most diverse transitions. The 2013-2019 period showed stability, with very few sites transitioning out of their states. There were 15 sites remaining at a low tree cover state between 2013 and 2019 and 14 sites that remained open. The most distinct shift in tree cover between 2013 and 2019 was two sites becoming open from a high tree cover, when they were manually cleared.

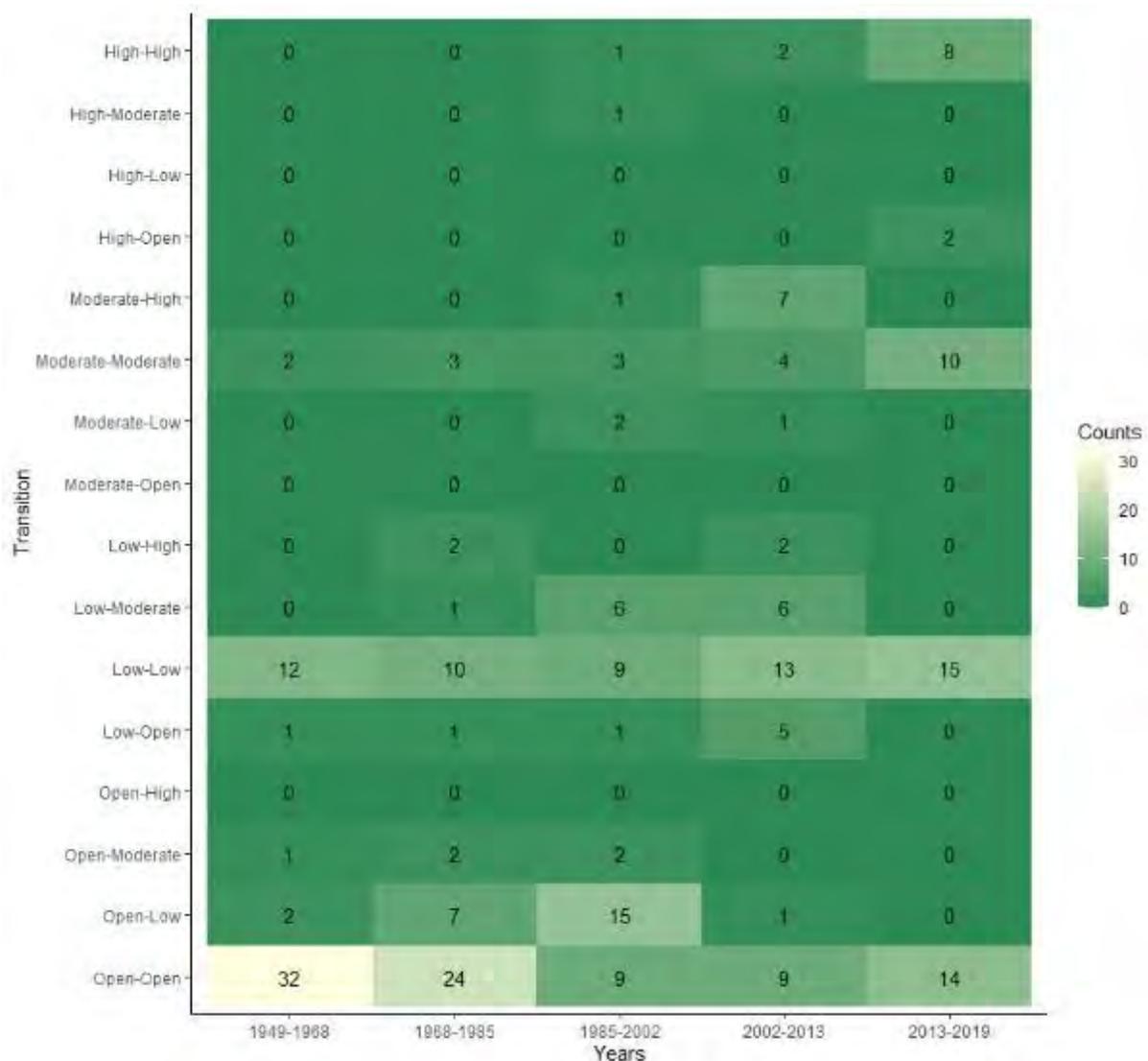


Figure 2. 8: Heatmap showing the number of sites that have transitioned into various states of tree cover (y-axis) between periods of years (x-axis- 1949-1968, 1968-1985, 1985-2002, 2002-2013, 2013-2019).

2.5.3. Rainfall and canopy cover change

There was an interchange between periods of above average rainfall and below average rainfall in the period between 1949 and 2019. There was a prolonged period of below average rainfall between 1952 and 1968 (Figure 2.9), where all the years recorded below average rainfall, representing the longest period of below average mean annual rainfall for this study (between 1949 and 2019). The period starting from the early 1972 up until the 1975 had above average rainfall years which were followed by a period of below average rainfall until 1985. The drought between 1977 and 1984 was followed by a period of high rainfall that was interrupted by a year with rainfall below 400 mm. Mean annual rainfall was high for the years between 2004 and 2006 and there was a short period of low rainfall represented by a single trough in the year 2009, followed by a series of below average rainfall years until 2013. The average annual rainfall between 1949 and 2019 was 722 mm. The maximum rainfall (1105 mm) was recorded in 2006, with the minimum rainfall (371 mm) recorded in 1949. Periods of below average rainfall were 1958-1968, 1980 -1985 and 2013-2019. Periods of above average rainfall were 1970-1979 and 1990-2013. Foley's index (1y/2 y/3y cumulative) show that the driest period was between 1949 and 1968 (Figure 2.9; Table 2.3).

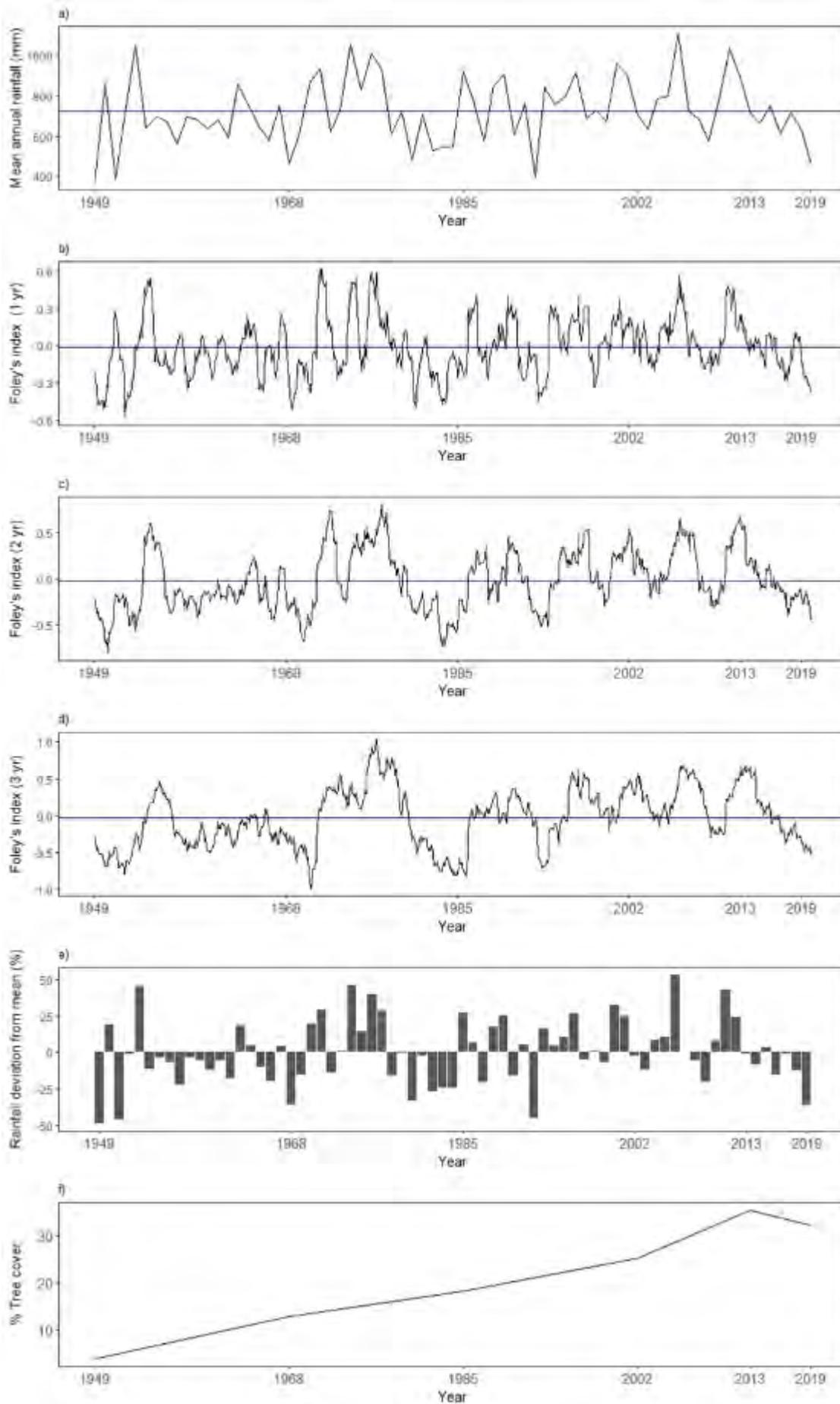
The mean annual rainfall, Foley's index in all the periods between 1949 and 2019 and the periods before the dates were related to the rates of tree cover change. There was a general increase in mean annual rainfall over each period between aerial photos between the years 1949 and 2013, but the period between 2013 and 2019 was drier than average (Table 2.2). There were notable peaks indicating above average rainfall events between 1968 and 1985. The rainfall experienced before the 1968-1985 period was mostly below average (Figure 2.9 a). The average canopy cover on specific sites on the farm (at the 51 sites sampled) shifted from 3.80% in 1949 to 32.29% in 2019. Mean rainfall for previous periods (10 years prior) showed an increasing trend between the years 1968 and 2019. The highest mean annual rainfall in the period preceding aerial imagery is highest for the 1949-1968 (792 mm).

The mean Foley index was positive in the periods 1985-2002 (0.044) and 2002-2013 (0.084). The period with the lowest rainfall was the average between the years 2013 and 2019 (633 mm) and this period also had the lowest canopy cover change (-0.52 % y⁻¹). The mean annual rainfall 10 years prior to 2013-2019 was the lowest at 676 mm. The rate of canopy cover change was the highest in the period 2002-2013. The 2002-2013 period had the highest mean annual rainfall (792 mm), and a positive Foley's index during the period (0.043) and 10 years

before the period (-0.053). There was a notable decline in the rate of tree cover change from the periods 1949-1968 (0.47 % y⁻¹) to 1968-1985 (0.32 % y⁻¹). The mean Foley's index 10 years before the beginning of a period was highest in 1949-1968 (0.092), this period also had the second highest rate of canopy cover change increase (0.47% y⁻¹). The lowest tree cover change (0.32 % y⁻¹) was estimated between 1968 and 1985, the mean annual rainfall during that period was 742 mm and the mean annual rainfall in the previous period (10 years) before 1968-1985 was 693 mm. Mean Foley's index for 2 and 3 years cumulative was greatest for the period 2002-2013 (0.18 and 0.25 respectively).

Table 2. 3: Rate of woody cover change (the average canopy cover for all 51 sites was taken), mean annual rainfall during a period (rainfall averaged from the first year to the last), mean rainfall 10 years prior a period (mean annual rainfall averaged for 10 years before the start of a period), and Foley's index (1, 2, 3 year cumulative) during the aerial photo periods and for the previous period (1-year cumulative deficit).

Period	Rate of woody cover change (% y ⁻¹)	Mean annual rainfall (mm)	Mean rainfall 10 years prior period (mm)	Mean Foley index (1 y cumulative)	Mean Foley's index (2 y cumulative)	Mean Foley's index (3 y cumulative)	Mean Foley index (1y) 10 years prior period
1949-1968	0.47	664	766	-0.092	-0.16	-0.24	0.092
1968-1985	0.32	742	693	-0.0084	-0.032	0.060	-0.097
1985-2002	0.41	754	776	0.044	0.053	0.011	-0.053
2002-2013	0.93	792	796	0.084	0.18	0.25	0.043
2013-2019	-0.06	633	676	-0.086	-0.03	0.024	-0.086



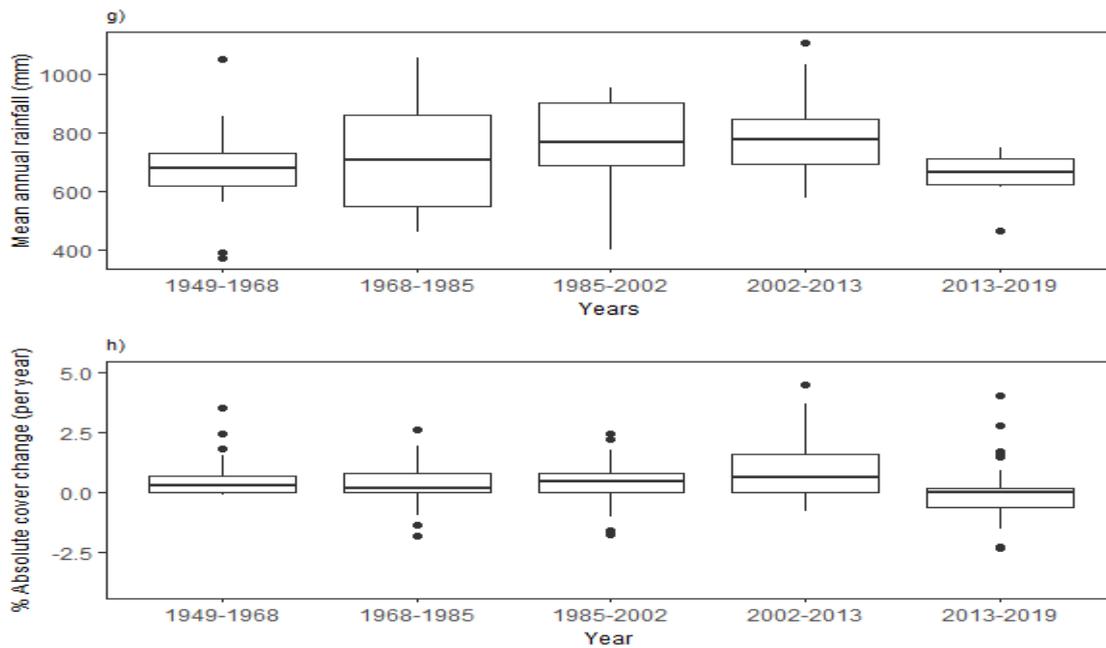


Figure 2. 9: a) Average annual precipitation (mm) with a blue line indicating the period’s average, b) Foley’s index 1 year surplus/deficit (relative to annual mean) c) percent deviation from long term mean, d) Average aerial tree cover, e) Boxplot of mean annual rainfall (mm) for each period. The median is drawn as a line inside the boxplot. Outliers are indicated as dots and the maximum and minimum as lines on the boxes, f) Boxplot of absolute rate of tree cover change /year for each period. The mean annual rainfall for the period between 1949 and 2020 was 732 mm, Median 712, mean 722, 1st quartile 617 mm, 3rd quartile 834mm.

2.6. Discussion

2.6.1. Changes in tree cover

Historical aerial photography provided evidence for increasing canopy cover over several decades on Endwell farm. This study showed that bush encroachment had been occurring in some patches since 1949 on the farm, confirming various studies that have documented tree cover increases in the Eastern Cape in the 20th century (O’Connor & Crow, 1999). These changes could be interpreted as savanna thickening, which is the increase of savanna tree species while C₄ grasses are kept intact, or thicket expansion, which is the increase in broad-leaved tree species, excluding the C₄ grass layer (Parr *et al.*, 2012). Both bush thickening processes have consequences for the overall functionality of the system as they change the structure of the canopy layer and tree interactions with the herbaceous layer (Scholes & Archer, 1997).

The average canopy cover of the sites sampled was 3.80 % in 1949 and it increased tenfold to 32.29 % in 2019. This indicates major shifts in the canopy structure of many sites. The density plots shown in Figure 2.7 showed shifting distributions in woody canopy cover over the years. There were two peaks in the canopy cover of the years 2013 and 2019, with an abundance of low and high tree cover sites. Even as the peaks in tree cover shifted between the years, sites with a tree cover ~50% were rare in all years. Staver *et al.* (2011a) found that sites with intermediate tree cover (50 – 75 %) were rare at the scale of sub-Saharan Africa. They found that tree cover does not increase continuously with rainfall and that tree cover is either constrained to low (< 50 %, “savanna”) or high tree cover (> 75 %, “forest”). Although this current chapter focused on a few selected sites, representing different tree cover classes in 2019, it is still evident from all the years that sites generally tend to have either high or low tree cover. This pattern suggests that there are complex interactions between various factors on the farm, resulting in the formation of alternative stable states in tree cover.

The rate of canopy cover change was different for each site, with some sites showing evidence of clearing/thinning events in some years and others remaining open. Other events of tree mortality can take place during periods of drought (Fensham *et al.*, 2009; Archer *et al.*, 2012). Sites are also expected to show different rates of tree cover increases due to environmental factors. Studies have shown that topography and soils tend influence woody cover formation (Hoffman & O’Connor, 1999; Colgan *et al.*, 2012). The small differences in topography and soils in which sites were found may have resulted in the differences in woody cover formation. Other factors could include proximity to established thicket (sources of propagules, Skowno, 2018). Woodland increase was found to occur incrementally along an advancing “tree front”. Treeless grasslands located 1.5 km away from woody patches would be limited by seed dispersal of encroaching woody species (Skowno, 2018). At the same time, rugged and incised sites that are located near valleys generally have a woody community which becomes seed providers to open sites (Skarpe, 1991; O’ Connor & Crow, 1991). It can be confirmed (aerial photographs, Figure 2. 4) that sites with high canopy covers in earlier years were located near densely wooded valleys, supporting the theory that wooded patches provide tree seedlings to adjacent open landscapes.

2.6.2. The impact of rainfall events on tree canopy cover

The differences in canopy cover class transitions between each period also suggested that encroachment was triggered by some external events in each period (Figure 2.9). For example,

most of the sites had remained open or at a low tree cover in the periods 1949-1968, and 1968-1985, and this transition became less common in the periods 1985-2002 and 2002-2013. The period with the most transitions was between 2002-2013, which saw more sites increasing in tree cover (Figure 2.8, Appendix A).

Above average rainfall events following a below average rainfall period are expected to lead to woody plant encroachment (Dean *et al.*, 1995; O'Connor, 1995; O'Connor & Crow, 1999; Kraaij & Ward, 2006; Joubert *et al.*, 2008). Rainfall was generally high in the period preceding 2002-2013 and this may have influenced the growth and establishment of trees. With an exceptionally wet year in 2006 (the wettest year in the whole record) and notably a wet 2-year period in 2001-2002 and 2011-2012, germination during the 2011-2013 period would not have reflected in the 2013 aerial photo but seedlings that established in the wet year of 2006 would have had good conditions for survival and growth in the subsequent years. There was a notable decline in the rate of tree cover change from the periods 1949-1968 to 1968-1985 (Table 2.3). The mean annual rainfall was low (664 mm) in 1949-1968 and could have influenced the rate of canopy cover increase in 1968-1985. The rate of canopy cover change is lowest between 1968-1985, and this implies that there was a low rate of tree recruitment in the previous period, which can be linked to the lowest rainfall between 1949-1968. The most dominant tree at Endwell farm was *V. karroo*. The tree has been reported to be responsible for the invasion of grasslands in the Eastern Cape and KwaZulu-Natal (Hoffman & O'Connor, 1999; Mucina & Rutherford, 2006). It has been shown that *V. karroo* has a limited seedling survival probability at MAP below 500 mm (O'Connor, 1995a, 1995b). Therefore, the low tree cover change observed between some years can be explained by longer periods with MAP below 500 mm in some years. The lower canopy cover change in more recent periods may be explained by Axelsson & Hanan (2018) who found that rates of encroachment are highest where initial cover relative to potential maximum cover is highest (i.e., where there is a high "woody cover deficit"). This would mean that where woody cover is already high, the rate must slow down as there is less "room" for more cover to be added.

Lag phases followed by a sharp increase in growth of a population are common for invasive species (Richardson *et al.*, 1994) - a pattern attributed to changing rainfall patterns. There was an abrupt increase in the rate of canopy cover between 2002-2013, following slower tree cover changes. As stated in chapter 1, a series of dry years, followed by several wet years may cause an increase in the recruitment of the woody component (O'Connor & Crow, 1999). Below average rainfall was recorded 10 years before 2002. Small individual trees were probably able

to take advantage of the weakened grass competition that may have occurred after high mortality rates of grasses after a drought (Danckwerts & Stuart Hill, 1988; O'Connor 1994).

Previous studies that quantified rates of canopy cover change such as O'Connor *et al.* (2014), using aerial photography report ranges between $-0.13\% \text{ y}^{-1}$ to $1.28\% \text{ y}^{-1}$ of canopy cover increases. Skowno (2018) studied the rates of tree cover change in mesic and arid savanna sites and reported ranges between $-0.04\% \text{ y}^{-1}$ and $1.13\% \text{ y}^{-1}$ for an arid and mesic savanna site in the Eastern Cape. In Skowno's (2018) study, the arid site's rate of tree cover change ranged from $-0.041\% \text{ y}^{-1}$ to $0.492\% \text{ y}^{-1}$. This chapter found a different range in the rates of canopy cover change ($-0.52\% \text{ y}^{-1}$ to $0.93\% \text{ y}^{-1}$) and this can be explained by the fact that 51 individual sites were selected on the farm instead of focusing on the entire area. Sites chosen in our study were also those that had undergone considerable changes over the years and some that had remained the same. The differences in the methods employed to quantify canopy cover and the selection of individual sites thus led to a biased calculation of canopy cover in this current study. The average rate of canopy cover change in this chapter ($0.32\% \text{ y}^{-1}$) is still comparable to the rate of woody cover change which was reported to be $0.37\% \text{ y}^{-1}$ in a commercial farm from 1963 to 1986 in Kei Road (Eastern Cape) (O'Connor *et al.*, 2014). The mean rate of change in African savannas is $0.25\% \text{ y}^{-1}$ (O'Connor *et al.*, 2014). Differences in average rates of change are expected in different areas with varying land use and some grassland system may remain open due soil properties, presence of mega-herbivores and frequent fires (Kellman, 1984; Belayneh & Tessema, 2017). O'Connor *et al.* (2014) found that encroachment was most rapid on small, protected areas, intermediate under commercial tenure and slower under communal tenure and big natural environments that still have mega-herbivores.

2.6.3. Other explanations for increasing tree cover

There are other reasons for increases in woody cover which cause debates among researchers. There seems to be multiple drivers that are interacting to cause bush encroachment (Devine *et al.*, 2017). It is however difficult to determine how rising CO₂ levels may have contributed to the increases in canopy cover over the past decades studied in this chapter (1949 – 2013). Rising CO₂ levels affect C₃ plant photosynthetic efficiency. Zhu *et al.* (2008) showed that ambient temperatures are linked to photosynthetic efficiency in C₃ plants with increasing CO₂ concentrations. The current CO₂ concentrations only give C₃ trees an advantage over C₄ plants when temperatures are below 20 °C (Bond & Midgley, 2012). Temperature can get low during winter in this region, thus rising CO₂ may have contributed to vegetation changes. Rising CO₂

levels may also improve water use efficiency in C₃ plants (Ainsworth & Rogers, 2007). In arid systems, CO₂ enrichment, increases water availability and reduces the limitations on maximum woody cover, propelling woody plant establishment (Devine *et al.*, 2017). Some decades experienced below average rainfall, and C₃ trees may have had an advantage over C₄ grasses during this period.

There have been other environmental changes that have taken place in the Eastern Cape over the past 50 years which could have influenced the changes in vegetation between 1949 and 2019 (O'Connor & Crow, 1999). Changes in livestock systems to those that were based on selective grazers (sheep and cattle) decreased browsing pressure and the removal of small-mouthed feeders may have aided seedling recruitment (Prins & Van der Jeugd, 1993). Fire was also frequent in South African savannas during the 19th century. The suppression of fire through changes in management practices in subsequent years may have promoted increases in woody cover at a rate determined by the potential growth of a site, which is a function of mean annual rainfall (Rutherford, 1978).

2.6.4. Conclusions: Evidence of bush encroachment on Endwell

There is evidence that canopy cover has increased in many sites on the farm. Some sites remained open, while others had rapid increases in canopy cover over the years (1949-2019), suggesting that there are other factors acting on the vegetation in this area. The year with the highest mean annual rainfall and high mean annual rainfall 10 years to the period (and a high Foley's index) was between 2002-2013. The same period was observed to have recorded the highest rates of canopy cover change in another study (Skowno, 2018). Bush encroachment may continue as fire continues to be suppressed and livestock populations increase, reducing grass cover and giving advantages to tree populations. This chapter indicated that there is a consistent bush encroachment process taking place within the farm. Whether the process taking place in some sites can be described as savanna thickening or thicket expansion can be determined by analysing the composition of trees (Chapter 3) and the herbaceous layer (Chapter 4) in those sites. Evidence of distinct stable vegetation cover states would be investigated by analysing canopy structure components such as LAI, light transmittance, tree composition linked to the 2019 canopy cover states (Chapter 3)

Chapter 3

Changes in Tree Composition, Canopy Structure and Light Dynamics with Changing Canopy Cover

3.1 Introduction

3.1.1. Bush clump succession and changes in the light environment

Bush clump succession is reflected in the increase in stem density, shifts in species composition and the growth of tree crowns, causing a change in light attenuation underneath canopies (Smith, 1991; Brown & Parker, 1994). The expansion and densification of *Vachellia karroo* in Eastern Cape grasslands has been well documented (Acocks, 1953; O'Connor, 1995; O'Connor, 1999; O'Connor & Crow, 2009; O'Connor *et al.*, 2014). An increase of *V. karroo* density in savannas may facilitate the establishment of other woody species, which may consist of broad-leaved, bipinnate microphylls, and evergreen species (Jordaan, 2010), often in the form of bush clumps (O'Connor & Chamane, 2012). Clumps that have formed for a longer period, are expected to be dominated by late-successional, mostly shade-tolerant, forest species (Jarvel & O'Connor, 1999; O'Connor & Chamane, 2012, Jamison-Daniels *et al.*, 2021). These compositional changes may cause further changes in light dynamics in the understory, impacting the abundance of C₄ grasses.

A notable difference between thicket and savanna systems is light availability in the understory (Charles-Dominique *et al.*, 2018). The thicket understory has low light, higher air humidity, lower temperatures, low fuel loads and low ground temperature (Redding *et al.*, 2003). Thicket and forest tree species are therefore adapted to closed canopy, low light conditions, and thus have plant traits that are different to those of savanna trees. The seedlings of forest species have lower chance of survival in savannas due to greater water stress and fire frequency, while savanna tree seedlings have lower chance of survival in forest or thicket habitats due to their shade intolerance (Hoffman *et al.*, 2004; Gignoux *et al.*, 2016). As the woody component in grasslands increases, it may lead to a biome shift from grassland to scrub forest or thicket (Briggs *et al.*, 2005; Brook & Bowman, 2006; Bowman *et al.*, 2010; Wigley *et al.*, 2010; Parr *et al.*, 2012) with a different species assemblage because of changes in the

environment. Successional changes through this increase in the woody component will further promote the development of clumps (O'Connor & Crow, 1999).

A positive feedback loop is apparent as tree cover increases in savanna systems. Increasing tree cover causes a reduction in available light, and this causes a reduction in herbaceous biomass (especially of grasses), and this facilitates tree recruitment leading to closed canopies if not disturbed. The threshold point at which tree cover suppresses fire is estimated to be 45-50% (Hennenberg *et al.*, 2006; Archibald *et al.*, 2009; Staver *et al.*, 2011). Some studies have also found that understory light variability peaks at 40% canopy cover and decreases with increasing canopy cover (Dupre *et al.*, 2002; Ligot *et al.*, 2016). It is important to identify the points where thresholds take place, and what happens beyond these points. The threshold points may have consequences for the herbaceous layer as the vegetation becomes dense and land managers may want to prevent significant changes from occurring in the rangeland system.

3.1.2. Changes in species composition influencing light variability in woody vegetation

A change in tree species composition causes a response in light transmittance because light transmittance at the stand level is determined by the species differences in canopy architecture and LAI, and the number and size of trees (Canham *et al.*, 1994; Drever & Lertzman, 2003; Sonohat *et al.*, 2004). Differences in tree species aboveground growth patterns influence canopy positions in time and space (Anten & Hirose, 1999; Ishii *et al.*, 2013), and this may influence light capture at the community level (Sapijanskas *et al.*, 2014). Some studies suggest that stands with a mixed composition of tree species have denser canopies than monocultures because of the different crowns complementing each other (Pretzsch, 2014; Sapijanskas *et al.*, 2014). There will be differences in light attenuation between mixed and homogenous stands of trees because spaces in canopies are determined by interspecific and intraspecific variability in crown morphology (Pretzsch, 2014). Architectural complementarity among the crowns of different tree species and a more multi-layered exploitation of light explain growth enhancement in mixed tree stands (Erskine *et al.*, 2006; Pretzsch & Schütze, 2009). It is also shown that trees will adapt to size-asymmetric competition by morphological shifts to mitigate the light limitation (Grams & Anderson, 2007). Changes in the morphology of trees in response to light availability is documented in many studies (Sterck & Bongers, 2001; Valladares *et al.*, 2007). In homogenous tree stands, trees compete with similar behaviour for the growing space and resources. In mixed tree stands, differences in shading or mechanical constraints caused

by differences in tree species, can affect a tree species' architecture, which will also affect its ability to capture light.

The spatial variability in light transmittance in tree stands is largely due to canopy characteristics (Martens *et al.*, 2000; Tinya & Odor, 2016). Overstorey characteristics, which include the height, stand structure, pattern of overstorey layer (regular or regular pattern of trees), tree species composition and tree cover of woody plants cause light variability in the understory environment (Martens *et al.*, 2000; Valladares & Guzmán, 2006). Different types of forests or woody savannas will display different light regimes, due to differences in stand structure and species composition (Bartemucci *et al.*, 2006). For example, the arrangement of trees in a packed manner allows trees to capture light more effectively, leaving less light below the canopy (Ligot *et al.*, 2016; Forrester *et al.*, 2017). The difference in the light regime can also exist within the same stand of trees due to gaps, depending on the dominant tree species found in the stand (e.g., deciduous or shade-tolerant species; Muscolo *et al.*, 2014). Light availability is fine scaled within older, heterogeneous, closed stands which is a result of the structural and composition of the overstorey layer (Tinya & Odor, 2016).

The position of the sun throughout the year, the position of gaps before and after leaf expansion, the timing of bud bursts and the period of spring before leaves expand all influence the light transmittance below the canopy in temperate regions to different degrees (Wirth *et al.*, 2001; Sercu *et al.*, 2017). Differences in the timing of leaf expansion create large differences in below-canopy light transmittance between stands differing in their species composition (Wesolowski & Rowinski, 2006; Bobinac *et al.*, 2012). Leaf area index, which is the total one-sided area of leaf tissue per unit ground surface area (Watson, 1947) is a key parameter to consider when analysing the effect trees have below their canopies. An increase in canopy leaf area, which can be linked with increasing canopy cover, will be accompanied by a reduction in the amount of light reaching the ground received (Breda, 2003; Ryu *et al.*, 2010).

3.1.3. Plant traits distinguishing savanna and thicket species

Trees that grow in forests or closed canopies are compositionally and functionally distinct from savanna trees (Hoffman *et al.*, 2012a; Charles-Dominique *et al.*, 2018), with savanna trees being more tolerant of competition with grasses, water stress and frequent fires. Functional traits can be response traits (such as shade or fire tolerance) or effect traits (such as light interception or flammability (Lavorel & Garnier, 2002)). The transition from a savanna to a

thicket should be marked by a change in plant traits, which influence light transmittance in the understory. Canham *et al.* (1994) found that variation in light extinction was strongly correlated with shade tolerance and the succession status of the species. Shade tolerant species were found to cast the deepest shade, while earlier successional species allowed greater light attenuation in the understory (Charles-Dominique *et al.*, 2018).

Leaf properties such as phenology, which is the study of plant activity (Diaz, 1998) is a relevant factor to consider when studying differences in light transmission between tree stands of varying canopy cover. *Vachellia karroo* trees are deciduous, with a distinct canopy structure from other tree species in this study area. This may result in light transmittance differences between stands that are dominated by evergreen, broadleaf tree species characteristic of thicket and those dominated by deciduous, microphyllous (small leaved) *Vachellia karroo* trees.

3.2. Objectives, Aims and Hypothesis

In Chapter 2, it was shown that most of the sites had been open seven decades ago (2019-1949), and many of these had undergone rapid bush encroachment in the subsequent decades, especially from the year 2002 onwards. The general aim of this chapter was to examine the compositional and structural changes that occurred as canopy cover increased, and how canopy cover and tree composition affected the light environment. In addition, this chapter aimed to elucidate the successional sequence, whether continuous or made of distinct stages in terms of tree composition, and how the light environment changed as it progressed. I also looked for evidence of a threshold in canopy cover associated with a switch from savanna (predominantly *V. karroo*) to thicket (predominantly a mixed community of broadleaf species). I used a structural equation model to examine the complex relationships between canopy structure variables (canopy area, canopy volume, maximum canopy area, density of trees, density of trees > 3m), canopy cover and light dynamics. I also examined whether canopy volume and light transmittance were influenced by woody species composition and more specifically if the later successional (broadleaf, evergreen) species had a disproportionate effect on light transmittance and leaf area index (LAI) due to their leaf and canopy traits.

I hypothesized that there would be more tree species, taller trees, and a more diverse assortment of trees with an increase in canopy cover, while sites that have remained in fairly open and moderately dense sites would have fewer tree species, with less diversity, and would be dominated by *V. karroo*. The proportion of broadleaved, evergreen trees would increase as

canopy cover increases, and this would result in decreased light transmittance. I expected that higher tree cover sites would have larger trees (higher canopy volume and area), indicating a longer length of growth. The broadleaf species found at the densest sites (and which have been encroached the longest) would have a proportionately greater effect on LAI and light transmittance.

3.3. Methods

The percentage canopy cover at the 51 sampling sites was estimated from a 2019 Google Earth satellite image as described in Chapter 2. Percent canopy cover in 2019 was used to represent the current vegetation status of the 51 sites for this study. This chapter examines the relationships between aerial canopy cover, woody species composition, tree species diversity, density of trees, density of trees > 3m, maximum height of trees, canopy area, canopy volume, light transmittance and LAI at each site.

3.3.1. Sampling design and data collection

A sampling plot was laid out in the centre of each of the 150×150 m sites described in Chapter 2. In some cases, the sampling plot was placed at a reasonable distance away from the centre of the site to ensure it was representative of the vegetation structure of the whole site (for example, where the centre of the plot had a lower density of trees than the entire site). Sampling took place during the summer growing season to ensure tree canopies were fully leaved, in November 2019, March 2020, and November 2020. Each 15 m × 6 m sampling plot consisted of ten 3 m × 3 m subplots laid out using 50 m measuring tapes (Figure 3.1). Coordinates were recorded at the start, mid- and endpoint of the long axis of each plot and pins were left at the start of each point to mark the area for re-sampling. Spray paint was also used to mark trees in each plot to allow sites to be relocated for sampling the herbaceous vegetation in March 2020.

Canopy volume and area were estimated using tree size measurements. For all woody species > 50 cm height, I measured total height, height to the base of the canopy, and canopy diameters. The diameter measurements were taken to capture the widest canopy extent (D1) and the other measurement (D2) was made perpendicular to D1. These measurements were used to estimate the sum of canopy area and canopy volume at each site. Trees were identified on site or at the Schonland Herbarium (GRA) in Makhanda. I classified all species as “evergreen” or “deciduous” using Palgrave’s (2002) tree descriptions. Evergreen species are

those that keep their leaves throughout the year and are never without leaves. Deciduous plant species have leaves for some months and begin to lose their leaves during the dry season. All species bore leaves at the time of sampling.

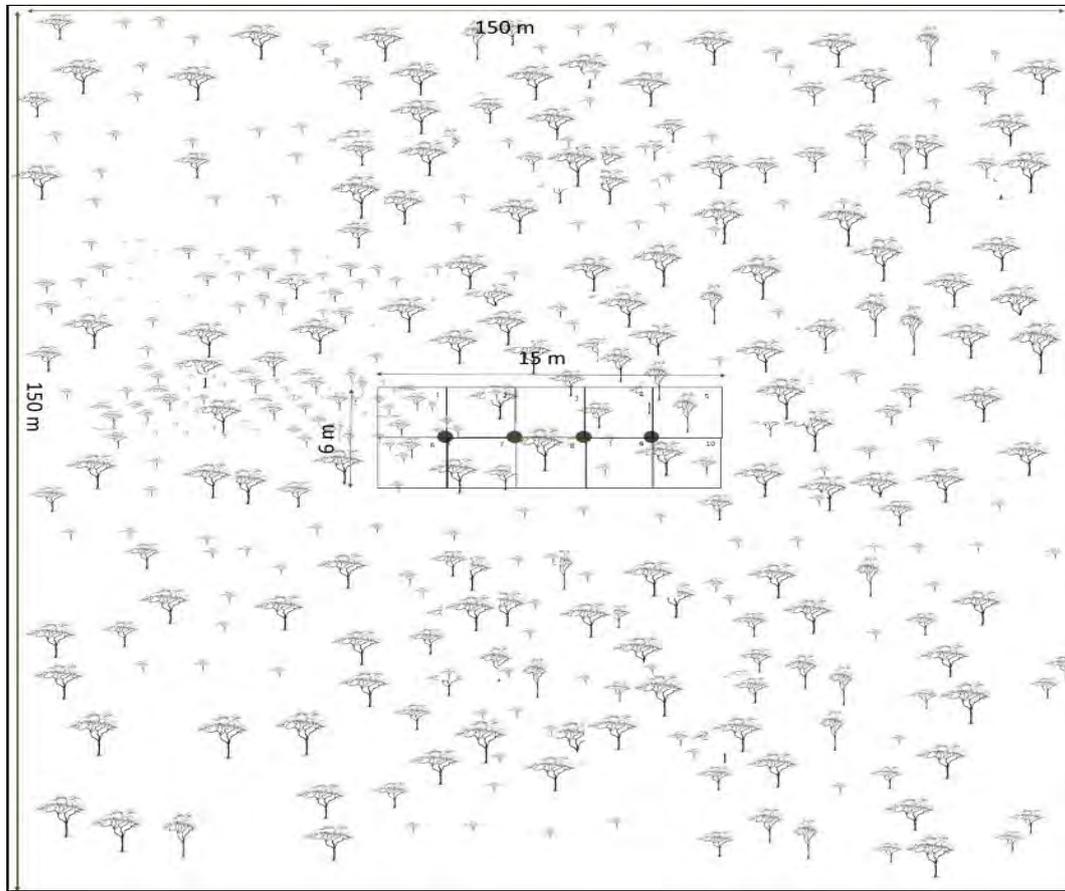


Figure 3. 1: A diagram showing the 150 m×150 m (51) sites and the 3×3m plots, divided into 10 subplots. The green circles represent the 3m intervals at which photographs were taken.

Canopy volume consisted of the entire canopy of a tree from the bottom of the crown to its highest point and from its centre to its furthest tips- D1 and D2. I assumed that the shape of the canopy was constant, that it had a solid geometric outline, and that equations could be applied to predict canopy area and volume of the tree. I also assumed that the shape of trees was consistent across different tree species.

$$\text{Canopy area} = \pi \times (D1/2) \times (D2/2)$$

$$\text{Canopy volume} = \text{Canopy area} \times \text{height of canopy (crown height)}$$

The total canopy area and canopy volume within a plot was determined by summing the canopy areas/volumes of individual trees within a plot. The data was summarised for each of the 51 plots.

To represent species diversity, I calculated the Shannon diversity index (Table 3.1)

I used hemispherical photographs to determine light transmittance and LAI. Hemispherical photography has been used in studies of canopy structure and forest light transmission (Frazer *et al.*, 1999). Hemispherical photographs were taken using a Pentax K30 DSLR camera and fisheye converter lens (180° angle) at 3 m intervals along the long axis of the plot (shown by the green circles in Figure 3.1). Each photograph was taken at ~10 cm above the ground by placing the camera on a small beanbag. The camera was set to self-timing, where the shutter delay was set to 10 seconds to allow me to move away from the frame. The camera was placed with the fisheye lens facing upwards, producing circular photos. A compass was used to fix the camera's direction to the North. Hemispherical photographs are sensitive to high light conditions and were thus taken on cloudy days or when the sun was not overhead to enable a standardized background.

Photographs were analysed using Gap Light Analyzer 2.0 (GLA, Simon Fraser University, British Columbia, 1999) following the GLA manual (Frazer *et al.*, 1999). The photos were configured by inputting the site location coordinates, growing season (September- April), sky region brightness and atmospheric conditions of the nearby town of Fort Beaufort. Each image was then classified into sky and non-sky. To improve the classification, the blue plane provided by the application was used. An analysis of canopy structure and gap light transmission data was generated and exported to a spreadsheet. The LAI estimated at ring 4 was used in this study.



Figure 3. 2: Examples of images obtained from hemispherical camera, illustrating a gradient from low to high canopy cover sites. Percentages of light transmittance were estimated from sky vs non-sky in the images.

3.4. Statistical analyses

3.4.1. Changes in species composition with increasing canopy cover and decreasing light transmittance

All statistical analysis were conducted in R (R Core Team, 2019). Canopy cover and light transmittance data were grouped into classes to determine patterns in tree compositions between sites belonging to the same group ranges. I used the same tree canopy cover classes as in Chapter 2, viz. open (0%-15%), low (16%-30%), moderate (31%-50%) and high (51%-100%). These classes agree with Puttick *et al.* (2014) who defined closed woodland as having trees making up more than 50 % of the vegetation. The woody cover indicating an unstable state in Chapter 2 was found to be ~50%. Others have also shown the threshold point for fire presence to be at 45- 50 % tree cover (Hennenberg *et al.*, 2006; Archibald *et al.*, 2009; Staver *et al.*, 2011). The sites were also grouped according to light transmittance using the hemispherical camera data: A (91-100%), B (81-90%), C (71-80%), D (51-70 %), E (20-50%). Kernel density plots were drawn to show the distribution of canopy cover values in each light transmittance class and the distribution of light transmittance values in each light transmittance class.

A tree species composition plot was generated following Torondel *et al.* (2016) using the package *ggplot2*. A species abundance matrix (sites vs species) was used to determine the proportions of species contributing to the total number of species at each site. All dominant trees found in this study were included in the species composition plot. The sites were grouped according to light transmittance classes.

Non-metric multi-dimensional scaling (NMDS) is an ordination reduction technique used to simplify multivariate data into fewer axes dimensions (Wagner *et al.*, 2007; Vathy-Fogarassy & Abonyi, 2009) that employs rank order information of a computed matrix of similarity or difference metrics between collected pairs of samples. Brays-Curtis distance measures were used in this chapter from the *metaMDS* package. To compare the similarity in tree species composition and relate them to the classes of canopy and light transmittance, tree abundance data set was used for 45 sites (6 sites had no trees). A Bray-Curtis similarity matrix based on the number of stems of each tree species at each site was generated using log transformed data to generate the NMDS plots.

A one-way multivariate analysis of variance (MANOVA) was used to compare multivariate sample means between light transmittance and canopy cover classes using tree species

abundance scores (Package *vegan*). *Vegan*'s *adonis* function was used for a permutational multivariate analysis of variance (PERMANOVA) to test whether the centroids and dispersions of the groups (light transmittance and tree cover classes) differed. The *adonis* function partitions the distance matrices among sources of variation. A permutation test with pseudo-F-ratios was generated through the *adonis* function fitting linear models.

To identify relationships between sites belonging to the same canopy cover and light transmittance classes, a dendrogram representing a two-dimensional cluster similarity matrix was constructed. The dendrogram was constructed with the *pheatmap* package in R. The data was in a form of a species abundance matrix (sites vs. species) and external environmental factors (sites vs. environmental factors). The abundance values were \log_{10} transformed to even out the abundance scores. Hierarchical clustering using the clustering distance "manhattan" and the "complete" method was performed in the *pheatmap* function. The output generated was a heatmap with a dendrogram with each square on the heatmap representing the abundance level of a species at each site. The dendrogram shows how sites clustered according to tree species abundance similarity. The environmental factors (light transmittance and aerial canopy cover classes) were added onto the branches of sites. Groups were ordered according to tree species composition similarity as canopy cover increased (decreasing light transmittance).

3.4.2. Bivariate relationships between canopy and light variables

Paired correlations were performed to explore the relationships between Shannon index of tree species, density of trees, density of trees > 3m, maximum height, canopy area, canopy volume, maximum height, maximum canopy area, light transmittance (%), LAI and tree cover in 2019 to determine relationships between these variables. The function on R, *ggpairs* produced a matrix of scatter plots and their corresponding x and y regression formulae, R and Spearman correlations (p value). A function was generated to colour Spearman correlations according to level of significance. The three assumptions for a correlation and regression are normality, linearity, and homoscedasticity. These assumptions were not always met and a \log_{10} and a square root transformation was first applied to the data. However, these transformations did not result in an improved linearity. The Spearman's rank-order correlation was used to analyse the data instead of the Pearson correlation that measured the strength and direction of the linear relationship. Spearman's correlation coefficients (p and R) measured the strength and direction of associations between canopy variables. A Smoothing method (LOESS) was used to draw regressions on the graphs. The LOESS (locally estimated scatterplot smoothing) fitted a

smooth curve using weighted regression through the scatter plots. The aim for the pair plot was to highlight significant relationships to be used in the SEM (Structural Equation Model) (see the next section).

3.4.3. Bivariate relationships between common tree species and canopy variables

Bivariate relationship plots were constructed to analyse the relationships between the stem density of common species in this study (*Gymnosporia buxifolia*, *Olea europaea* subsp. *africana*, *Scutia myrtina* and *V. karroo*) and light transmittance, LAI and total woody canopy cover. Correlations were also performed to assess the relationships between the dominance of plant phenological types (evergreen or deciduous) with light transmittance, LAI, canopy area and canopy cover in 2019. The p values from Spearman correlations and R values were generated for all the correlations.

3.4.4. Analysing pathways between canopy structure, canopy cover and light transmittance

A partial least squares structural equation model (PLS-SEM) was constructed to analyse the structural relationships between canopy structure variables, canopy cover and light dynamics using the package *semPLS* in R. Outer correlations, weights were calculated using Pearson correlations. The factor scores, outer weights, path coefficients and total effects were generated and drawn as a model. A meta-model (Figure 3.3) was first constructed that represented the hypothesis based on theoretical propositions. The model was guided by the hypothesis that both canopy structure and canopy cover would influence light transmittance. The inner model in the PLS-SEM shows the relationship between the latent variables and the arrows (Figure 3.3) head in a single direction (Hair *et al.*, 2011). There were nine observable indicator variables (rectangles) and three latent variables (circles). Canopy structure was modelled using maximum canopy height, total canopy volume, tree diversity, density of trees, density of trees > 3m, and maximum canopy area. Canopy cover is the percent aerial tree cover in 2019. The latent variable “Light” was modelled using LAI and light transmittance. A goodness of fit test was applied to the model which generated R^2 values inserted on the model. The variables that resulted in the highest overall R^2 value were chosen for the final SEM model.

Table 3. 1: The variables examined in the pairwise analyses and in the structural equation model and their descriptions.

Variable (units)	Description
Shannon index	<p>A measure of diversity which accounts for both abundance and evenness of the species present.</p> <p>Shannon Index (H) = $-\sum_{i=1}^s p_i \ln p_i$</p> <p>$p_i \ln p_i$, where p_i is the proportion of individuals of one species (n) divided by the total number of individuals found (N)- (n/N), \ln is the natural log, and \sum is the sum of calculations and s is the number of species.</p>
Tree density (ha ⁻¹)	The number of trees > 50 cm found in sampling plots per hectare
Density of trees >3m (ha ⁻¹)	The number of trees with a height greater than 3m in sampling plots per hectare
Canopy area (m ²)	Sum of canopy area on each plot
Canopy volume (m ³)	Sum of canopy volume on each plot
Maximum height (m)	Height of the tallest tree in each plot
Maximum canopy area (m ²)	The largest canopy area in each plot (for an individual tree found at the site)
Light transmittance (%)	A measure of the percentage of light passing through canopies (leaf, branches, or stems), calculated from hemispherical photographs taken at 3m intervals in the middle of the plots (Figure 3.1).
LAI	Estimated leaf area index using hemispherical photographs
Canopy cover 2019 (%)	Aerial canopy cover in the year 2019 for each site, estimated from Google Earth satellite images

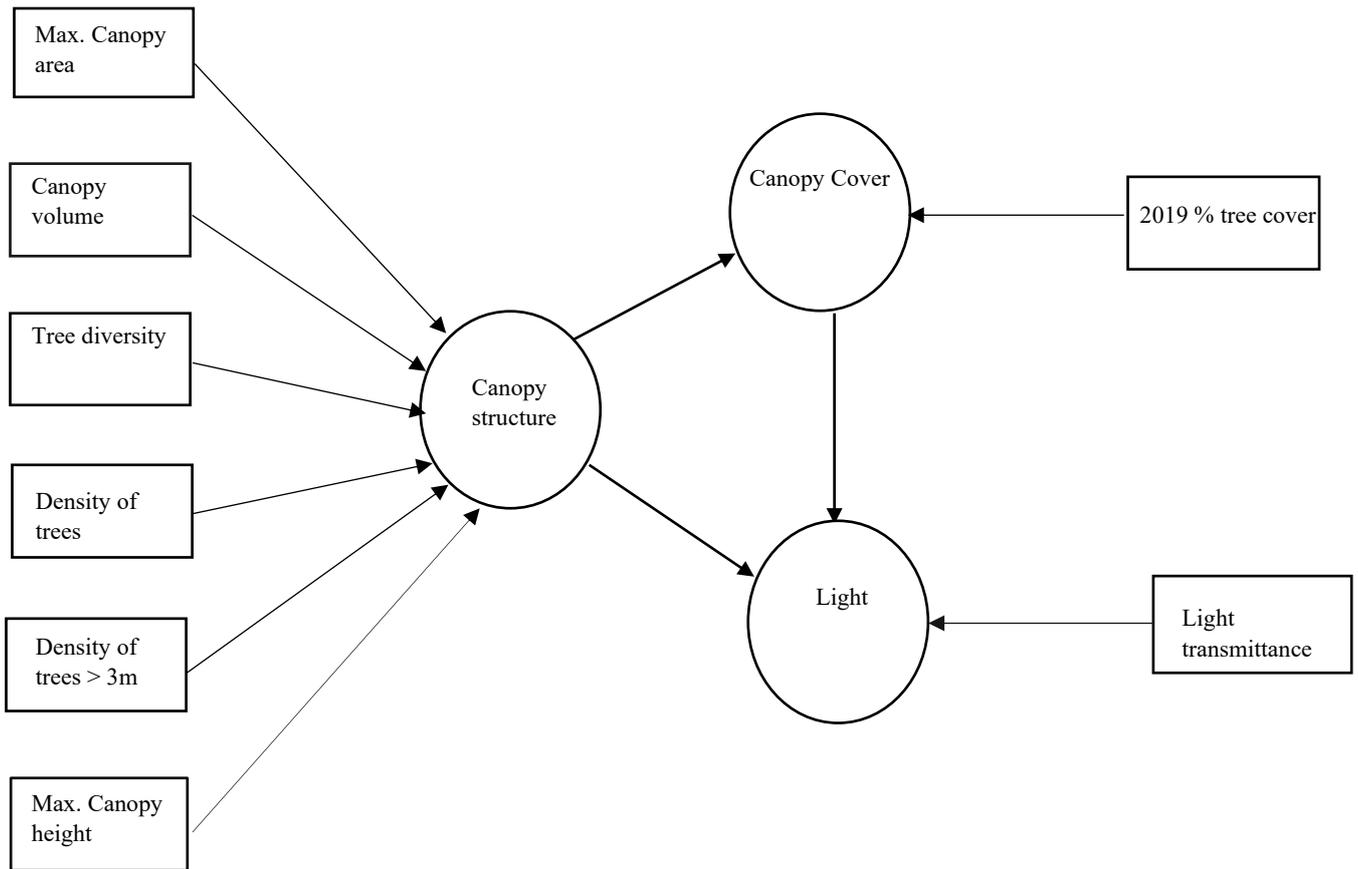


Figure 3. 3: The framework which guided the SEM analyses. The model shows the structural relationships between three latent variables: canopy structure (maximum canopy area, canopy volume, tree diversity, density of trees, density of trees >3m, maximum canopy height) the aerial canopy cover and light variables (Light transmittance). Measured variables are represented by rectangles and latent variables by circles. Arrows represent the expected direction of influence which will have path coefficients estimated.

3.5. Results

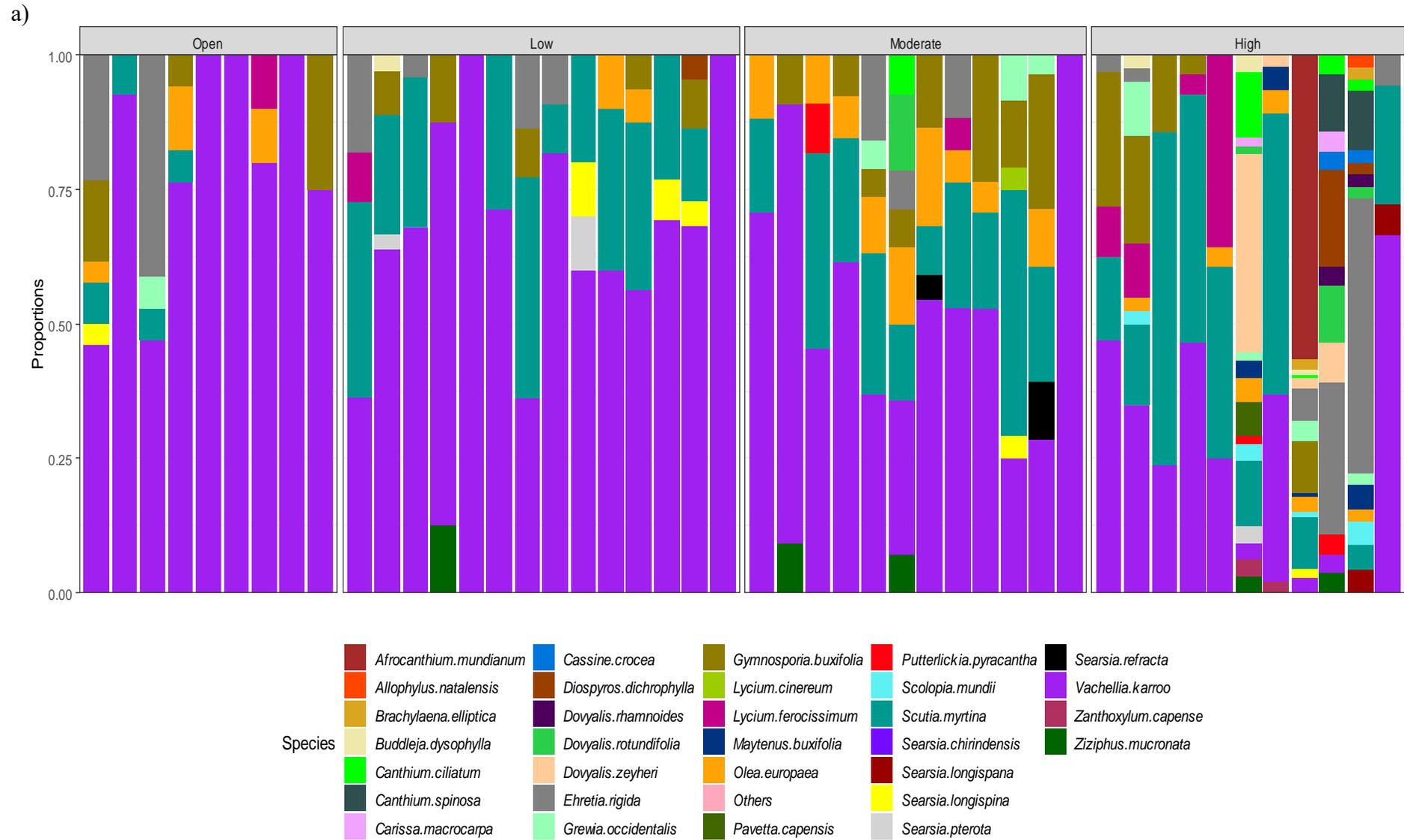
3.5.1. Changing tree composition with increasing canopy cover and decreasing light transmittance

Tree composition changed with increasing canopy cover and with decreasing light transmittance (Figures 3.4a and 3.4b). The most notable differences in tree composition were observed between sites with high (51-100%) tree cover and the lower tree cover classes. Similarly, composition was most distinct, and included more tree species in sites with the lowest light transmittance (class E; 20-50%) compared to all the other transmittance class ranges. It is evident that *V. karroo* and *S. myrtina* are the dominant tree species across all sites

because they make up more than 50% of trees in most of the sites. *Vachellia karroo* is present in all the sites but is less prominent in the high canopy class sites. *Gymnosporia buxifolia* and *Olea europaea* subsp. *africana* contribute less to tree abundances in the open tree cover class sites.

A two-dimensional NMDS plot represented the variation in species composition among the 51 sites surveyed in the study. The final stress score for the model was 0.14 (non-metric fit $R^2 = 0.98$, linear fit: $R^2 = 0.94$). There was a gradient in the positioning of sites from high light transmittance (A) to low transmittance levels (E) (Figure 3.5 a). Sites with high light transmittances (belonging to A, B, C, D) tend to cluster together, while four of low light transmittance (class E) sites were positioned far apart from the rest. There was a site with a low light transmittance class that was omitted from the plot due to its difference in species composition. It is evident from the NMDS plot that tree species composition differed amongst sites with low light transmittance but was similar between sites that had open to moderate canopy covers (light transmittance). As also evident from the composition plots, light transmittance captured compositional stages better than woody canopy cover from the aerial photographs. Figure 3.5 b shows the same NMDS plot with canopy cover classes superimposed. Sites belonging to the open, low and moderate canopy cover classes overlapped with each other and had similar species compositions, while three of the five sites with high canopy cover were positioned separately from the rest of the classes. Some sites in the high canopy cover class clustered with the open, low and moderate canopy cover classes (Figure 3.5 b).

A MANOVA test showed that there was a significant compositional difference between light transmittance classes ($R^2 = 0.33$, $F = 5.02$, $p < 0.001$; Table 3.2). A PERMANOVA pairwise test showed significant ($p < 0.05$) differences between the two highest transmittance classes (A and B) and between the lowest transmittance class (E) and each of the lower transmittance classes (A-D). There was a significant compositional difference between the different canopy cover classes ($R^2 = 0.20$, $F = 3.40$, $p < 0.001$; Table 3.3). A trend was apparent from Figure 3.5 b, indicating that there were changes in species composition with an increase in canopy cover (decreasing light transmittance). A PERMANOVA pairwise test showed that open and low cover sites were similar to each other, as were moderate and high cover sites. All other pairwise comparisons showed significant differences ($p < 0.05$) between open or low and moderate or high cover sites.



b)

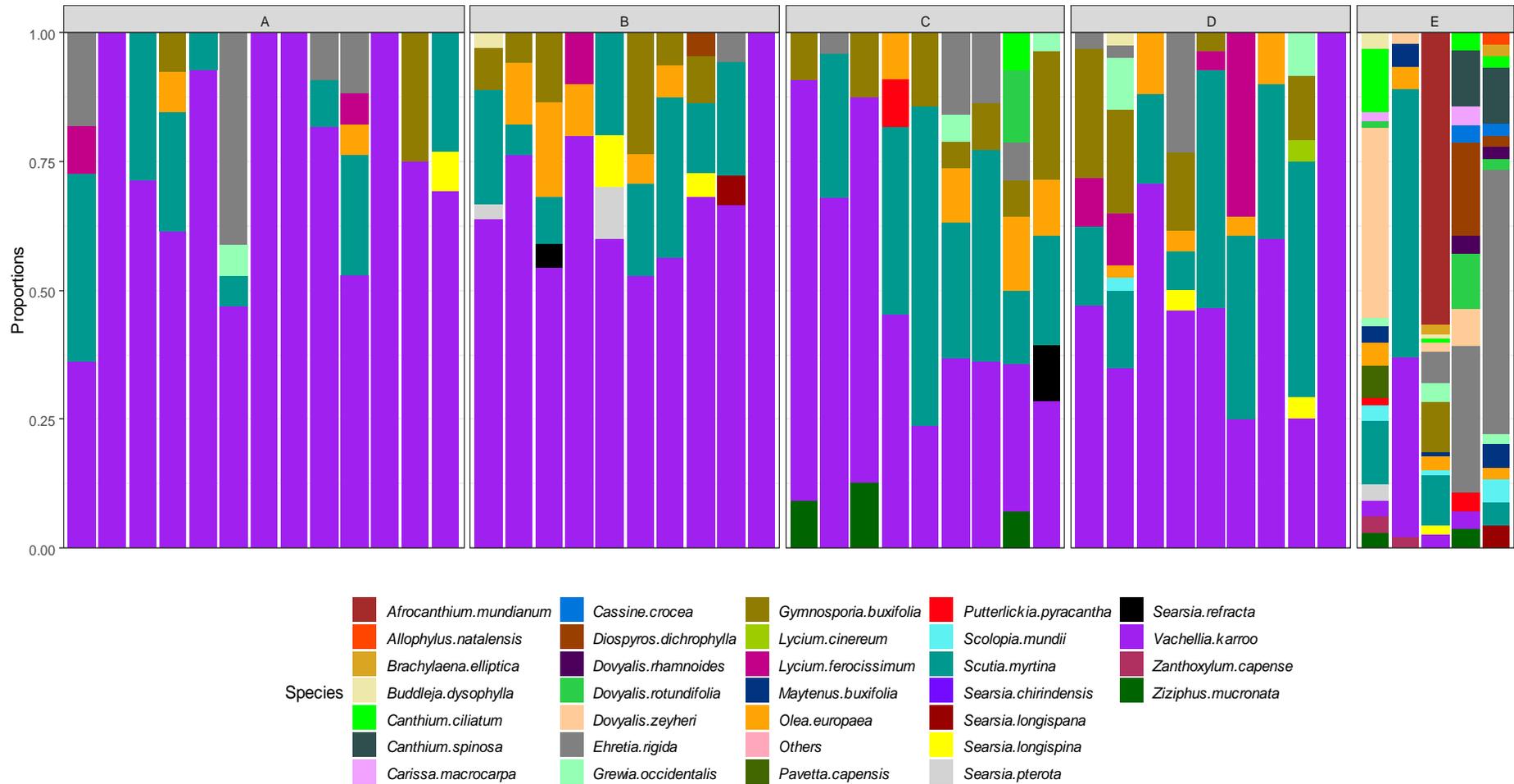


Figure 3. 4 a and b: Species composition plots showing the proportion of 32 tree species contributing to the tree composition in the site. a) The groups were divided according to aerial canopy cover classes: Open (0-15%), Low (16-30%), Moderate (31-50%), High (51-100%). %. b) The groups were divided according to light transmittance groups: A (91-100), B (81-90%), C (71-80%), D (51-70 %) and E (20-50). Each colour on the plot represents a different woody species. Tree species found in this study are listed in Appendix F.

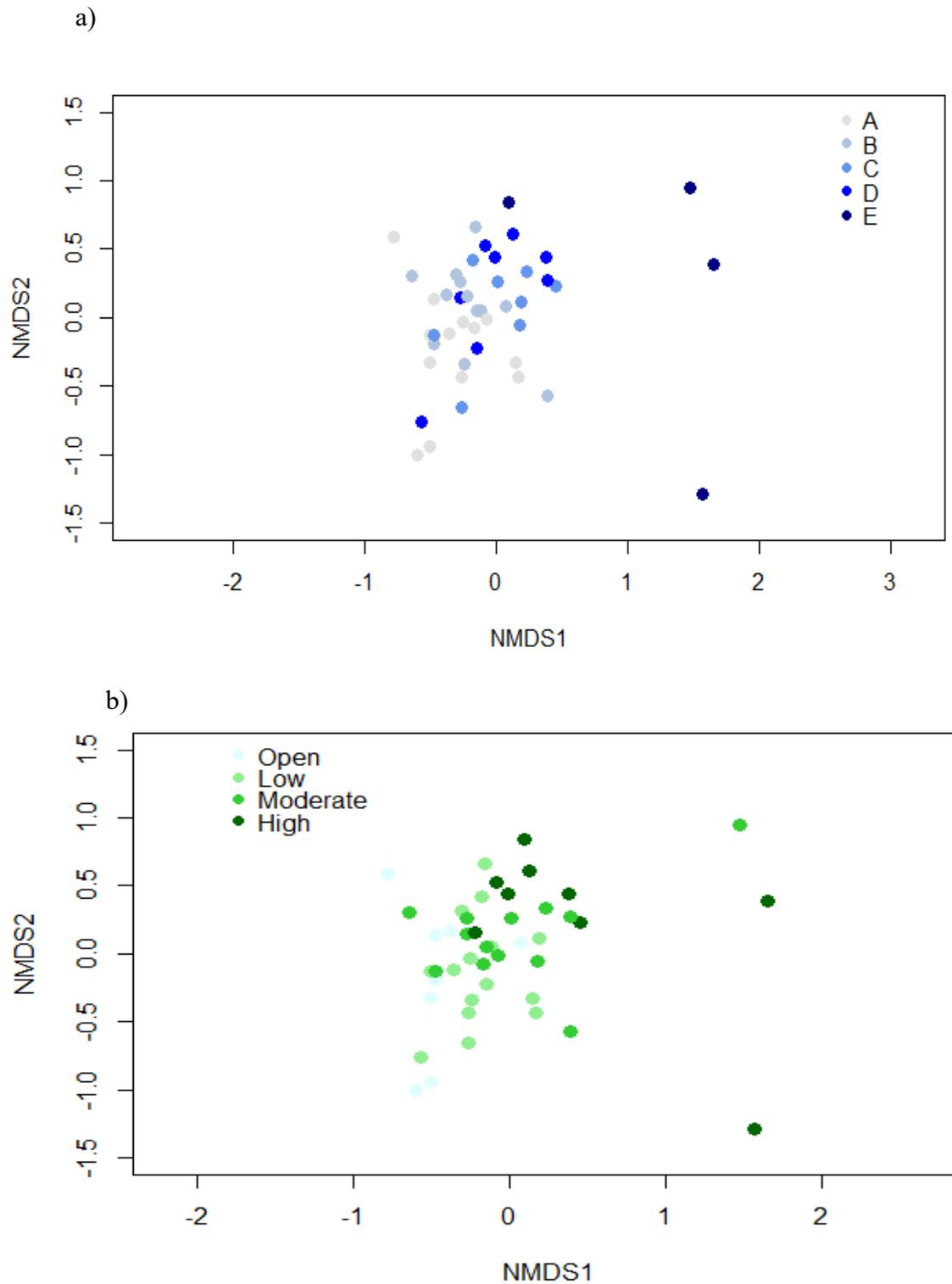


Figure 3. 5 a and b: Non-metric multidimensional scaling (NMDS) plot based on the Bray-Curtis distances of 51 sampling sites using tree species abundance data. a) light transmittance levels were coloured as: A (91-100), B (81-90%), C (71-80%), D (51-70 %), E (20-50). b) tree cover ranges from aerial photographs were: Open (0-15%), Low (16-30%), Moderate (31-50%), High (51-100%).

Table 3. 2: Results of pairwise PERMANOVA analysis between light transmittance ranges: A (91-100), B (81-90%), C (71-80%), D (51-70 %), E (20-50). Significant differences ($p < 0.05$) are highlighted.

		A	B	C	D
Light transmittance	B	0.028	-	-	-
	C	0.060	0.738	-	-
	D	0.112	0.738	0.738	-
	E	0.010	0.010	0.028	0.010

Table 3. 3: Results of pairwise PERMANOVA analysis between canopy cover classes: Open (0-15%), Low (16-30%), Moderate (31-50%), High (51-100%). Significant differences ($p < 0.05$) are highlighted.

		High	Moderate	Low
Canopy cover	Moderate	0.096	-	-
	Low	0.024	0.027	-
	Open	0.006	0.006	0.096

A clustering pattern based on woody species composition emerged among sites belonging to the same light transmittance and canopy cover classes (Figure 3.6). The clusters 1 to 6 indicate a general decrease in light transmittance corresponding to an increase in canopy cover—although some sites with low light transmittance (E or D ranges) were clustered with sites with high light transmittance. This suggests that sites belonging to transmittance classes A (91-100), B (81-90%), C (71-80%), D (51-70 %) were very distinct from group E, with the two far left groups in the cluster being the most distinct from all the others. Sites in the open, low, and moderate canopy cover classes appeared to cluster together, and most high tree cover sites clustered separately and some with other tree cover classes. The most evident cause for clustering of groups is the abundance of *V. karroo* and *S. myrtina* at a site. The clustering pattern showed some high tree cover sites clustered amongst low cover sites because they had an abundance of *V. karroo* trees without many other species. The clustering pattern suggests a woody thickening sequence reflected by changing tree composition. The open and treeless sites (not shown on the heatmap as these have no trees) form one group. Group 1 from Figure 3.6 was *V. karroo* dominated and featured few sites with *G. buxifolia* and *S. myrtina*. Group

2 was characterised by an increase in *V. karroo*, and an increase *O. europaea* subsp. *africana* and *S. myrtina* trees. Group 3 was dominated by tree species: *V. karroo*, *S. myrtina*, *Gymnosporia buxifolia*, *Olea europaea* subsp. *africana* and there were sites with *Ehretia rigida* and generally more trees (evergreen thicket species). Group 4 is characterised by a lack of *V. karroo* and *S. myrtina* and a high abundance and diversity of other species (evergreen thicket tree species).

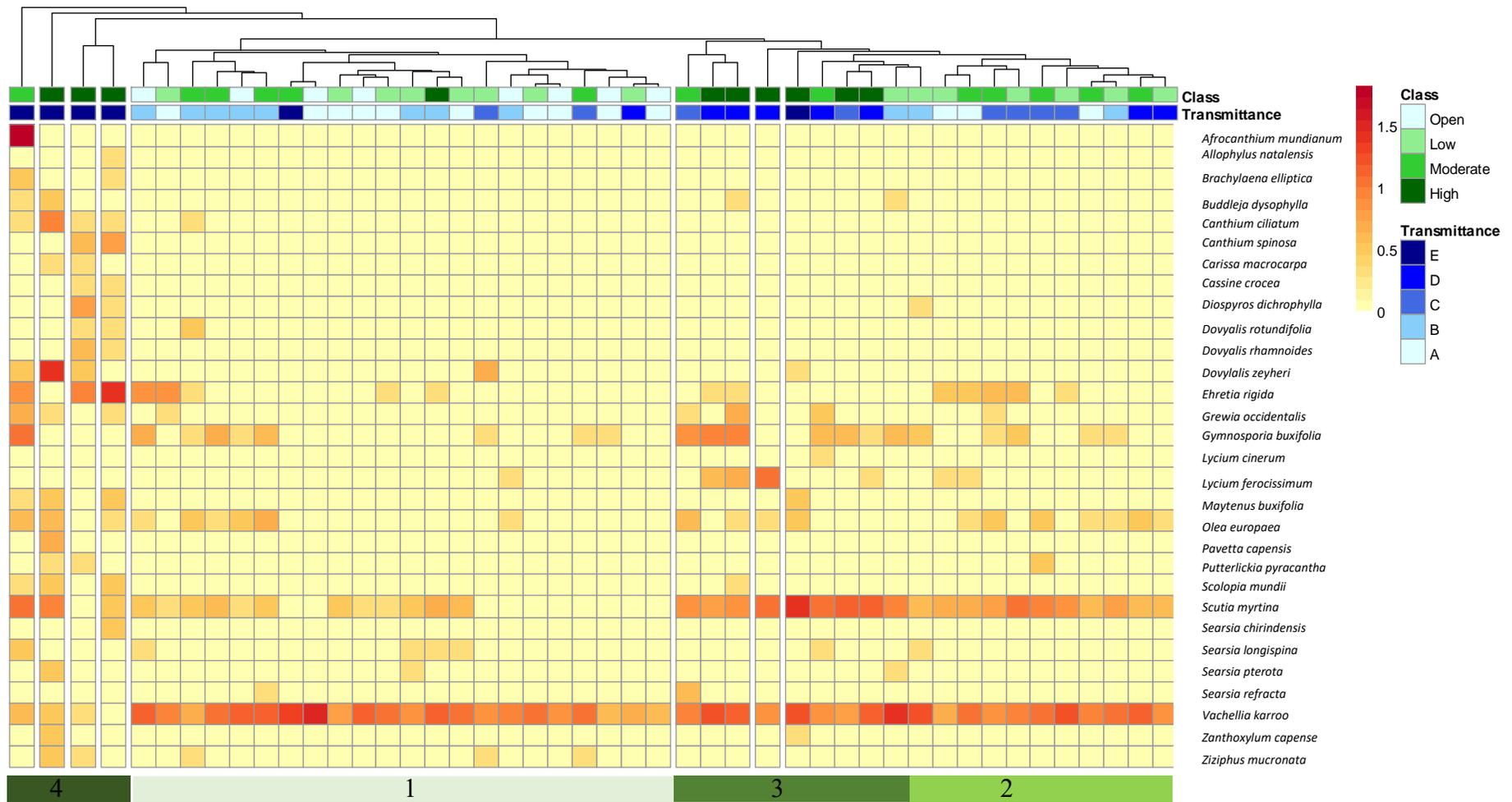


Figure 3. 6: Dendrogram and heatmap showing the abundances scores (\log_{10} transformed) of tree species (rows) and the sites (columns). The sites were clustered using Bray-Curtis distances using the complete method. The legend shows a gradient of green blocks from light green to dark green representing the canopy cover classes from aerial photographs: a) open (0-15%), low (16-30%), moderate (31-50%), high (51-100%) b) light blue to dark blue dots correspond to sites belonging to light transmittance classes: A (91-100), B (81-90%), C (71-80%), D (51-70%), E (20-50). On the heatmap, lighter yellow and orange colours represent the lower bounds of the species abundance and the darker red represents a high abundance of the species. The woody thickening sequence is revealed in the clusters (numbered from 1-4, showing how sites are grouped according to tree species similarity).

3.5.2. Relationships between woody composition, vegetation structure and light environment

The relationship between the stem density of *G. buxifolia*, *O. europaea* subsp. *africana*, *S. myrtina*, *V. karroo* and a) light transmittance, b) canopy volume, c) tree diversity (H) and d) canopy cover in 2019 differed across the species (Figure 3.7). As the density of *O. europaea* ($R = -0.43$, $p < 0.05$), *G. buxifolia* ($R = -0.29$, $p < 0.01$), and *S. myrtina* ($R = -0.41$, $p < 0.01$) increased, the light transmittance decreased. *Vachellia karroo*, which was the dominant tree species on the farm, decreased insignificantly ($R = -0.13$, $p > 0.05$) as light transmittance increased, which corresponded to an increase of the other, broadleaf species as the encroachment sequence progressed (Figure 3.6).

As the density of *G. buxifolia* ($R = 0.76$, $p < 1 \times 10^{-4}$), *O. europaea* ($R = 0.66$, $p < 1 \times 10^{-4}$), *S. myrtina* ($R = 0.34$, $p < 1 \times 10^{-4}$), *V. karroo* ($R = 0.76$, $p < 1 \times 10^{-4}$) increased, the total canopy volume at the site increased. The diversity (H) of trees increased significantly with an increase in the density of *G. buxifolia* ($R = 0.34$, $p < 0.05$), *O. europaea* subsp. *africana* ($R = 0.42$, $p < 0.05$), *S. myrtina* ($R = 0.34$, $p < 0.05$), but showed no significant trend with an increasing density of *V. karroo*. As the density of *S. myrtina* and *O. europaea* subsp. *africana* increased, total canopy cover also increased. However, an increase in the density of *V. karroo* did not correspond to a significant increase in canopy cover.

The proportion of deciduous trees affected the availability of light in the understorey and LAI (Figure 3.8). Higher canopy volume and aerial tree cover in 2019 were accompanied by a decrease in the proportion of deciduous trees (mainly *V. karroo*). An increase in the proportion of deciduous trees corresponded to a significant increase in light transmittance ($R = 0.60$, $p < 0.001$) and a decrease in LAI ($R = -0.54$, $p < 0.001$). Sites with a higher proportion of deciduous trees (*i.e.* dominated by *V. karroo*) had a lower percentage canopy cover ($R = -0.72$, $p < 1 \times 10^{-4}$) and lower total canopy volume ($R = -0.66$).

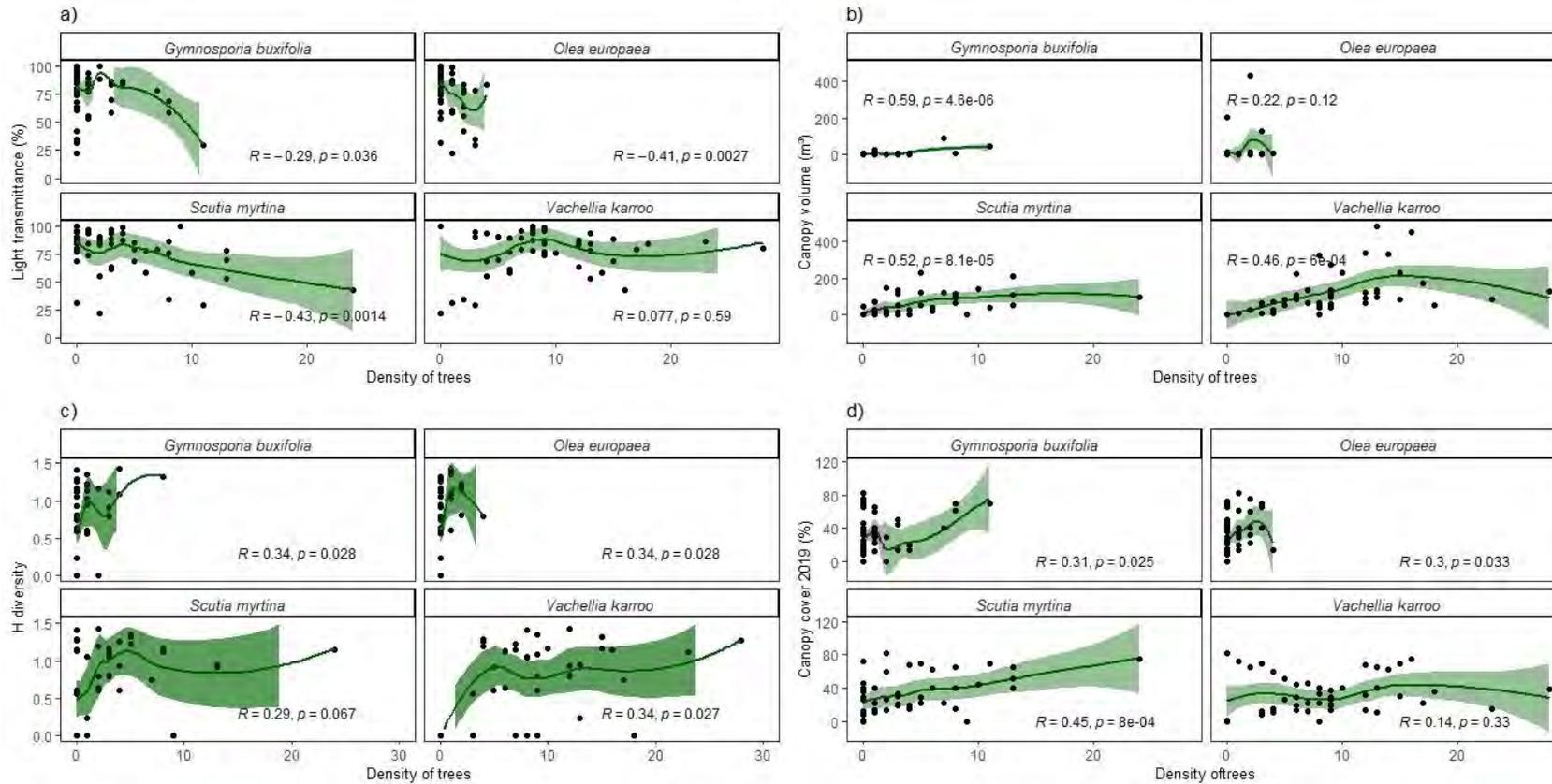


Figure 3. 7: Relationships between a) light transmittance, b) canopy volume (m³), c) (Shannon) diversity, d) canopy cover in 2019 and the density of trees (*G. buxifolia*, *O. europaea* subsp. *africana*, *S. myrtina* and *V. karroo*). The p values from Spearman correlations and R values are shown. The loess and lm methods were used to compute a smooth regression represented by the dark green and dark cyan lines respectively.

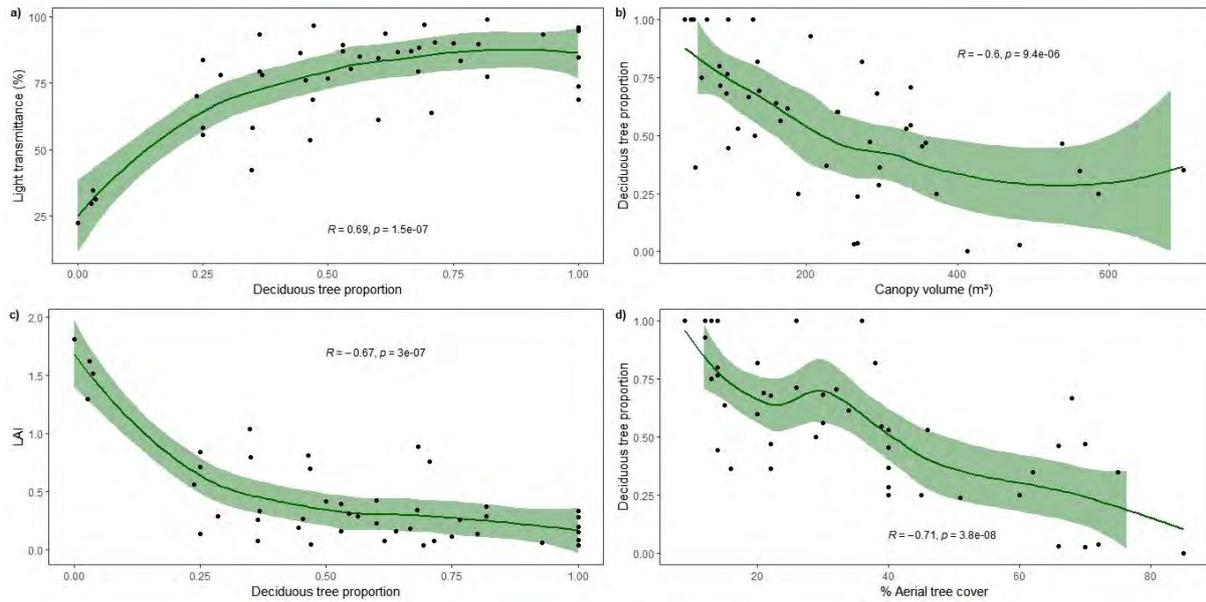


Figure 3. 8: Light transmittance increased (a) and LAI decreased (c) as the proportion of deciduous trees increased. Higher canopy volume (b) and aerial tree cover in 2019 (d) were accompanied by a decrease in the proportion of deciduous trees. The p values from Spearman correlations and R values are shown. The LOESS and linear regression methods were used to compute a smooth regression represented by the dark green and dark cyan lines.

3.5.3. Relationships between woody vegetation structure, canopy cover and light environment

Most of the relationships between woody cover, structure, diversity and light variables indicated strong and highly significant relationships (Figure 3.9). The pairwise comparisons showed a gradient from open sites with fewer, smaller trees and lower canopy cover, canopy volume and area to sites with taller and more trees, with higher canopy cover, canopy volume and canopy area. Particularly strong relationships were found between canopy area and canopy cover in 2019 ($R=0.82, p < 1 \times 10^{-11}$), canopy cover and LAI ($R= 0.80, p < 1 \times 10^{-11}$), and canopy cover and light transmittance ($R= -0.79, p < 1 \times 10^{-11}$). As expected, given their derivation from the same images, LAI and light transmittance were also strongly correlated ($R= -0.92, p < 0.001$).

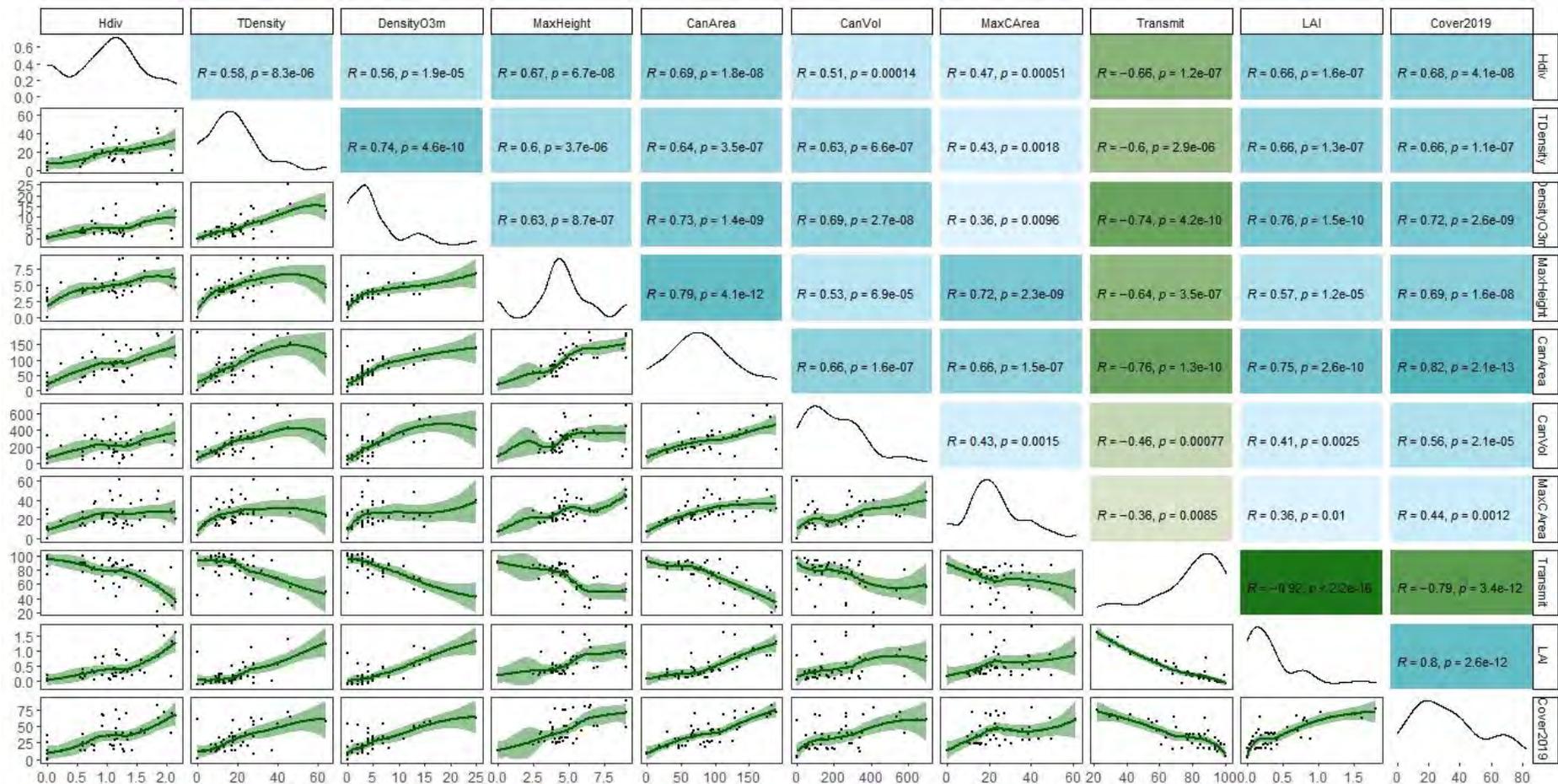


Figure 3. 9: Correlations between the variables: tree diversity (Tdiv), density of trees (TDensity), density of trees >3m (DensityO3), maximum height (Max Height), canopy area (CanArea), canopy volume (CanVol), maximum canopy area (MaxCArea), light transmittance (Transmit), LAI (Leaf Area Index) and aerial %tree cover in 2019 (Aerial canopy cover from 2019). The p values from Spearman correlations and R values are shown on the upper half of the figure. The significance of the linear relationship indicated by colours from dark dark cyan (positive) to dark green (negative). The LOESS method was used to compute a smooth regression represented by the dark green line.

The gradient of increasing canopy cover, estimated from aerial satellite imagery in 2019 on Endwell farm correlated strongly with increasing tree density, density of trees greater than 3m (Figure 3.9). Meanwhile, the increase in the density of trees corresponded significantly to an increase in canopy area and canopy volume. The maximum height (the tallest tree on a plot) was strongly correlated with an increase in the density of trees on a plot. The canopy area had the strongest positive relationship with canopy cover, and this relationship was weaker for canopy volume. Light transmittance decreased with an increase in tree density but was the least impacted by maximum canopy area (the largest canopy area of a tree on a plot).

In the final SEM, the canopy structural variable ‘maximum height’ was removed due to its low contribution to the woody vegetation structure variable. “Light” was also represented by light transmittance and LAI was removed. Figure 3.10 shows the final modes with the variables retained. Woody vegetation structure (representing the effects of canopy area, canopy volume, tree diversity, density of trees, density of trees > 3m, maximum canopy area) explained 73% of the variation in canopy cover in 2019, and together with aerial canopy cover explained 73 % of the variation in light transmittance directly. Hair *et al.* (2014) considers R^2 values 0.7 to be substantial and 0.50 to be moderate. The model results indicated a strong effect of canopy structure and on aerial canopy cover ($\beta = 0.86$). The strength of the direct effect of canopy cover on light transmission is stronger ($\beta = -0.62$) than its effect via aerial canopy cover ($\beta = -0.26$).

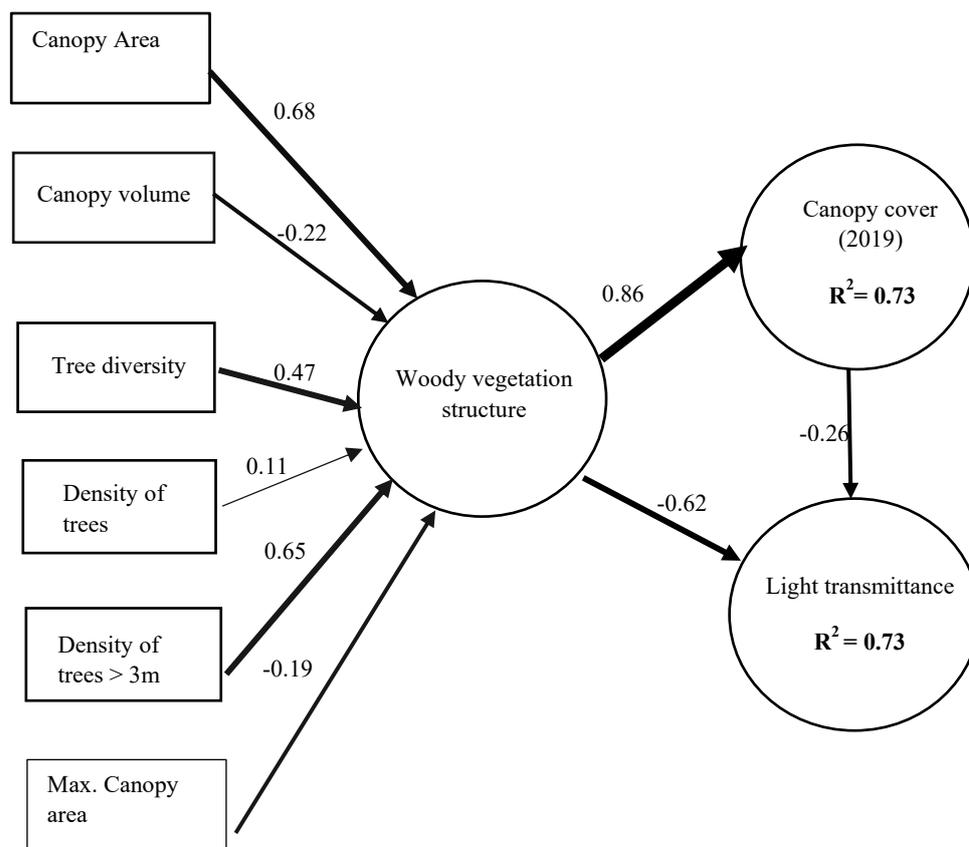


Figure 3. 10: Structural equation model (SEM) examining the effect of woody vegetation structure (Canopy area, Canopy volume, Tree density, Density of trees >3m, Maximum Canopy area (Max. Canopy area) on Canopy cover (2019) from aerial satellite imagery and on Light transmittance from hemispherical photography.

3.6. Discussion

3.6.1. The sequence of woody thickening and its effect on the light environment

The decline in savanna tree species (*Vachellia karroo*) as canopy cover increased, indicated that thicket clump formation was occurring on some sites on the farm. Sites with the highest canopy cover and lowest light transmittance had a greater variety of tree species dominating the species proportion plots (Figure 3.4a and 3.4b). The species proportion plot showed that *V. karroo* and *S. myrtina* were the dominant tree species in areas with a light transmittance > 50 % (high canopy cover) and they became less frequent at lower transmittance levels

when other tree species became dominant, suggesting that *S. myrtina* is the first of the broadleaf thicket precursors to establish, usually in association with *V. karroo* (similar to O'Connor & Chamane, 2012). There were sites with high canopy cover that bore a resemblance to sites with moderate canopy cover, and these represented an advanced stage of savanna thickening dominated by *V. karroo*. In chapter 2, two sites had a moderate canopy cover in 1949, which increased (Chapter 2, Figure 2.4 a) to a higher canopy cover in 2019. One of these sites was dominated by *Afrocanthium mundianum* and had a more diverse assemblage of thicket tree species, different from the rest of the sites (Figure 3.6). The other site had a more diverse assemblage of thicket tree species, with a higher abundance of *Dovyalis zeyheri*. The higher diversity of thicket tree species at these sites is explained by the length of time these sites had been encroached. Sites with high canopy cover generally had fewer *V. karroo* trees and there was an increase of *V. karroo* dominance as the canopy cover decreased. The savanna trees, represented by *V. karroo* trees on the farm, may increase in density on a site indicating that savanna thickening is taking place (with C₄ grasses still intact) (Parr *et al.*, 2012). However, an increase in savanna trees may be the first phase of thicket clump formation which was shown to occur in Eastern Cape savannas, pioneered by *V. karroo* trees (O'Connor & Chamane, 2012). Bush clumps formed beside open savannas through a process of succession (O'Connor & Chamane, 2012), where individual trees encroached open sites, changing environmental conditions (soils, light and nutrients), inviting more tree species which were more suitable to the changed environment (Belay *et al.*, 2013; Schönbeck *et al.*, 2015; Jamison-Daniels *et al.*, 2021).

The NMDS showed a general trend of increasing light transmittance assortment of sites on the x axis, thus further confirming the hypothesis that tree species composition changes with changing light transmittance (Sercu *et al.*, 2017). There was a distinction between sites with estimated light transmittance levels < 50% and those with light transmittance > 50%. This point represented the threshold between vegetation dominated by *V. karroo* and a few thicket pioneer species, and more diverse communities with very little *V. karroo*. In low-light environments, there is selection for rapid height gain to compete for light (Archibald & Bond, 2003). Savanna species are adapted to growing in environments where light is not limited, and herbivory and fire select for their growth forms in those environments (Archibald & Bond, 2003). Species composition will therefore influence light transmittance within and among stands (Messier & Bellefleur, 1988; Canham *et al.*, 1994; Kabakoff & Chazdon, 1996) due to differences in canopy and growth forms of trees on either side of the

boundary. Cardoso *et al.* (2020) found differences in tree species composition and functional traits along the savanna-forest mosaics of Lope National Park, Gabon (Cardoso *et al.*, 2020). Belay *et al.* (2013) also found that the diversity, richness, and evenness of tree species increased with increases woody plant density, and this was attributed to increased spatial heterogeneity and soil microclimate improvement.

Overall, sites with light transmittance > 50% were similar in species composition and this was evident in the clustering patterns (Figure 3.4 a and 3.5 a). Sites that had a light transmittance < 50% had slightly different tree compositions and formed separate clusters. These represent sites that have undergone significant thicket development with a variety of woody species such as *Afrocanthium mundianum*, *Dovyalis zeyheri*, *Afrocanthium mundianum*, *Ziziphus mucronata*, *Diospyros dichrophylla* and *Searsia longispani*.

3.6.2. Changes in tree species composition impacting light transmittance

Scutia myrtina and *O. europaea* subsp. *africana* were found in both high tree cover and low tree cover environments and this was reflected in their stem density's strong positive correlation with increasing canopy cover (Figure 3.7). The density of *V. karroo* tends to decrease insignificantly with increasing light transmittance. It should also be noted that the density of trees generally decreases with an increase in light transmittance, and the poor response of *V. karroo* tree densities to increasing canopy cover suggests that it was restricted in dense sites. The differences in these trends indicate that tree species respond differently to changing canopy environments, and some trees may be more tolerant to changes in the light environment. The positive but weak relationship between the density of *V. karroo* and diversity also suggests that *V. karroo* becomes less dominant at sites with a higher diversity of trees (possibly sites with a higher density of trees). The other trees had significantly positive responses as the diversity of trees increased (Figure 3.7 c). Since *V. karroo* is dominant in the open savanna and is thought to be the main species encroaching grasslands, it was expected that its numbers at each site would have the strongest relationship with canopy volume (m³).

A strong correlation was observed between light transmittance, canopy volume and the proportion of evergreen trees (Figure 3.8). Sercu *et al.* (2017) found that increased diversity of trees led to increased canopy packing and decreased spatial light heterogeneity in forest floors and they also found that light transmittance differed amongst different tree species

and timing of leaf expansion. Figure 3.4a and 3.4b showed the decline in the dominance of *V. karroo*, and the increase in the dominance of other tree species which are mostly broad-leaved trees. The decrease in light transmittance with an increase in evergreen trees supports the theory that light transmittance tends to decrease in mixed stands-which is where evergreen trees dominated (Sapijanskans *et al.*, 2014; Sercu *et al.*, 2017). Light transmittance will also be impacted by seasons and sites with more deciduous trees will receive more light in dry seasons (Uemura, 1994; Lieffers *et al.*, 1999). The increase in the number of evergreens, broad leaved species with an increase in tree cover, indicates the process of a savanna system transitioning from an open system to a closed system with a different set of tree species than the original.

3.6.3. Changes in canopy structural dynamics with increasing tree cover

Chapter 2 showed that many sites had undergone bush encroachment in the past seven decades and this Chapter showed that this resulted in a change in canopy characteristics. The pair plot showed there were changes in the canopy structure and light characteristics, as canopy cover increased (Figure 3.9). Canopy structure characteristics were influenced by the density of trees in the system, and the density of trees in the system were related to the state of bush encroachment (canopy cover) of the system. The canopy area and canopy volume increased with an increase in the density of trees on a plot (Figure 3.9), impacting the amount of light available in the understory.

The SEM model showed that the number of tall trees (< 3m) had the greatest impact on the tree composition influencing canopy cover and light dynamics (Figure 3.10). Canopy cover had the strongest influence on light dynamics than tree canopy structure. The same result was observed on the pair plots (Figure 3.9), where canopy cover showed the strongest relationships with LAI and light transmittance. An increase in the density of trees was not always accompanied by a decrease in light transmittance because there could have been large numbers of small or average sized trees in some sites. There were also plots with fewer but large trees that had higher light transmittance values. Therefore, canopy cover, in this case would be an important variable to consider when analysing variables that influence light (SEM results). The variable that had the strongest relationship with canopy cover was canopy area. Canopy area is a measure of the diameter size of trees, which is what canopy cover accounts from a bird's eye-view perspective. A high tree cover may also suggest a longer period of encroachment and therefore sites that had a high tree cover would also have

older trees that are bigger, accounting for the high canopy areas in those sites. As a result, canopy area had a strong positive response to increasing aerial canopy cover.

There were sites that had very large, but few trees. *Olea europaea* subsp. *africanais* one of the common trees found on the farm which often grows very tall and wide. The presence of such large trees in some plots may have increased the canopy area/volume. Large trees are also unlikely to be accompanied by larger trees due to competition (Gutierrez & Fuentes, 1979; Wiegand *et al.*, 2005).

Light transmittance decreased significantly with the density of trees > 3m and canopy area. Canopy cover and LAI increased significantly with increasing tree diversity (negatively with light transmittance). This confirms the finding from Figure 3.4 that bush encroachment results in a higher tree diversity on the farm. O'Connor & Chamane (2012) studied the successional patterns of bush clumps initiated by *V. karroo* in the Eastern Cape. It was shown that increasing clump size, led to an increase in woody basal area, species richness and diversity. Another study in the Cerrado region of central Brazil found that Basal area and LAI declined significantly from a forest to a savanna system (Geiger *et al.*, 2011). There were differences in species composition between the two biomes, where most savanna species were absent in the forest. The results obtained in this study also support Nondlazi's (2016) study, which found that light transmittance (%) was a function of tree cover, tree height, tree architecture and the phenology of trees found at a site.

3.6.4. From savanna thickening to thicket formation – evidence for a threshold associated with shifts in tree functional type

The tree composition was diverse below 50% canopy cover, suggesting that 50% light transmittance was the point where a clear transition could be seen between the ranges of transmittance. It is not clear whether 50% canopy cover marks a transition in tree species composition since there were sites in the high tree cover classes that were similar to those in low tree cover classes. This study has shown that a canopy cover of certain species describes the state of encroachment, and not aerial canopy cover per se. Chapter 4 will investigate how the changes in tree species composition impact the composition of the herbaceous layer. The diversity and abundance of herbaceous species at certain levels of canopy cover and light transmittance will clarify the threshold points determined in this chapter. It has been clear from this chapter that canopy cover alone cannot explain the state of encroachment, and that the type of tree species found at a site, influence light

transmittance and therefore cause a change in the type of plants that can exist at a site. The increasing dominance of thicket tree species signified a change in the canopy structure of the sites. A canopy cover of 50% by *Vachellia karroo* represented savanna thickening, albeit at an advanced stage. A 50 % canopy cover of mainly broadleaf species suggested a threshold between savanna thickening and thicket formation. The theoretical threshold tree cover beyond which fire does not spread is estimated to be 40% (Archibald, 2010; Scholes, 2003). The threshold should be reflected by changes in tree species composition, from fire tolerant savanna tree species to shade tolerant thicket species. *Vachellia karroo* was the dominant tree species in low canopy sites this study, and it became less prominent in higher tree cover sites. Woody thickening, by encroaching *V. karroo* may have occurred in some clumps-early clump formation and these sites were therefore different from clumps that had experienced thicket expansion (encroachment by thicket species). An explanation for differences in threshold canopy cover found in this study and other studies could be the fact that canopy cover was determined manually from aerial photographs and could therefore result in different canopy cover estimates than studies that employed satellite images. This chapter showed that threshold points in tree compositions do exist where the system changes from savanna to thicket type of vegetation. The next chapter builds on this chapter's finding that thicket vegetation appears at light transmittance of 50 %.

Chapter 4

Response of herbaceous species composition to changing canopy cover

4.1. Introduction

4.1.1. Increasing tree cover and savanna system functioning

Several studies have shown the negative impact of increasing tree cover on the diversity and richness of grassland species (Zodel *et al.*, 1994; Frelechoux *et al.*, 2007; Koch *et al.*, 2015). An important feature of a savanna is the dominance of C₄ grasses in the herbaceous layer. A change in the composition of the grass species that affect fire regimes will ultimately change the integrity of a savanna system. It is proposed that high fire frequencies promote high species richness by preventing competitive exclusion of grasses and forbs by woody plants (Huston, 1994). Furthermore, trees in savannas suppress herbaceous plant production through light reduction (Martens *et al.*, 2000; Funk & McDaniel, 2010; Cardoso *et al.*, 2020). Open canopies in savanna allow a lot of light in the understory, which promotes a drier micro-climate and the accumulation of flammable grasses (Bond & Van Wilgen, 1996; Hoffmann *et al.*, 2012c; Scholes & Archer, 1997; Biddulph & Kellman, 1998). Open canopies are therefore ideal for the maintenance of high species richness and diversity of savanna herbaceous species.

Tree species composition also changes along a thicket successional gradient due to changes in environmental conditions (Schönbeck *et al.*, 2015; Jamison-Daniels *et al.*, 2021). The increase in broad-leafed trees and evergreen species may further diminish light in the understory. These changes in microclimate (increased humidity, lower temperatures, lower temperature variation, etc.) during clump succession may negatively impact herbaceous species establishment (Archer, 1995). A Critical transition at LAI ~ c. 1.5 was identified in Hluhluwe-iMfolozi Park, where grass composition shifted from C₄ to C₃ pathway and this transition was linked to shifts from savanna tree species to forest tree species (Charles-Dominique *et al.*, 2018). A threshold point at LAI ~c. 0.5 represented a shift in C₄ in photosynthetic subtype and a loss in flammability. The savanna in the Brazilian Cerrado was found to have undergone an increase in tree cover over the past 30 years, largely due to

fire suppression policy. There had been an increase in vegetation as areas that were once savanna in 1986 had turned into forests (Abreu *et al.*, 2017). The increase in tree biomass was accompanied by a decrease in the richness of herbaceous plant species, and savanna specialists were the ones mostly affected. The loss of savanna species also occurred when the vegetation reached a stem basal area of $\sim 15\text{m}^2\cdot\text{ha}^{-1}$ and LAI of 2.2. As the number of forest specialists increased, savanna species declined. The result of this was a strong trade-off between ecosystem carbon stocks and species richness across savanna forest gradients (Abreu *et al.*, 2017).

Tree size is an important factor impacting the interactions between trees and grasses. The period in which a tree has been growing in its habitat will influence its soil properties, and microclimate (Archer, 1995). The positive influences that trees may have on the herbaceous layer may not occur until some years have passed since the tree establishment (Scholes & Archer, 1997). Conversely, the negative impact of trees on grasses may also not occur until the tree reaches a critical age (Engle *et al.*, 1987; Cameron *et al.*, 1989; McPherson *et al.*, 1993; Fuhlendorf, 1997). Competition starts to play a greater role as the trees become larger and they overshadow facilitation and as a result, negatively impact the herbaceous layer (Aguiar & Sala, 1994; Archer, 1995). On a landscape level, tree density and tree size are important factors to be considered. The apparent positive and negative impacts of trees on herbaceous layer diversity suggest that productivity and diversity of the herbaceous layer may be higher where there are scattered trees than where there are no trees (Stuart-Hill *et al.*, 1987; Moore & Dieter, 1992). An increase in tree density to a critical point will still result in a change in the diversity and productivity of the herbaceous layer.

4.1.2. Effect of increasing tree cover on forb and grass diversity and composition

Studies on the effects of woody species on understory grass productivity have been the focus for decades and both negative and positive effects have been reported (Belsky *et al.*, 1989; Ludwig *et al.*, 2001). Net primary productivity is also increased by woody encroachment, and this often has negative consequences for plant diversity in herbaceous communities (Grime, 1973; Tilman & Pacala 1993; Clark *et al.*, 2007; Harpole & Tilman 2007; Ratajczak *et al.*, 2012). Some plant communities may respond differently to woody encroachment. The interaction may be negative (competition) and positive (facilitation) (Scholes & Archer,

1997). Shrubs in semi-arid ecosystems may create “islands of fertility” where shrubs provide shelter for species sensitive to low nutrient availability (Schlesinger *et al.*, 1990). The presence of an overstorey canopy can increase herbaceous production during a drought (Frost & McDouglass, 1989) and enhance the production of cool-season species (Clary & Morrison, 1973).

Forb species contribute significantly to the total species richness of the herbaceous layer in savanna and grassland systems (Turner & Knapp, 1996; Trollope *et al.*, 2014; Scott-Shaw & Morris, 2015; Siebert & Scogings, 2015; Van Oudtshoorn, 2015). Herbaceous community changes are often governed by forb species responses to either selective pressures on the grass component (e.g., herbivory) or abiotic factors (drought, fire or nutrient-enriched shaded habitats) giving forb species an advantage over the grass layer (Siebert & Dreber, 2019). Furthermore, changes in the composition and structure of the woody layer may cause a change in the species abundance, diversity, and biomass in favour of forbs in the understory (Siebert & Dreber, 2019). Forbs dominate the herbaceous layer under specific environmental conditions *i.e.*, under moderate to heavy grazing pressure (Scholes, 1987; Cowley *et al.*, 2014), after a drought event (Fynn & O’Connor, 2000; Buitenwerf *et al.*, 2011), on nutrient-rich soils (Reich *et al.*, 2003; Van Coller & Siebert, 2015) and beneath tree canopies (Linstädter *et al.*, 2016).

Forbs display a distinct and diverse morphological, life history, ecophysiological characteristic to C₄ grasses (Martin *et al.*, 1992; Turner *et al.*, 1995). These characteristics make forbs resilient to different environmental conditions (Turner & Knapp, 1996). Savanna forbs are better adapted to shaded micro-habitats than grasses and may be expected to persist as tree densities and grass biomass increase (Belsky, 1987; Turner & Knapp, 1996; Mlambo *et al.*, 2005). Forbs may contribute up to 40% -50% of the total herbaceous biomass under tree canopies (Ludwig *et al.*, 2004; Linstädter *et al.*, 2016; Mlambo *et al.*, 2005) and have a smaller contribution in sites outside of the canopy zone (Belsky *et al.*, 1993; Ludwig *et al.*, 2004; Mlambo *et al.*, 2005; Linstädter *et al.*, 2016). Other factors that may benefit forb species under canopies is the increased nutrient availability under canopies as they have been shown to make use of improved soil conditions (Jacobs *et al.*, 2007). The effect of trees on forbs and grasses may vary as a result of tree species composition (Mlambo *et al.*, 2005). Since high light conditions favour C₄ grasses, the availability of light to forbs will be determined by the productivity of dominant grasses (Turner & Knapp, 1996).

Forbs are favoured by drought because they possess a variety of drought-tolerant traits such as underground storage organs (Siebert *et al.*, 2019). Therefore, the loss of forbs in a grassland system may impact the resilience of that system. Forbs are often clumped into one category when assessing changes in herbaceous species composition (Scott-Shaw & Morris, 2014). The grouping of forbs into a single category has made it difficult to identify which forb species persist in the savanna habitat with changing environmental conditions- because of their drought tolerance traits or their tolerance to shade- which bring about resilience in a savanna system.

The effects of tree cover on grass composition and biomass production have been well studied but much less attention has been paid to the non-graminoid plants that make up most of savanna biodiversity (Siebert & Dreber, 2019). In large open grasslands, the productivity of the subdominant forbs varies strongly with topographic position and burning regime (Turner & Knapp, 1996). Since high light conditions favour C₄ grasses, the availability of light to forbs will be determined by the productivity of dominant grasses (Turner & Knapp, 1996).

4.1.3. Responses of C₃ and C₄ grasses to shade

The relationship between trees and understory plants may range from positive to negative, depending on the ecophysiological characteristics of the trees or grasses, photosynthetic pathways, phenology (evergreen, deciduous) and even the canopy architecture and root patterns (Scholes & Archer, 1997). Therefore, it is difficult to predict how certain herbaceous species will respond to increasing tree density and canopy sizes. In open habitats there is a higher exposure to solar radiation and temperature that favours C₄ plants with their great water-use efficiency (Ehleringer & Monson, 1993; Sage, 2004). Alternatively, C₃ grasses are more favoured in densely wooded environments because they can tolerate the low light environments (Sage *et al.* 1999).

In subtropical and temperate systems, C₃ grasses and herbaceous dicots may occur beneath tree canopies, with C₄ grasses dominating in areas with open canopies (Heitschmidt *et al.*, 1986; Scifres, 1992; Fuhlendorf *et al.*, 1997). It has also been shown that the distinction in species composition beneath and away from canopies is more distinct in low rainfall regions (Belsky *et al.*, 1989; Belsky *et al.*, 1993). Therefore, a slight increase in tree cover will not necessarily lead to a decrease in herbaceous species abundance, diversity, or richness, but

could lead to the presence of both shade and open-canopy tolerant herbaceous species. The increase in productivity usually occurs under canopy or near-canopy environments, and it results from higher concentrations of soil nutrients, low evapotranspiration rates under canopies, improved soil properties (Tiedmann & Klemmedson, 1977). Thus, environmental gradients are prominent in habitats where effects of the radiant energy regime or root competition have greater influence on species interactions (Scholes & Archer, 1997).

4.1.4. Aims and Hypotheses

Chapter 3 showed that there was a sequence of thicket formation, which was accompanied by increased canopy cover, more woody diversity, larger trees and less light transmittance. The impact of increasing tree density and canopy structure on the herbaceous layer would explain how transitions from open to closed canopy states occur, through the changes in herbaceous composition. In this chapter, I investigated the characteristics of the woody vegetation that affect the composition, richness and diversity of the herbaceous vegetation, including the species-specific responses of the most common grass species and the diversity and richness of the forb community.

An objective of this study was to analyse the changes in herbaceous species composition which accompany changes in tree density (which changes light transmittance and correlates positively to aerial tree cover). High canopy cover sites with low light transmittance were expected to have a distinct assemblage of herbaceous species, as would open sites. Tree species composition was found to change drastically at around 50% light transmittance (Chapter 3, Figure 3.4), and the same outcome is expected for herbaceous species. Additionally, a difference in the assemblage of grasses was expected, with C₃ grasses dominating in low-lit environments and C₄ grasses dominating in open sites. Furthermore, this chapter's objective was to explore the relationship between herbaceous plant diversity, richness, and basal cover have with changing canopy characteristics quantified in chapter 3 (number of trees, number of trees > 3m, canopy area, canopy volume, LAI, light transmittance, and aerial % tree cover). I predicted that species richness, basal cover and diversity would decrease as tree density, canopy area, canopy volume, density of trees >3 m, % tree cover increases, and leaf area index (LAI) decreases, while increasing with light transmittance.

The net effect of tree density on the herbaceous layer is generally negative (Scholes & Archer, 1997; Riginos *et al.*, 2009), but the presence of few trees may benefit shade-loving

herbaceous species (Stuart-Hill *et al.*, 1987; Moore & Dieter, 1992) and lead to a mosaic of microhabitats with different light and microclimatic conditions. Herbaceous species richness and composition were therefore expected to increase at intermediate tree cover, but to decrease beyond certain levels of tree canopy cover and LAI. The lowest herbaceous diversity was expected at the sites that had undergone transformation to almost closed-canopy thicket, with a loss of open savanna. The response of key grass species to changes in light transmittance (%) and aerial canopy cover was also analysed to investigate critical threshold points. The critical threshold points percent (tree canopy cover, LAI or light transmittance) would be indicated by a significant decline in the abundance and basal cover of both herb and grass species. Sage (2004) suggested that tree canopies that obstruct 80% of light (in a South African savanna) should be able to exclude grass. This threshold may differ for this study since it was carried out in the semi-arid savanna of the Eastern Cape in South Africa.

4.2. Methods

4.2.1. Data collection and sampling design

Tree cover from 51 sites was estimated (Chapter 2). These same sites were sampled to determine herbaceous composition, richness and diversity. Light transmittance, LAI, canopy volume, canopy area, number of tall trees (> 3m) and the number of trees at each site were determined (as reported in Chapter 3) and were used to investigate their relationships with the herbaceous community in this chapter.

The plot sampling for herbaceous species took place during the summer growth season from late February until April 2020. The same plots in chapter 3 were sampled (Figure 3.1). The exact coordinates of the plots were recorded on previous visits and the exact location marked using spray paint and pins. Plots consisted of 10 subplots (3m × 3m) in the middle of each site. All herbaceous species in the subplots were identified and their aerial cover was estimated. The percentage aerial cover of each species in each subplot was given a score of either 1 (<1%), 2 (between 1 and 10%) or 3 (>10%). Thus, for each of the 51 plots, the total abundance score of any species present could range from 1 (< 1% cover in only one subplot)

to 30 (> 10% covers in all ten subplots). All plants were identified using field guides and in the Schonland Herbarium (GRA) in Makhanda.

A pin drop frame (Levy bridge; Levy & Madden, 1933) with 10 pins was used to estimate herbaceous basal cover. The Levy bridge was placed at the center of each of the ten 3m × 3m subplots. The pins were pushed onto the ground, and for any pins that struck the roots of a plant I recorded the name of the plant that had been struck while the remaining pins were recorded as having struck bare ground. Basal cover was calculated as

$$\% \text{ basal cover} = \frac{\text{Number of pins that touch a plant's base}}{\text{Total number of pins}}$$

The summed total abundance score (range: 0-30) for each species in the 51 plots was used to calculate species richness and diversity. The vegan package in R was used to calculate species richness, abundance (using the aerial cover abundance scores), and diversity. The results were combined with canopy characteristics data (Light transmittance, LAI, canopy area, canopy volume, number of trees, and the number of trees > 3m).

4.3. Statistical analyses

4.3.1. Changes in herbaceous species composition with increasing woody cover

The 51 sites were grouped according to light transmittance (see Chapter 3): A (91-100%), B (81-90%), C (71-80%), D (51-70 %), E (20-50%). Woody canopy cover classes were categorised as in Chapter 2 based on the 2019 data: open (0%-15%), low (16%-30%), moderate (31 %-50%) and high (50%- 100%).

A species composition plot was generated in R following Torondel *et al.* (2016). A species abundance matrix (sites vs. species) was used to determine the proportions of herbaceous species at each site and grouping them by the specified canopy cover and light transmittance classes.

4.3.1.1. Herbaceous species composition in relation to canopy cover and light transmittance

A non-metric multi-dimensional scaling (NMDS) plot was generated to analyse similarities between sites belonging to different classes of canopy cover and light transmittance using

herbaceous species abundance scores. Brays-Curtis distances were used in the metaMDS package in R for abundance scores in 51 sites. The total number of each herbaceous species score summed up in each site was tabulated and these were used to compute the similarity matrix on which the NMDS was generated.

A one-way Multivariate analysis of variance (MANOVA) was conducted to compare multivariate sample means between light transmittance and canopy cover classes using herbaceous species abundance scores (*Vegan*). *Vegan's* *adonis* function was used for a permutational Multivariate Analysis of Variance (PERMANOVA) to test whether the centroids and dispersions of the groups (light transmittance and tree cover classes) differed. A permutation test with pseudo-F-ratios was generated through the *adonis* function fitting linear models.

Dendrograms were created with the *heatmap* package in R to analyse relationships between sites belonging to different classes of light transmittance and canopy cover based on their grass composition and the composition of sedges and forbs. The data was in a form of species abundance matrices (sites vs species) and external environmental factors (Sites vs environmental factors). Hierarchical clustering using the clustering distance “manhattan” and the “complete” method was performed in the *heatmap* function. The output generated was a heatmap with a dendrogram with each square on the heatmap representing the abundance level of herbaceous species at each site. For showing the clustering of sites, the number of herbaceous species was limited to the 117 most abundant species. The dendrogram shows how sites (columns) clustered according to tree species abundance (rows) similarity. The environmental factors (light transmittance and canopy cover classes) were added onto the branches of sites.

4.3.2. Bivariate relationships between woody and herbaceous vegetation attributes

Pairwise correlations were performed to determine the strength and direction of relationships between diversity (Shannon index) of herbaceous species, abundance (from abundance scores), herbaceous species richness, tree density, density of trees > 3m, canopy area, canopy volume, light transmittance, LAI and tree cover in 2019. The R function, *ggpairs* produced a matrix of scatter plots and their corresponding p-value (Spearman correlation). The smoothing method LOESS (Locally Estimated Scatter Plot Smoothing)

was used to draw regression lines on the graphs. A function was generated to colour Spearman correlations according to level of significance. The variables canopy volume, canopy area LAI, light transmittance, number of trees/ha and number of trees/ha were not normally distributed, thus not meeting the assumption for linear regressions. Transforming the data did not fix the problem and the linear regression equations and coefficients need to be interpreted with caution for these relationships.

4.3.3. Relationships between woody canopy structure and cover, light transmittance, and herbaceous vegetation: PLS-SEM model

The bivariate relationships plotted were used to highlight significant relationships between canopy, light, tree cover and herbaceous composition. A model showing the influences of canopy structure variables on light dynamics and herbaceous species composition was constructed using the package *semPLS* in R. The first model was constructed using all canopy variables (density of trees, density of trees > 3m, canopy volume, canopy area, maximum canopy area, maximum height), all herbaceous composition data (abundance, richness, and diversity) and light (light transmittance). A conceptual model hypothesis was first constructed based on the relationship's variables (Figure 4.1). Latent variables (canopy structure, canopy cover, light and herb composition) were inferred from measured variables. Variables that resulted in higher path coefficients were selected for the final model. There was a total of 9 observable variables. The outer correlations, weights were calculated using Pearson correlations. The factor scores, outer weights, path coefficients and total effects were generated and drawn as a model. A goodness of fit test was applied to the model which generated R^2 values inserted on the model. The variables that resulted in the highest overall R^2 value were chosen for the final SEM model.

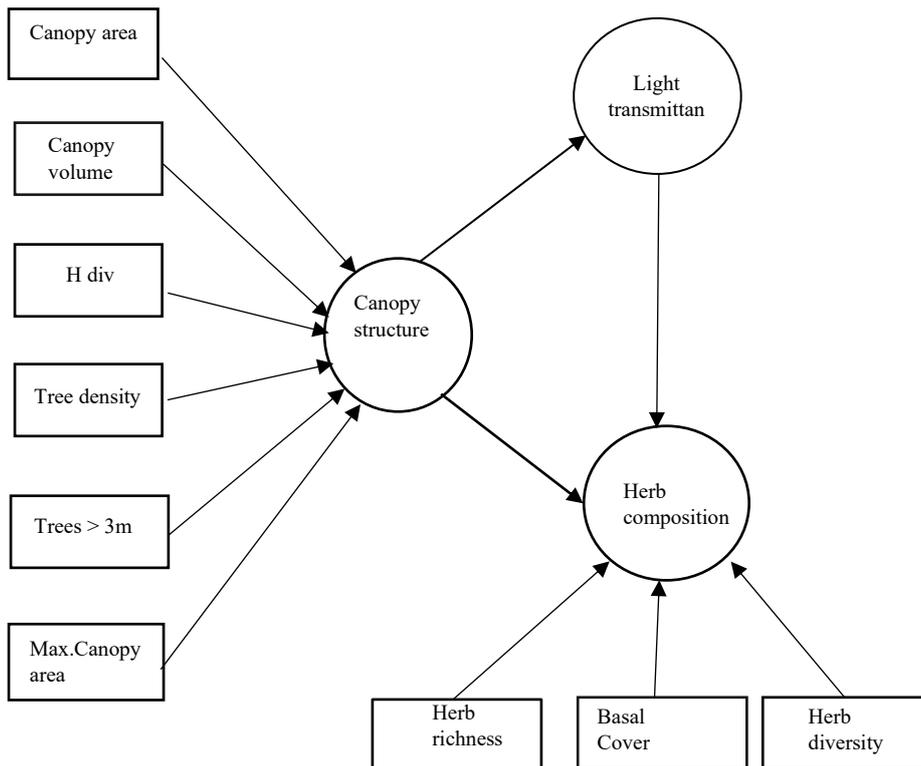


Figure 4. 1: Framework showing the influence between variables: canopy structure (canopy volume, tree diversity, density of trees and density of trees >3m), light (light transmittance) and herbaceous species composition (richness, abundance, and diversity). Measured variables are represented by rectangles and latent variables by circles. Arrows represent the expected direction of influence.

Light transmittance, LAI and canopy cover were correlated with the total summed up abundance scores of abundant grass species on each site. The LOESS smoothing method (Locally Estimated Scatter Plot Smoothing) was used to draw regression lines on the graphs. The p values from Spearman correlations, R^2 and linear regression formulae were generated for all the correlations.

Presence-absence data for the same grass species at each site was used to generate boxplots were to show the minimum, maximum, median, 75th and 25th quartiles for the occurrence of each species with increasing LAI, light transmittance, and canopy cover. Kernel density plots were also generated in *ggplot2* for common grass, all herb and sedge species responses along gradients of increasing LAI, light transmittance, and canopy cover and changes in basal cover with increasing LAI, light transmittance, and canopy cover.

4.4. Results

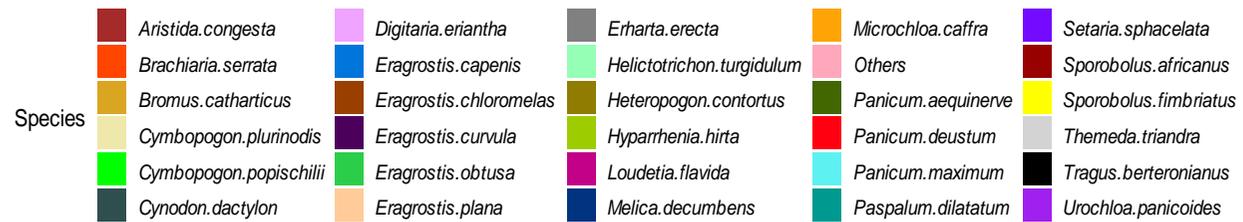
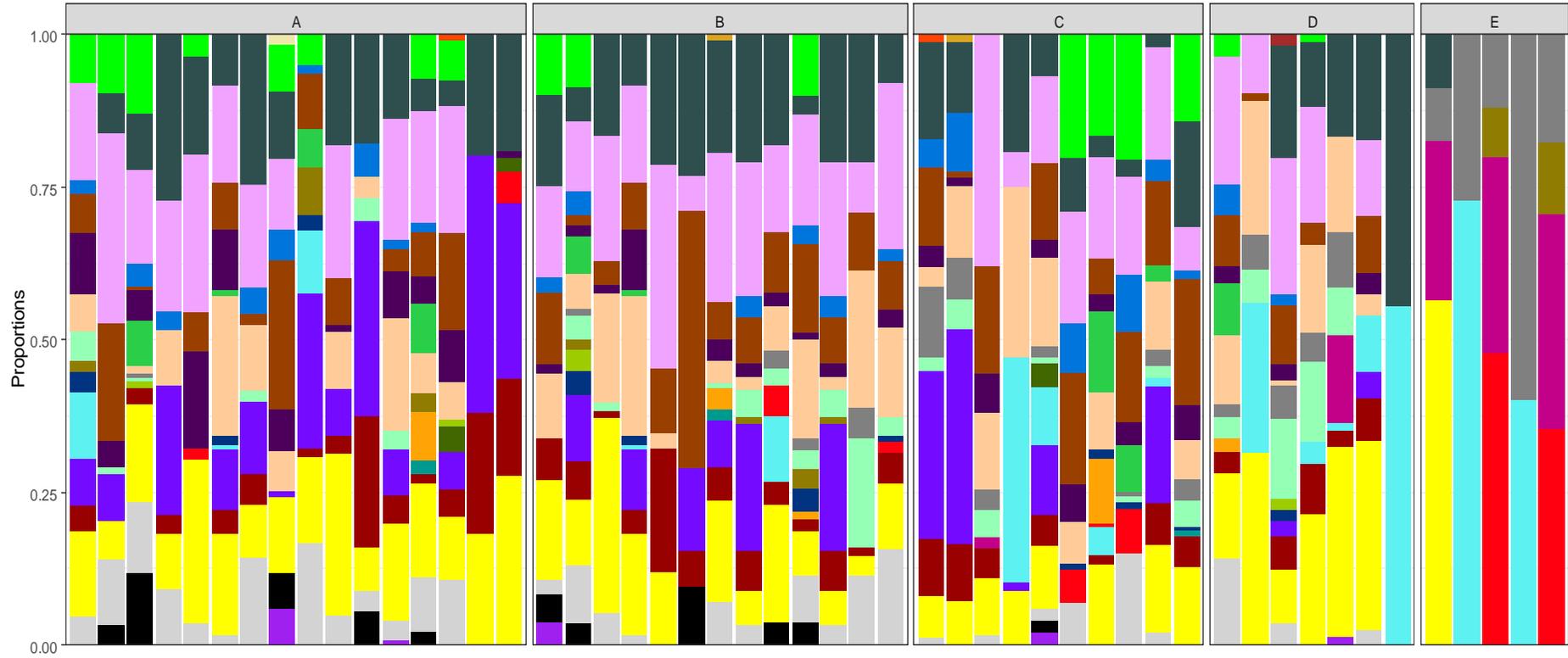
4.4.1. Changing herbaceous species composition with increasing tree cover

Tree cover and light transmittance had a significant effect on herbaceous species composition (Figure 4.2 a,b). Sites with low tree cover had similar herbaceous species compositions. Grass species: *Digitaria eriantha*, *Sporobolus fimbriatus*, *Themada triandra*, *Cymbopogon popischilii*, *Eragrostis plana*, *Eragrostis obtusa*, *E. capensis* and *E. chloromelas* were dominant at lower tree cover sites. Forb species *Berkheya* spp., *Ficinia* sp., *Hibiscus aethiopicus*, *Helichrysum dregeanum*, *Helichrysum nudifolium*, *Gerbera viridifolia* and *Eriospermum* sp., and *Selago corymbosa* were dominant in the sites with low canopy cover and high light transmittance and their presence declined with increasing light transmittance (increasing canopy cover, Appendix B). There was a clear difference in the composition of species in the high (> 50%) tree cover class and the open (0-15%) to moderate (31-50%) canopy cover classes (Appendix B). A few sites in the high tree cover class had the same species composition as sites in the low to moderate classes. In chapter 3, sites with light transmittance > 50% were dominated by *Vachellia karroo* and *Scutia myrtina* and had fewer tree species. These sites, dominated by *V. karroo* and *S. myrtina* had more grass and forb species than sites with a diverse species composition.

Clutia spp., *Pellaea viridis*, *Ehrharta erecta*, *Stachys aethiopica*, *Panicum maximum* and *Cyperus* spp. dominated high tree cover sites (low light transmittance) and were also found in low tree cover sites. *Oxalis pes-caprae* and *Polygala* sp. were also found in some high canopy cover but were dominant in low canopy cover sites. Sites in the E transmittance class were compositionally distinct from the rest of the transmittance classes. Grasses dominant in low light transmittance sites were *P. maximum*, *P. deustum* and *L. flavida* and these were fewer in sites with a high light transmittance (low canopy cover) and most grasses found in class A-D were absent at light transmittance class E. These high tree cover (light transmittance < 50%) were also dominated by thicket tree species (e.g., *Afrocanthium mundianum*, *Dovyalis zeyheri* and *Searsia longispina*) and had less of *V. karroo* featuring in the tree assemblages (Chapter 3, Figure 3.4).

A light transmittance of 50 % corresponded to LAI of ~1 and a canopy cover of ~70 % (Figure 4.2). The light transmittance cover class E (<50 %) is thus representative of conditions where LAI >1 and canopy cover is >70%.

a)



b)

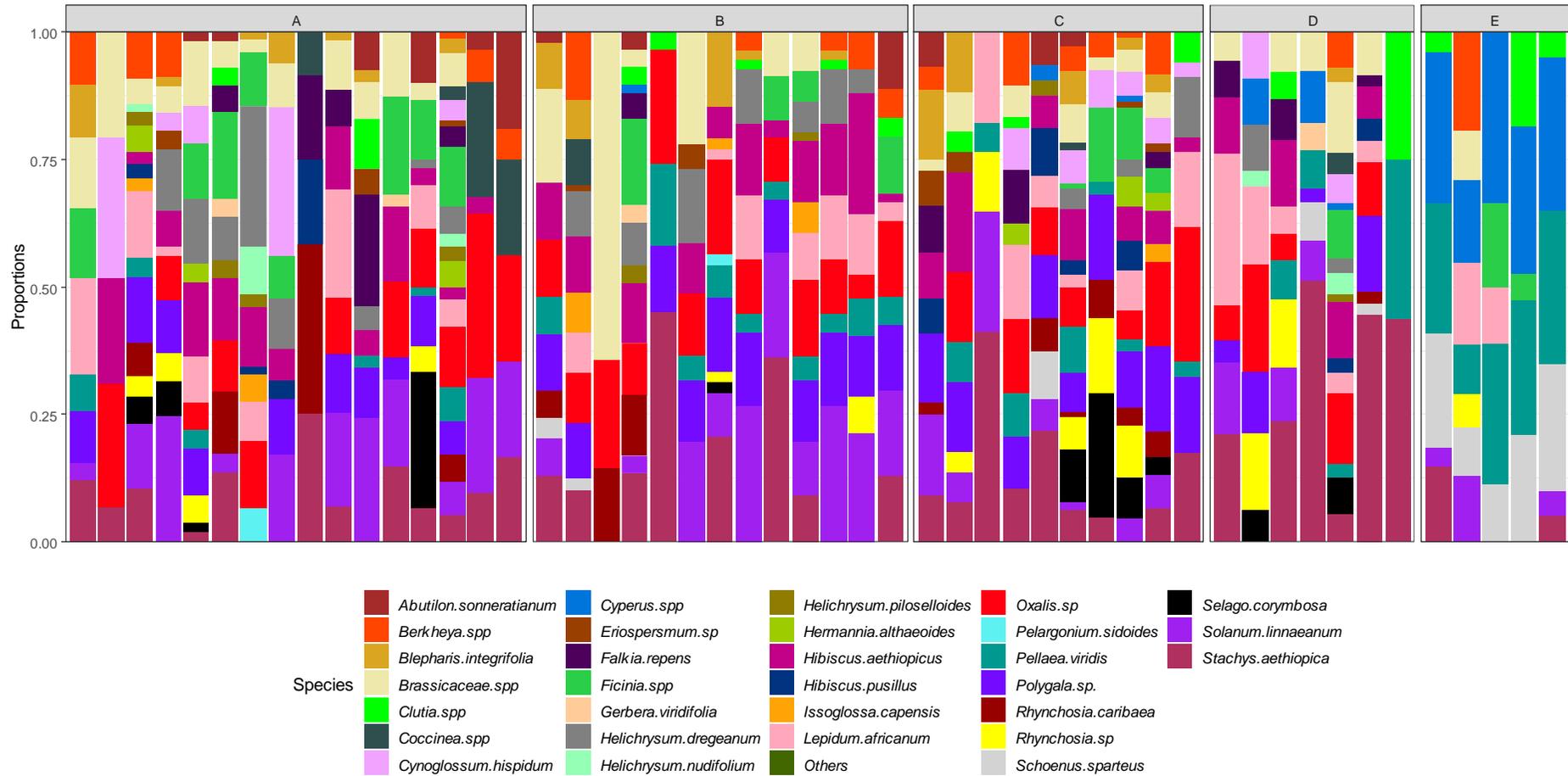
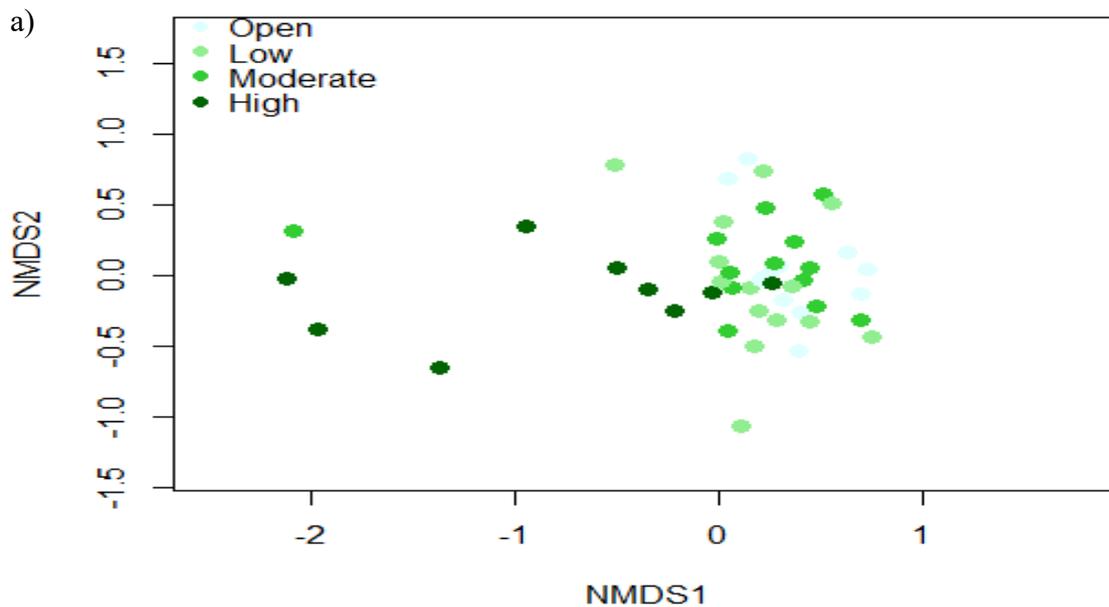


Figure 4. 2 a, b: The proportion of a) grass and b) forb found at 51 sites. Each colour on the plot represents a different forb species. b) and d) The groups were divided into light transmittance classes: A (91-100), B (81-90%), C (71-80%), D (51-70 %), E (20-50) (Appendix B). Each colour on the plot represents a different herb and grass species. Herbaceous species found in this study are listed in Appendi

A trend of changing herbaceous composition is evident from Figure 4.3 b) from low canopy cover to high canopy cover. A similar trend is observed from low light transmittance to high light transmittance. The low transmittance class (E; <50%) had a different herbaceous composition compared to the other classes (B, C, D, E). The high canopy cover class sites overlapped with some low canopy cover classes. The overlapping classes suggested a high similarity in species composition with some high canopy class sites having communities that were different from the rest of the classes. MANOVA test for Transmittance range classes showed that there was a significant difference in species composition between the classes ($R^2 = 0.21$, $F=2.91$, $p=0.001$). MANOVA test for canopy cover classes also showed that there was a significant difference between the classes ($R^2 = 0.11$, $F=1.91$, $p=0.004$). There was a significant difference between A and B, C, D, E ($p<0.05$) (Table 4.3). There was a significant difference between high-low, high-open and low-moderate canopy cover classes ($p<0.05$) (Table 4.3).



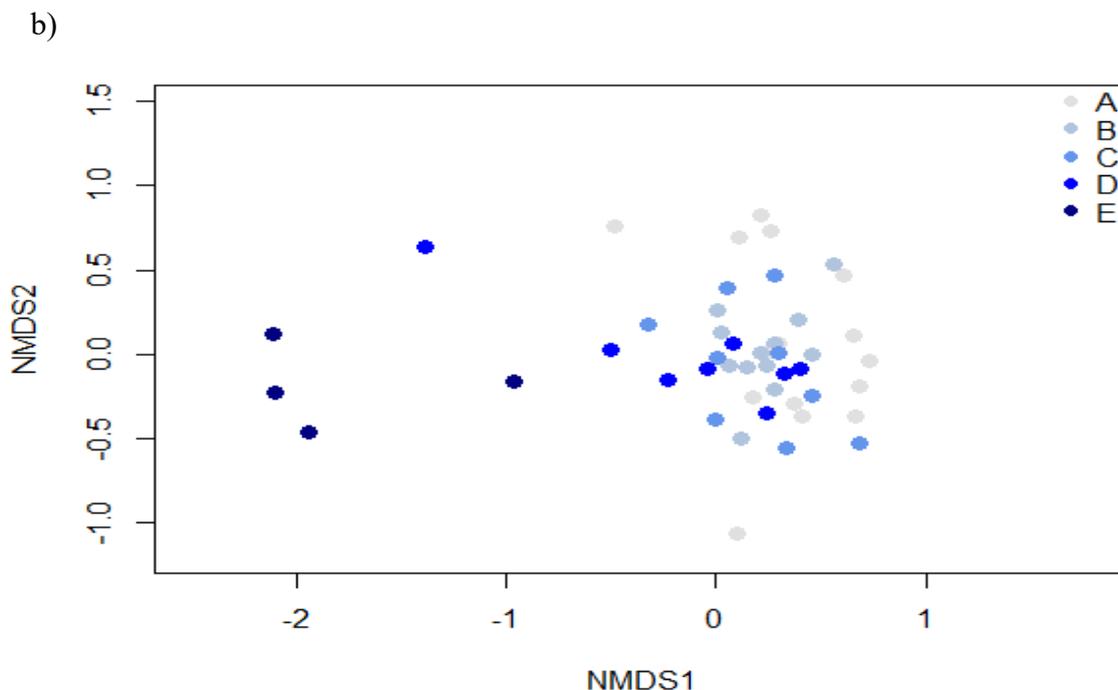


Figure 4. 3: Non-metric multidimensional scaling (NMDS) plot based on the Bray-Curtis distances among 51 sampling sites using herbaceous species abundance data (stress= 0.17). a). The gradient of green dots from light green to dark green represent the canopy cover classes from aerial photographs: a) open (0-15%), low (16-30%), moderate (31-50%), high (51-100%) b) light blue to dark blue dots correspond to sites belonging to light transmittance class A (91-100), B (81-90%), C (71-80%), D (51-70 %), E (20-50).

Table 4. 1: Pairwise tests of significance based on species composition between A, B, C, D and E light transmittance classes

Light transmittance		A	B	C	D
	B	0.201	-	-	-
	C	0.256	0.120	-	-
	D	0.036	0.075	0.256	-
	E	0.010	0.010	0.010	0.010

Table 4. 2: Pairwise tests of significance between open (0-15%), low (16-30%), moderate (31-50%) high (51-100%) tree cover classes.

Tree cover		Open	Low	Moderate
	Low	0.044	-	-
	Moderate	0.006	0.10	-
	High	0.006	0.28	0.682

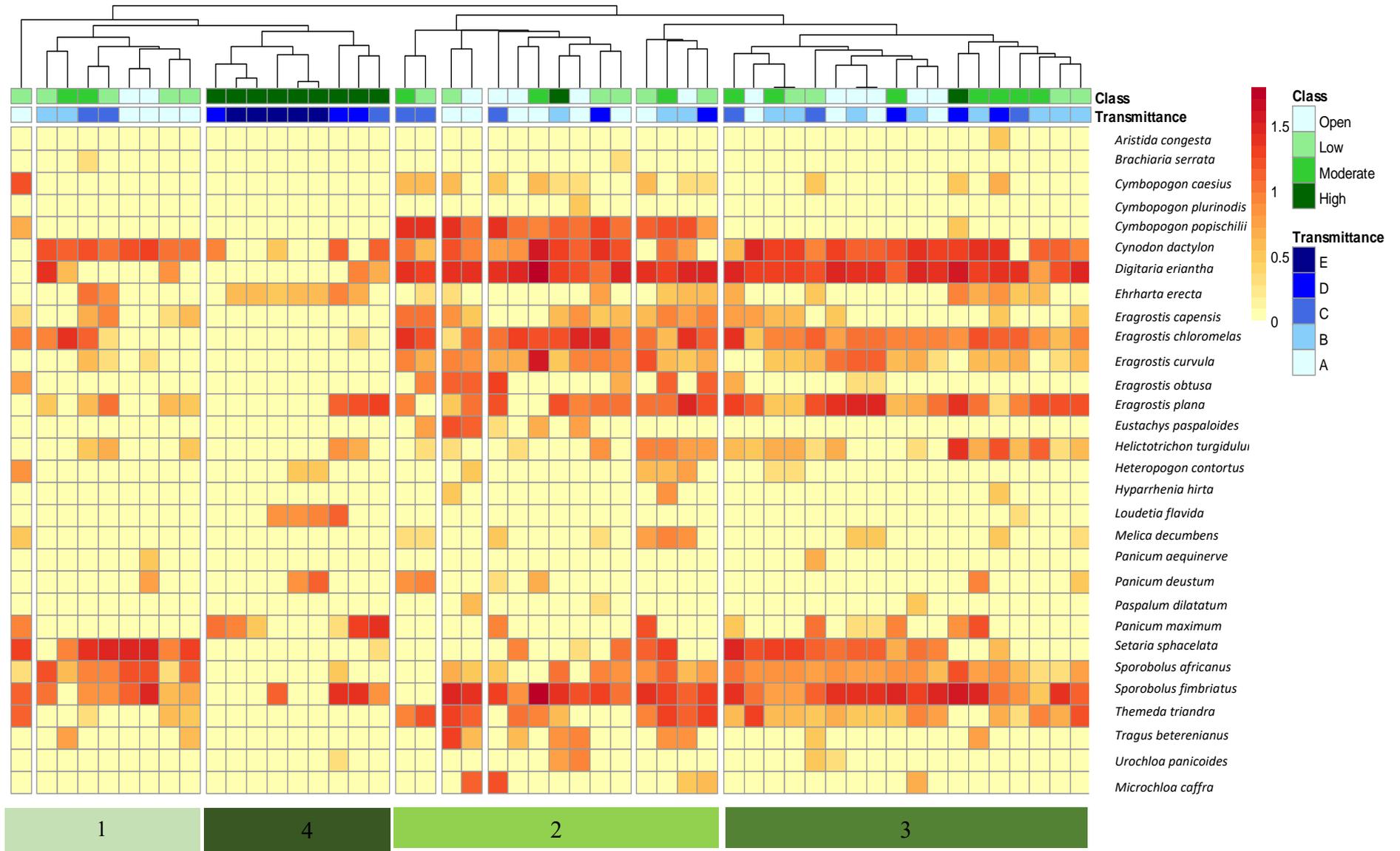
Hierarchical clustering based on herbaceous species abundance scores on each site in Figure 4.4 suggests that there were similarities in species composition between sites belonging to the same ranges of light transmittance. There was a clearer difference in species composition between sites with light transmittance >50 % (A-D) and group E (light transmittance < 50%). Sites that belong to the high canopy cover class and the light transmittance class E tree had a tendency of clustering together. Open, low and moderate canopy cover sites were found in the same clusters. Grass species that were common in low light transmittance (high canopy cover) classes were *Cynodon dactylon*, *Digitaria eriantha*, *Sporobolus fimbriatus*, *Sporobolus africanus* and *Themeda triandra*. Forb species that fell into low tree cover (high light transmittance) clusters were *Abutilon sonneratianum*, *Berkheya spp*, *Brassicaceae spp*, *Selago corymbosa*, *Helichrysum spp.*, *Lepidium africanum* and *Oxalis sp*, *Hibiscus aethiopica*, *Stachys aethiopica*. Species that were common amongst the high canopy cover class and light transmittance E (20-50%) were *Pellaea viridis*, *Cyperus spp.*, and *Schoenus sparteus*.

The pattern of cluster formation as a function of canopy cover and light transmittance class can be described according to changes in the abundance of forb and grass species. The groups formed from the clustering pattern were arranged from groups 1 to 4, and the sites falling into these groups generally represented a change from open to high canopy cover sites (Figure 4.4). In chapter 3, sites with a high abundance of *V. karroo* and *S. myrtina* belonged to the lower canopy cover classes (high light transmittance). Sites belonging to the same canopy cover and light transmittance classes were shown to have similar species compositions based on abundance data in Figure 4.3. suggesting that the herbaceous community responded to changes in canopy structure, that were observed in chapter 3. Group number 1 shown on Figure 4.4 a) consisted of sites that were mainly open and low canopy cover (high light transmittance) sites and the grass species that dominated these sites were: *Cynodon dactylon*, *Setaria sphacelata*, *Sporobolus africanus*, *Sporobolus fimbriatus* and there was a low abundance of *Themeda*

triandra. The second group consisted of mostly open and low canopy cover sites. This second group had three moderate canopy cover sites and one high canopy cover class (high light transmittance), these are sites with a high abundance of *Cymbogon popischilii*, *Cyndodon dactyon*, *Digitaria eriantha*, *Eragrostis capensis*, *Eragrostis chloromelas*, *Eragrostis curvula*, *Eragrostis plana*, *Sporobolus africana* and *Sporobolus fimbriatus*. The third group consisted of a mixture of open, low and moderate and one high canopy sites. The third group had more moderately covered sites than the second group. This third group lacked *Cymbopogon* grass species and had a higher abundance of *S. sphacelata* compared to the second group. The fourth group was composed mainly of high tree cover sites (with low light transmittance) and the grasses present at some sites were *Panicum maximum*, *Loudetia flavida*, and *Ehrharta erecta*.

The first group (1) on Figure 4.4. b) was composed of mainly low, open and moderate canopy cover classes that had high light transmittance (> 50%) and the forb species dominating at those sites were: *Abutilon*, *Berkheya* sp., *Brassicaceae* sp., *Selago corymbosa*, *Helichrysum* spp., *Lepidium africanum*, *Oxalis* sp. The second group was composed of low, open and two higher canopy cover sites which had a light transmittance > 50 % and was made of similar forb species to the first group, however it had higher abundance of *Helichrysum piloselloides* and a lower abundance of *Solanum linnaeanum* species. The third group had more high and moderate canopy cover sites, which also had more sites with a light transmittance < 50% than the first and second group. The third group was different from the first and the second because of a very low abundance in *Helichrysum* species and the *Polygala* sp. The fourth group was composed of only high canopy cover and low light transmittance (< 50%) sites which lacked species *Abutilon*, *Berkheya* spp., *Brassicaceae* sp., *Selago corymbosa*, *Helichrysum* spp., *Lepidium africanum*, *Oxalis* sp. The most dominant species in the fourth group was *Cyperus* spp., *Pellaea viridis* and *Schoenus sparteus*.

a)



b)

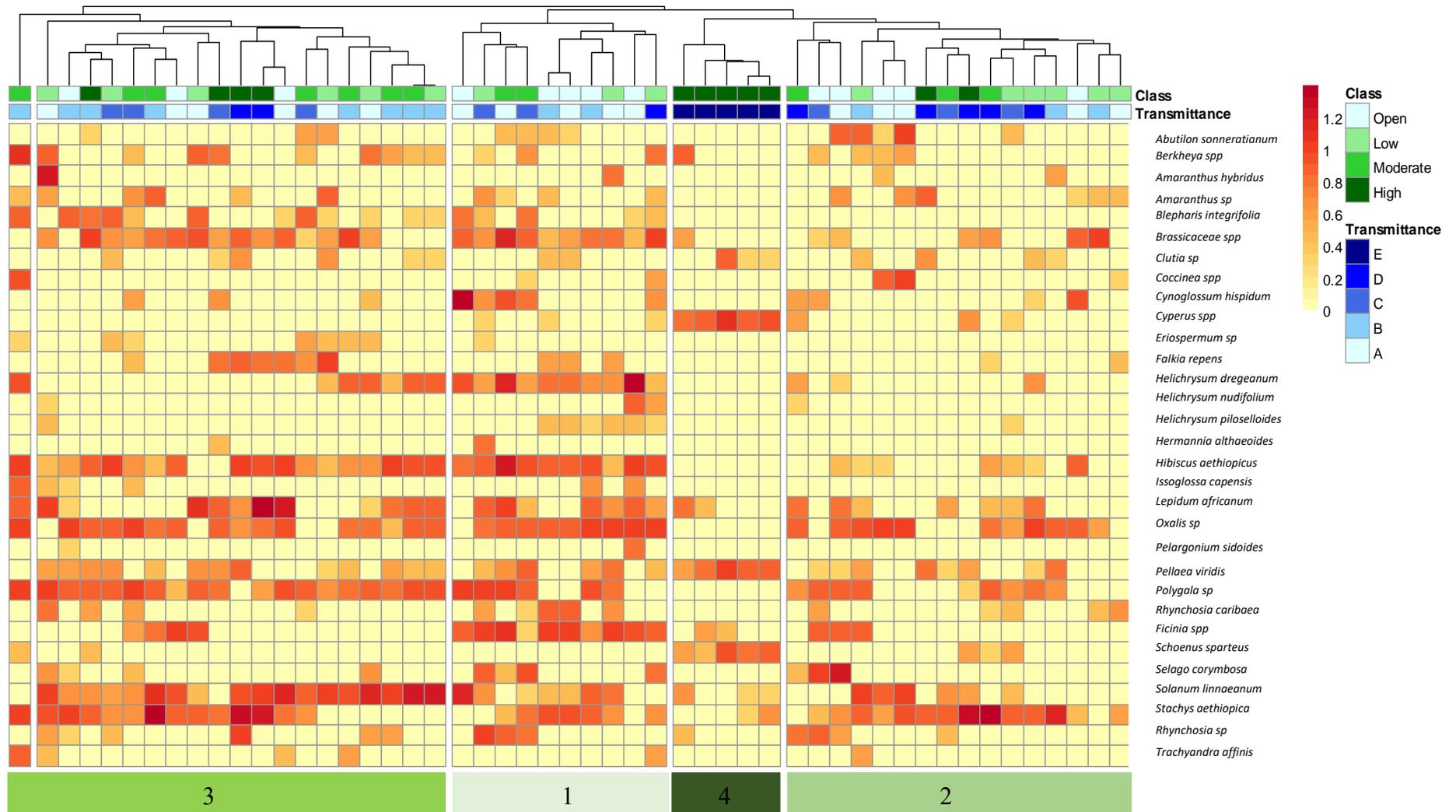


Figure 4. 4: Dendrogram and heatmap showing the abundances scores (log10 transformed) of herbaceous species- a) grasses and b) forbs (rows) and the sites (columns). The sites were clustered using Bray-curtis distances and using the complete method. The legend shows a gradient of green blocks from light green to dark green represent the canopy cover classes from aerial photographs: a) open (0-15%), low (16-30%), moderate (31-50%), high (51-100%) b) light blue to dark blue dots correspond to sites belonging to light transmittance classes: A (91-100), B (81-90%), C (71-80%), D (51-70 %), E (20-50). On the heatmap, lighter yellow and orange colours represent the lower bounds of the species abundance and the darker red represent a high abundance of the species. The gradient of light green to dark green blocks at the bottom of the figure represents the general clustering pattern of some sites with an increase in canopy cover (decreasing light transmittance).

4.4.2. Response of herbaceous species to canopy variables

The abundance, richness and diversity of herbaceous species increased markedly with decreasing canopy cover, LAI, canopy area, density of trees, density of trees > 3m, canopy volume and canopy area, and with increasing light transmittance (Figure 4.5). Significant relationships were shown between the forb species richness, herb abundance, herb diversity, diversity of trees, density of trees, canopy area, canopy volume, maximum canopy area, light transmittance, LAI and canopy cover from each of the 51 sites.

The diversity of herbaceous species showed the strongest negative relationships with canopy cover and LAI and the strongest positive relationship with light transmittance. Species richness had the weakest negative relationship with % tree cover, LAI, canopy area, number of stems >3m, number of trees and canopy volume and weakest positive relationship with light transmittance (%).

4.4.3. SEM: Effect of increasing tree cover on the herbaceous community

The structural equation model showed that the woody structure variable had a strong influence on the light variable as already shown in Chapter 3 (Figure 3.10), but a less strong direct effect on the herbaceous composition variable (Figure 4.6). The goodness of fit for the model was $R^2 = 0.62$. Woody vegetation structure (representing the effects of canopy area, canopy volume, tree diversity, density of trees, density of trees > 3m, maximum canopy area) explained 71% of the variation. Light and woody vegetation cover explained 53% of the variation in herb composition. Hair *et al.*, (2014) considers R^2 values 0.7 to be substantial and 0.50 to be moderate. The high R^2 value achieved in the model suggests that latent independent variables explain most of the variance in the endogenous variables. There was a negative direct influence of canopy structure (number of trees, number of trees > 3m, diversity of trees and canopy volume) on the herbaceous community ($\beta = -0.35$). The density of trees >3m at a site had the greatest influence ($\beta = 0.66$) on the canopy structure variable. Herb diversity had the greatest influence on herb composition ($\beta = -0.1.62$). Light had a positive influence ($\beta = 0.41$) on the herbaceous community's composition.

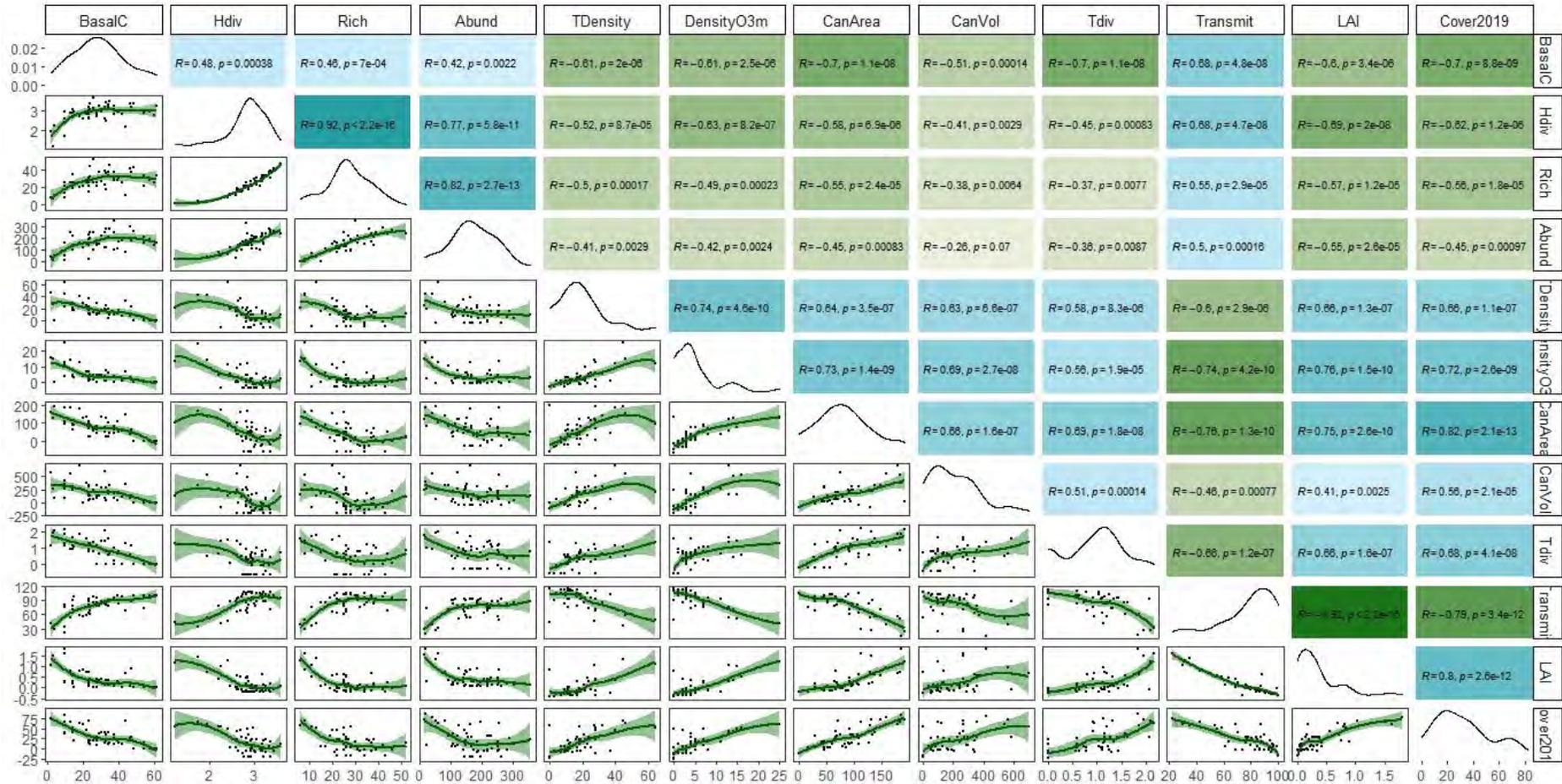


Figure 4. 5: The relationships between the BasalC (Basal cover), Hdiv1 (Herb species diversity, grass and forb species combined), Est.Rich (Estimated Richness), TDensity (Tree density at each site tree/ha), CanArea (Total canopy area), CanVol (Total canopy volume), Hdiv (Diversity of trees), Transmit (Light transmittance estimated from hemispherical photography) and LAI (estimated from hemispherical photographs and Cover2019 (Aerial canopy cover estimated from 2019 Google imagery). The p values from Spearman correlations and R values were generated for all the correlations. The loess method was used to compute a smooth regression represented by the dark green line.

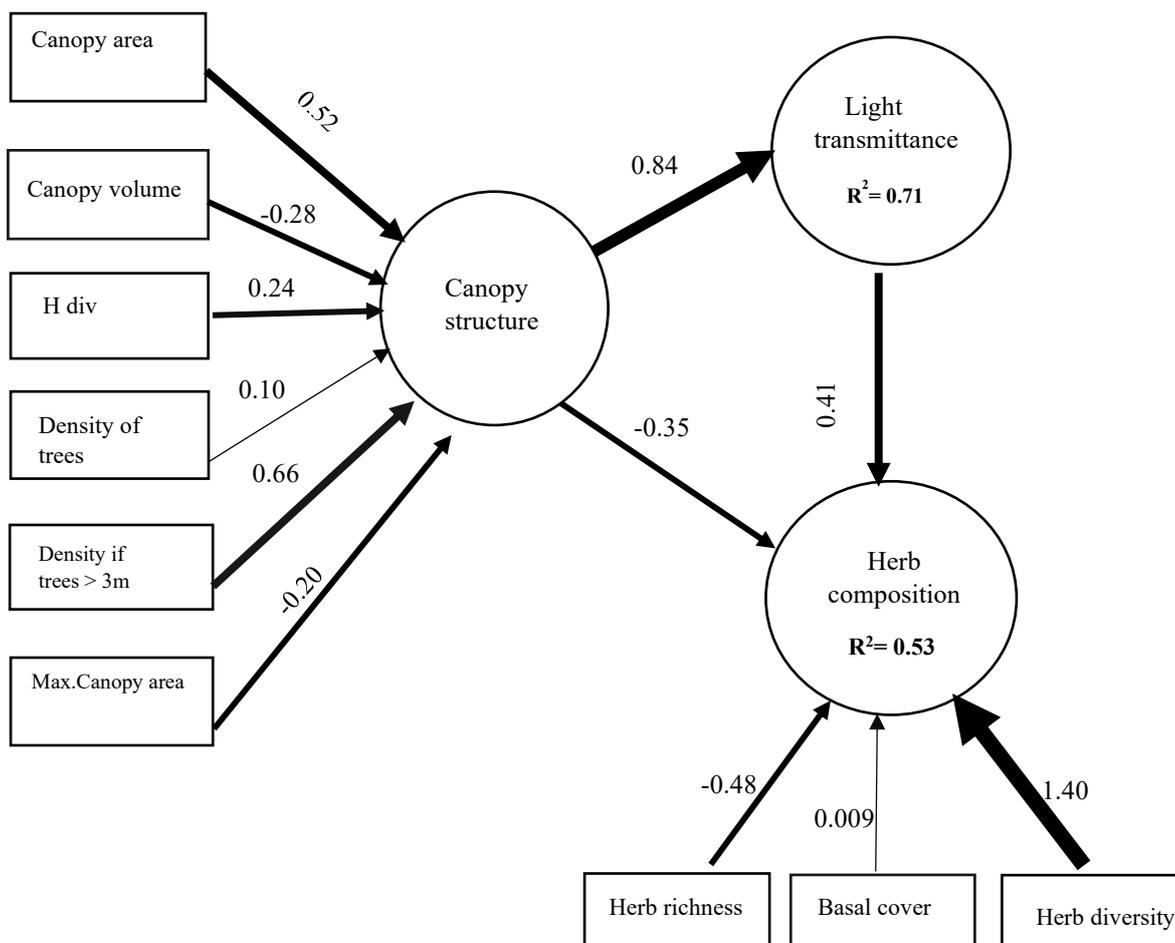


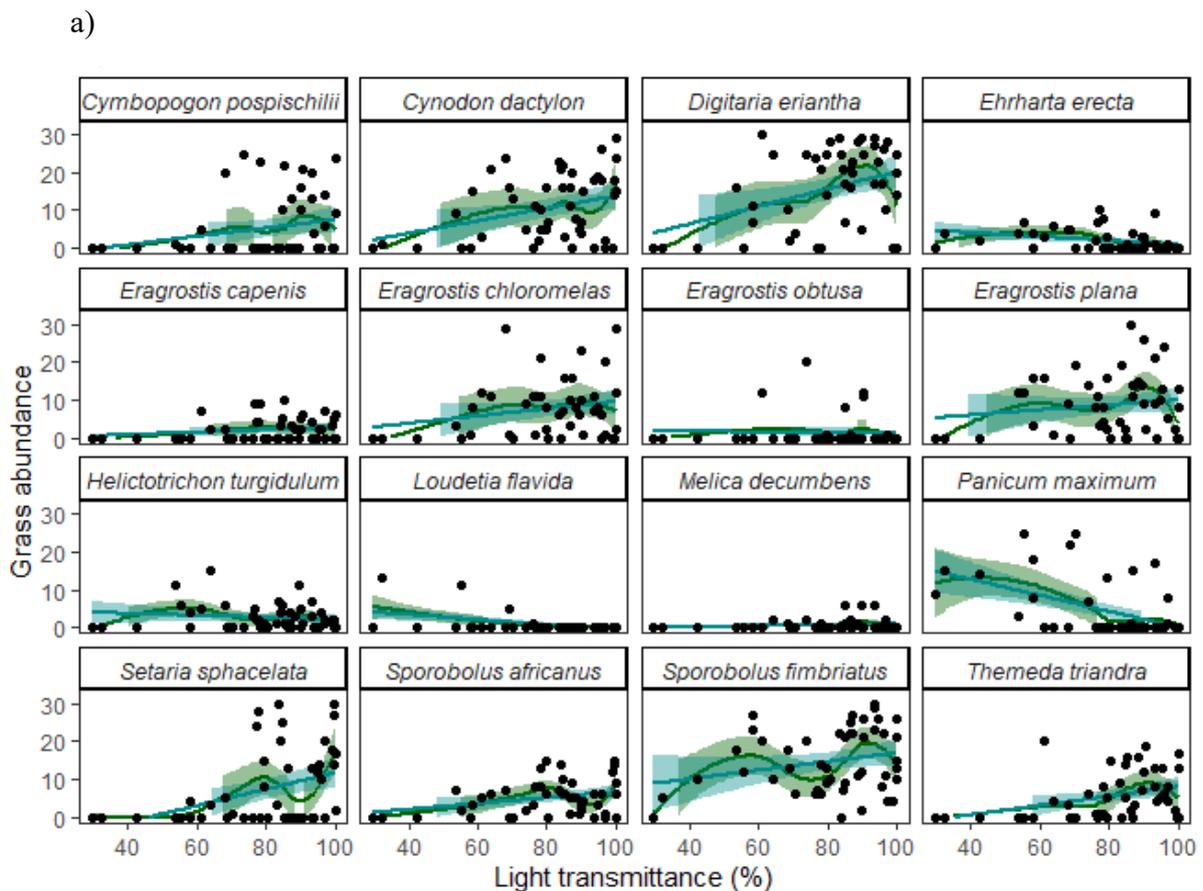
Figure 4. 6: The path diagram for structural equation model relating canopy structure (canopy volume, tree diversity, number of trees, number of trees >3m), light (Light transmittance) and herb composition (richness, abundance, and diversity). The path coefficients are shown as arrows, and the direction of the arrows indicate influence. Latent variables are represented as circles and observed variables as rectangles. The goodness of fit for the model, $R^2 = 0.66$ and the variables: Herb composition ($R^2 = 0.53$) and Light ($R^2 = 0.71$).

4.4.4. Responses of key grass species to changing woody cover

Grass species showed different trends in abundance scores (range: 0-30) with increasing canopy cover, LAI and light transmittance (Figure 4.7). More grasses had significant responses to changes in canopy cover than changes in LAI and light transmittance (Table 4.2). Grasses that were most dominant in most field sites were *D. eriantha*, *T. triandra*, *C. popischilii*, *E. chloromelas*, *C. dactylon*, and *S. fimbriatus* and these grasses showed significant changes with changing LAI, light transmittance and canopy cover. An increase in light transmittance was met by a significant increase

($p < 0.05$) in *S. sphacelata*, *T. triandra* and *S. africanus*. Grasses that decreased in abundance with increasing light transmittance were *E. erecta*, *P. maximum*, and *Loudetia flavida*. *Melica decumbens*, *E. obtusa* and *E. capensis* showed no change in abundance with changing light transmittance. The relationship between LAI and grass abundances is the inverse of the relationship between light transmittance and grass abundances. Only *P. maximum* and *L. flavida* increased with increasing LAI. *Cynodon dactylon*, *D. eriantha*, *S. sphacelata* and *T. triandra*, *S. africanus*, *E. chloromelas* had a negative correlation with canopy cover. The abundance of *P. maximum*, *E. erecta*, and *L. flavida* increased with canopy cover.

Figure 4.7 is consistent with a woody cover threshold of $\sim 40\%$, above which several species declined in abundance. Based on regressions shown in Chapter 3 (Figure 3.9), this corresponds to a light transmittance of $\sim 75\%$ and LAI of ~ 0.5 .



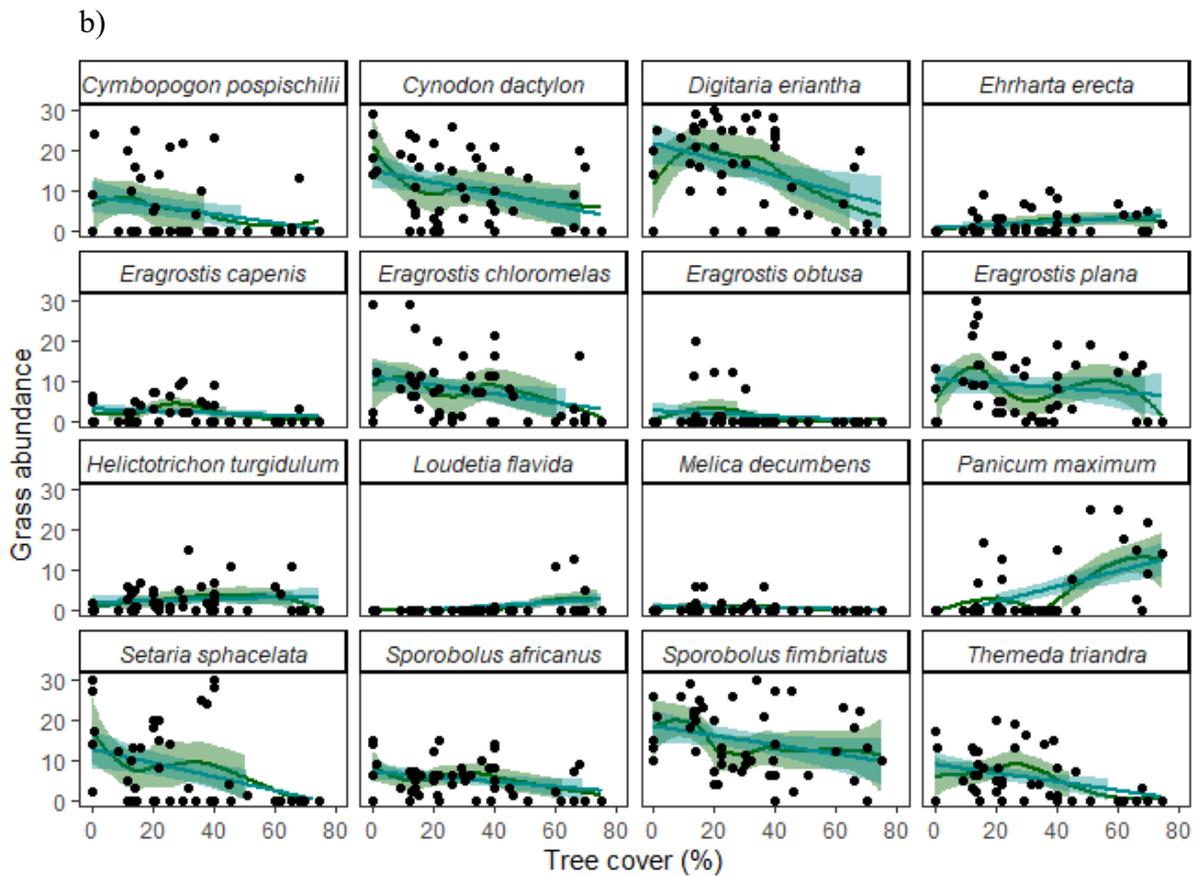


Figure 4. 7: Bivariate relationships between grass species a) Light transmittance, b) Tree cover (%). The LOESS and lm methods were used to compute a smooth and linear regression represented by the dark green and dark cyan lines respectively.

Some grass species were more common at higher LAI, canopy cover and lower light transmittance levels, while others showed the opposite trend. Grass species *Cymbopogon pospischilii*, *E. capensis*, *E. chloromelas*, *M. decumbens*, *T. triandra*, *S. sphacelata*, *S. fimbriatus*, *S. africanus*, *H. turgidulum* peak at LAI < 0.5, light transmittance > 75% and tree cover < 38% (Figure 4.8) and this pattern was also evident in Figure 4.4. The grasses that had LAI range > 1 were *L. flavida* and *P. maximum*. *Loudetia flavida* and *P. maximum* were also the only grasses with an optimum at LAI > 0.5, light transmittance < 75% and tree cover > 38% (Figure 4.8). Most of the grasses were only present at LAI < 1 and had their minimum at LAI = 0. Light transmittance maxima for most grass species (*T. triandra*, *S. fimbriatus*, *S. africanus*, *S. sphacelata*, *H. turgidulum*, *E. plana*, *E. obtusa*, *E. chloromelas*, *D. erianth*, *C. dactylon* and *C. pospischilii*) were at 100%. *Panicum maximum*, *L. flavida*, and *E. erecta* were the only grasses with a an interquartile range light transmittance < 40%. *Cymbopogon pospischilii* and *M. decumbens* had the lowest minimum light transmittance limit at 60%. There were outlying

sites at light transmittance < 40% for *S. fimbriatus* and *C. dactylon*. The majority of the grasses had a minimum at 0 canopy cover, except for *E. obtusa*, *L. flavida*, *M. decumbens*, and *P. maximum* whose minimum canopy cover were at higher tree covers (~15%). Grasses with maximum canopy cover ranges beyond 70% were *S. fimbriatus*, *P. maximum*, and *E. erecta*. Grasses with the lowest canopy cover maximum (< 50%) were *T. triandra*, *E. capensis*, *E. obtusa*, and *M. decumbens*.

Basal cover of herbaceous species declined with increasing LAI and canopy cover and increased with increasing light transmittance (Figure 4.7). All herbaceous species basal cover was at its highest densities at LAI < 0.5, which corresponds to light transmittance ~ 78% and canopy cover of 38%. All grasses decrease in cover with an increase in LAI, except for *S. fimbriatus* and herb species which have a second peak at LAI 0.5 < 1. All grass and herb species basal cover had the highest densities at >80% light transmittance. Grasses with lower peak basal cover densities were *E. chloromelas*, *S. sphacelata* and sedges.

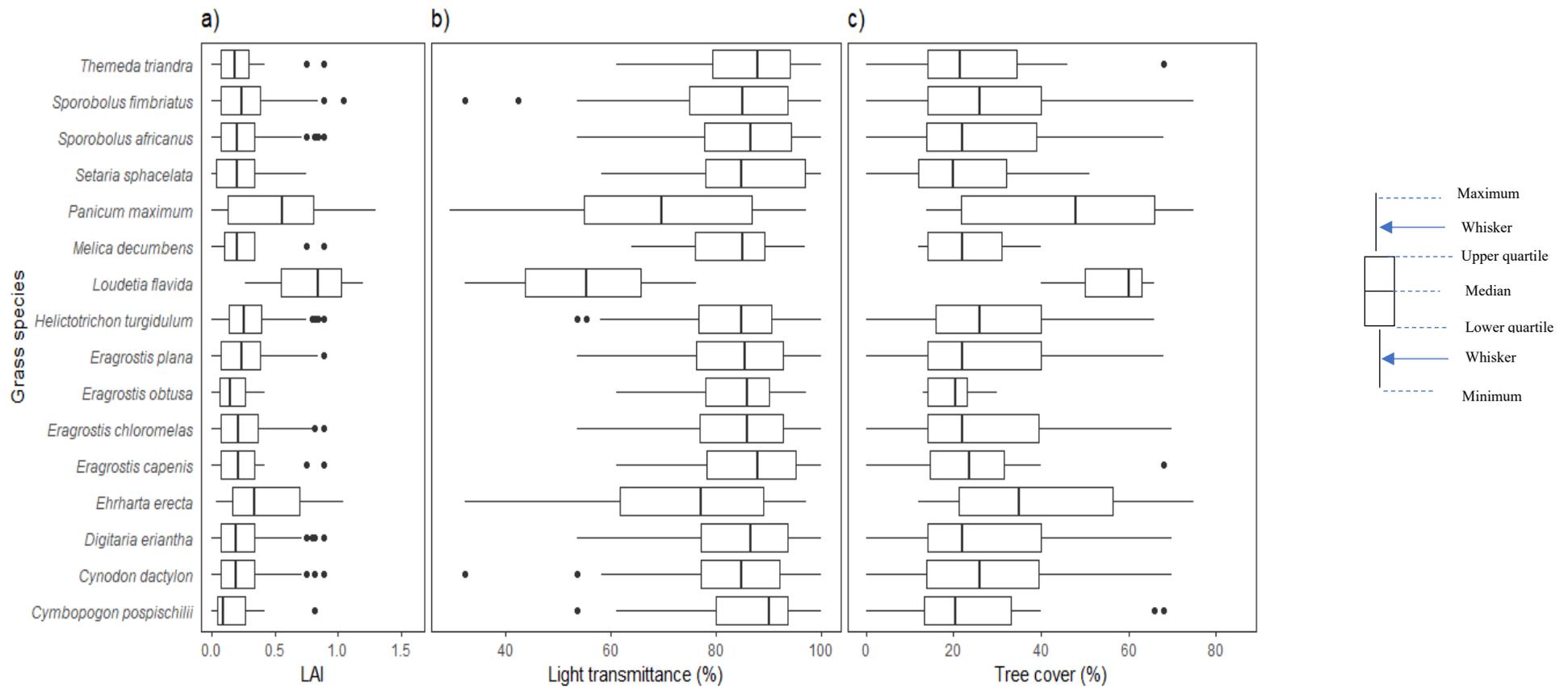
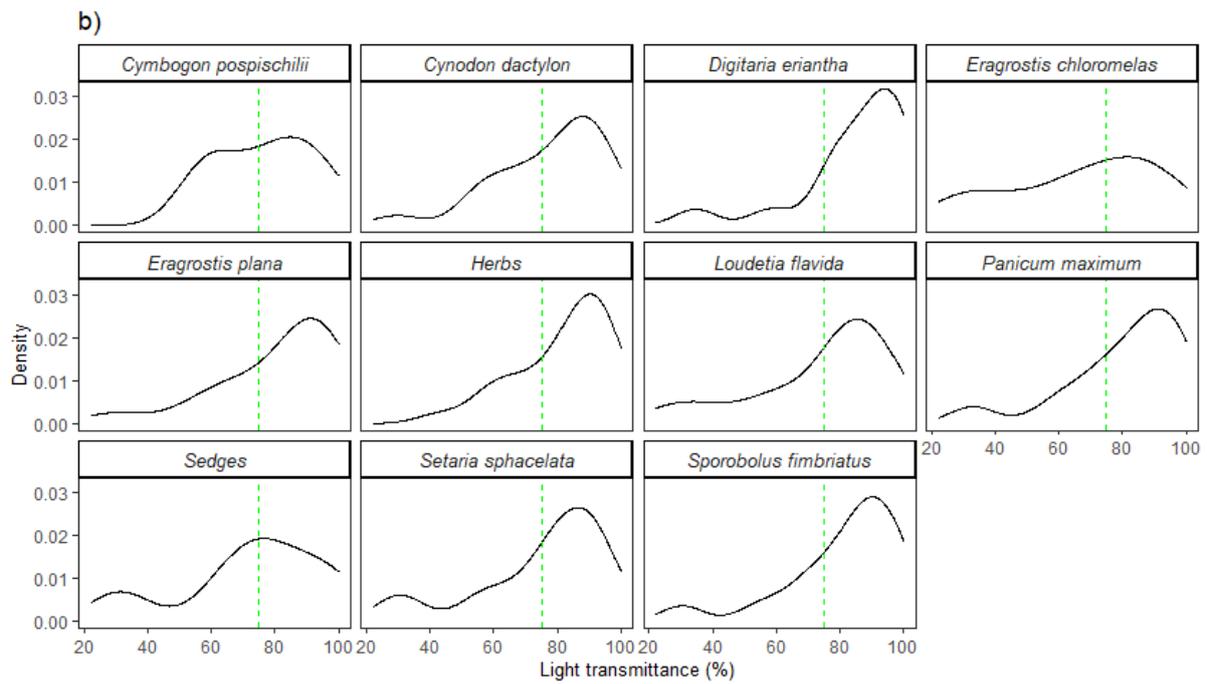
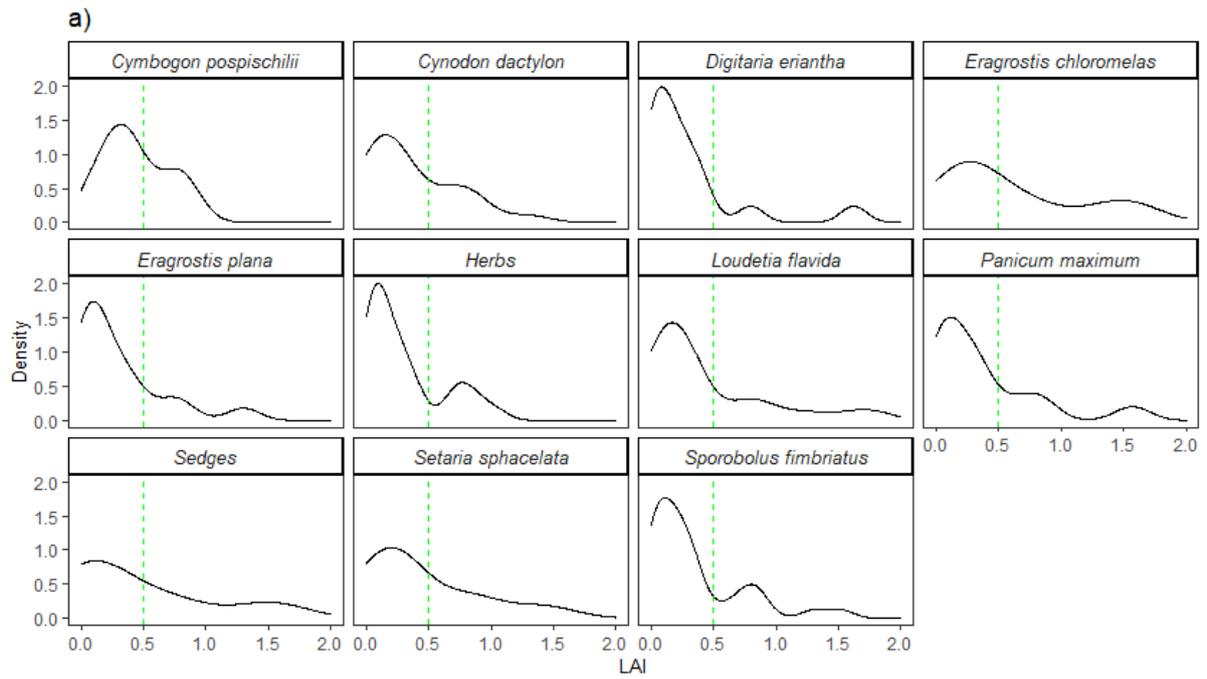


Figure 4. 8: The range of light transmittance (%), LAI, % tree cover where key grass species occur. The boxplots indicate the lower (Q1) and upper (Q3) quartiles. The median is drawn as a line inside the boxplot. Outliers we indicated as dots and the maximum and minimum as lines on the boxes



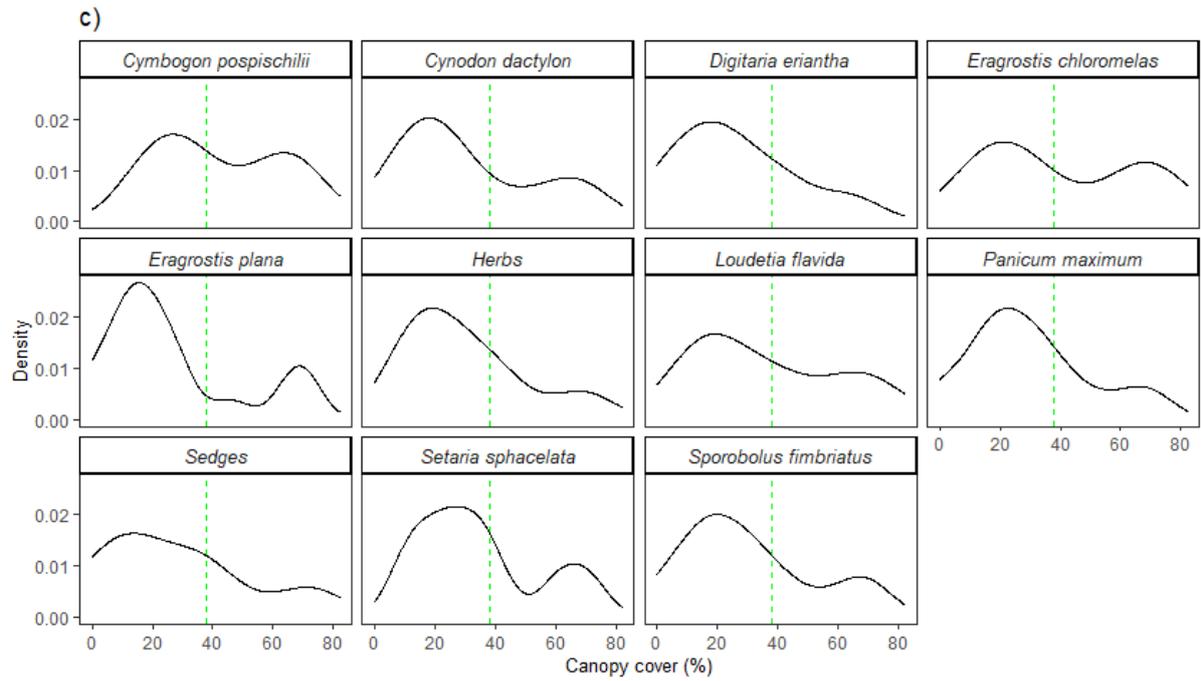


Figure 4. 9: Kernel density plot showing the distribution densities of basal cover for grass, forbs (herb) and sedge species with increasing a) LAI, b) Light transmittance c) Canopy cover (%) for individual grass species, grouped herb and sedge species. The green line indicating a threshold for maximum densities at a) 0.5 LAI and the corresponding b) light transmittance (78%) and c) canopy cover (38%) thresholds calculated from linear regression equations.

4.5. Discussion

4.5.1. Changing grass composition along changing light transmittance and % tree cover

The presence of forb species in savanna systems is important, not only for forage biomass, but for the resilience of the savanna system. The diversity of herbaceous species maintains the function of a savanna when environmental conditions change. For example, droughts are favourable to forb species (*H. nudifolium*, *G. ambigua* and *Eriospermum* sp.) that have underground water storage organs and other drought-tolerant traits (Siebert *et al.*, 2019). The change in herbaceous species was analogous to the change in tree species in chapter 3. Sites dominated with *V. karroo* and *S. myrtina* were low canopy cover sites with high light transmittance favouring a diverse assemblage of forb species and sites with a diverse assemblage of trees had fewer of the herbaceous species found in low canopy cover sites. The low light transmittance sites had fewer grass species, with *Panicum maximum*, *Loudetia flavida* and *Ehrharta erecta* being their most dominant grass species. The high light transmittance sites (low canopy cover) were dominated by C₄ grass species (Appendix D) and specific forb species (*Berkheya* spp., *Ficinia* sp., *Hibiscus aethiopicus*, *Selago corymbosa* and *Helichrysum dregeanum*, *Helichrysum nudifolium*, *Gerbera ambigua* and *Eriospermum* sp. (Figure 4.2). Sites with a light transmittance > 50% had similar compositions of herbaceous species, and this composition changed at light transmittance < 50% (Figure 4.2).

The differences in species composition could not only be due to differences in canopy structure characteristics, because there were sites that belonged to the same canopy cover class that had different herbaceous plant compositions. The composition of herbaceous and tree species may have been influenced by the local topography and geomorphology (Motta *et al.*, 2002), and the chemical properties of the soil (Reatto *et al.*, 2008; Ribeiro & Walter 2008). It has been shown that variation in plant community composition at local scales is related to environmental factors, altitude, moisture content, slope, soil types and pH (Birhanu *et al.*, 2021). Although the sites were located along the same slope, there could have been slight differences in topography and soils that may have influenced the differences in species composition for sites with same canopy cover and light transmittance ranges. For example, some of the sites that were densely covered for the longest period were located in areas near wooded valleys (Chapter

2). Other sites had only experienced bush encroachment in more recent years and their tree and herb species composition still resembled that of open sites.

The herbaceous layer composition did not change immediately, since sites with open, low and moderate tree cover or A, B, C, D light transmittance ranges had similar species compositions. The composition of grasses changed drastically beyond the 50% light transmittance mark, and this was indicated by deficiency of grasses dominant in the open sites. The change in the composition of forb and grass species as tree cover increased and light transmittance decreased beyond a critical level indicated that vegetation communities are different on either side of the light transmittance threshold. The denser vegetation sites were characterised by these common species and a general decline in herbaceous species on the ground, whereas open-moderate tree cover sites had more grass and forb species in the understory.

The NMDS plots also corroborated the trend of changing species composition from lower canopy cover/ light transmittance to higher canopy cover classes (Figure 4.3). Charles-Dominique *et al.* (2018) observed that a threshold of c. 1.5 marked the transition from a C₄ dominated system to a C₃ dominated system. The NMDS, and taxaplot figures generated from light transmittance range classes suggested that the point where C₄ grasses were excluded could be at ~50% light transmittance, which corresponds to an LAI of c 1. The difference in the composition of the herbaceous layer was also observed between encroached and non-encroached sites in Dirbaba *et al.* (2014) study in the areas of Borana Rangelands. Bush encroachment reduced herbaceous plant diversity, richness and biomass, which resulted in declining productivity of the rangeland (Dirbaba *et al.*, 2014).

Although the level of shading is usually attributed to tree density, it is suggested that forest/thicket trees could differ from savannas by casting deeper shade. The trees that dominated the open-moderate sites were *V. karroo* and *S. myrtina* and the composition of these trees changed with increase tree density (Chapter 3), a change that was also associated with an increase in broadleaved, evergreen tree species. Figure 3.4. in chapter 3, also showed that the composition of trees changed below ~50% light transmittance and this was also the same light transmittance point that resulted in a change in the composition of herbaceous species. Therefore suggesting that a change in tree species composition, signifies a change in the herbaceous layer composition.

The effect of bush encroachment on the herbaceous community was evident in the significant relationships between canopy structure variables (density of trees, density of trees > 3m, canopy area, and canopy volume) (Figure 4.4). Herbaceous plant communities were richer and more diverse in sites of lower tree cover, and lower tree density. The relationships observed in this study between herbaceous species composition and increasing canopy cover is supported in literature (Shirima *et al.*, 2015; Gobelle & Gure, 2018; Cardoso *et al.*, 2018). These results are also in line with previous studies that showed that increasing tree density correlated with a decrease in botanical composition of grass and basal cover of grass (Gemedo *et al.*, 2006; Teshome *et al.*, 2012; Niguse *et al.*, 2014). The reduction in grass and forb species richness and diversity in bush encroached sites might be due to the available aboveground light and below ground competition (Gobelle & Gure, 2018) as hypothesised.

4.5.2. Response of grass and forb species to increasing light transmittance

There was an indication of a threshold point of ~ 38% canopy cover (light transmittance~ 75% and LAI of c.~05), above which several species declined in abundance (Figure 4.7 and Figure 4.8). This indicated the optimum point where herbaceous species presences began to decline before switching to a different vegetation state. This was expected as trees can be beneficial to herbaceous species up to a critical tree density (Engle *et al.*, 1987; Cameron *et al.*, 1989; McPherson *et al.*, 1993; Fuhlendorf, 1997). Grasses such as *P. maximum*, *M. decumbens*, *E. erecta* and *L. flavida* were found growing underneath trees, even in low tree cover sites, adding herb richness to this community. C₃ species are found to be shade tolerant and an increase in these species as canopy cover increased was expected in this study. Grasses that follow the C₄ pathway (*C. popischilii*, *C. dactylon*, *D. eriantha*, *Eragrostis spp*, *P. maximum*, *S. sphacelata* and *T. triandra*-see Appendix D) occurred in sites with high light transmittance (low canopy cover). C₃ Grasses (*P. maximum*, *E. erecta*, *H. turgidulum*) following the C₃ photosynthetic pathway were mostly found in dense vegetation. The higher mean species richness and abundance found in sites that have a lower tree cover may be explained by the presence of sparse trees (Appendix E). Trees appear to be beneficial to the herbaceous community until a certain limit is reached. This finding is supported by Aucamp *et al.* (1983) study which illustrated that grass is unaffected by increasing bush densities up to a certain critical level, and as this critical level is reached, grass productivity then decreases with increasing tree density. Stuart Hill *et al.* (1987) also showed that leaf litter and shade of *V. karroo* trees stimulated grass

growth in the False Thornveld of the Eastern Cape and that may explain the high grass species richness in sites of low and moderate canopy cover.

Charles-Dominique *et al.* (2018) found that grass species were sorted on the light gradient according to their photosynthetic pathway. C₄-NAD-me grasses were dominant in open canopies of LAI values less than 0.4; C₄-NAD-me and C₄ PCK occupied intermediate levels of shading and C₃ grasses were found deep shades where LAI was greater than 1.5. The results of this study suggested a similar LAI of 0.5 limit where the grasses were highest in abundance (Appendix D). *Melica decumbens*, *Ehrharta erecta* and *P. maximum* still occurred in open sites underneath trees. The only grasses found to occur at LAI > 1 were *P. maximum*, *E. erecta* and *L. flavida*. Most of the grasses occurred within an LAI range < 1. Grasses that were present at a canopy cover beyond 70% were *S. fimbriatus*, *P. maximum*, and *E. erecta*. The sites being sampled were not always uniform. There were clumps of high tree cover adjacent to sparse tree areas. Some plots may have had low light and high light subplots, resulting in the presence of sun-loving herbaceous species.

The same limits for C₄ grass assemblages was observed for the forb species in this study. There was a high abundance of particular forb species in the open sites, and these forb species decreased at light transmittance <50 %. Basal cover of grasses, forbs and sedges was higher in lower tree cover, LAI and high light transmittance sites (Figure 4.9). The decline in the cover of herbaceous species can affect forage quality, the grazing capacity and the overall function of the savanna landscape. There was also increased tree density in sites with low light transmittance (high aerial tree cover), which makes it harder for grasses and forb species to establish. The increase in bare land cover due to bush encroachment (beyond a certain limit) highlights the need to support rangeland monitoring and evaluation as it poses a threat to the local grass and forb species available for livestock.

4.5.3. Conclusions: Impact of increasing tree cover on the herbaceous community

The SEM model showed that canopy characteristics such as the density of trees found in a plot, density of trees > 3m, diversity of trees and canopy volume had the largest effect on the composition of the herbaceous layer (Figure 4.6). Light had the second largest effect and canopy cover had the least. An increase in tree cover, does however have an impact on light dynamics in the understory environment. This study showed that species, basal cover, richness, abundance, and diversity changed markedly with canopy characteristics. The emergence of C₄

grasses was an adaptation to drier conditions (Pagani *et al.*, 1999; Edwards & Still 2008). The emergence of C₄ photosynthesis demanded that the grasses grow in open environments (Osborne & Freckleton, 2009) and therefore C₄ grasses rarely colonise densely vegetated habitats where there is less light and lower temperatures (Sage *et al.* 1999). Forest (or thicket) trees are broadleaved and accumulate leaf area quicker than savanna trees, creating an environment in the understorey that is unsuitable for savanna species, and thus making the transition to forest much quicker (Hoffmann *et al.*, 2012). It is thus important to understand the conditions at which savanna species fail to persist as it has implications for managing bush encroachment in savanna systems.

Chapter 5

Conclusion and Synthesis

5.1. The Implications of Changing Canopy Cover, Light Transmittance, and the Herbaceous Layer in Open Ecosystems

5.1.1. Photographic evidence of bush encroachment

This study was conducted in a semi-arid savanna and thicket system in the Eastern Cape. It was evident from aerial historical photographs that most of the sites had undergone an increase in tree cover over the past 70 years. Although the focus of the study was on a selected area on the farm, and there were 51 sites placed at various locations on the area, it can still be deduced that the sites are representative of the changes that have occurred throughout the farm. Most of the sites were open in 1949 (having a tree cover < than 15%), a few of these sites remained open in the subsequent years. Visual examination of the aerial photos suggests that there were two sites that had been cleared from high tree cover between the years 2013 and 2019 and these followed a different canopy cover increase trajectory to the rest. The sites that remained open indicated that the landscape is governed by different processes allowing the persistence of open landscapes in some sites and causing an increase in tree cover in other parts of the farm. One of the reasons explaining differences in woody thickening in some of the sites was the proximity of the sites to woody patches and valleys. Woody expansion was found to be more likely to occur at sites that are closer to woody patches that will provide seeds of encroaching woody species (Skowno, 2018). Open to moderate cover sites that were close to woody patches in 1949 were the ones that had high tree cover in 2019. One of the features of the Endwell farm landscape was its patches of dense vegetation along the valleys, and these patches of dense vegetation may have been a source of seed provision to adjacent open or moderately covered sites.

One of the processes that was proposed to be occurring on the farm was bush clump succession where *V. karroo* establishes and facilitates the establishment of more tree species causing clumps of high tree density (O'Connor & Chamane, 2012). This study aimed to identify the stages of bush clump formation as they occur in 51 sites on the farm. As the woody cover

changed between the years, some of the same peaks and troughs were observed in woody cover frequency distribution, even as most sites were increasing in canopy cover. This suggested that the cover classes that were more and less common across the years could be interpreted to represent more and less stable states. The canopy of ~ 50% was rare and indicated an unstable state. This result reflected Staver *et al.* (2011a) finding that sites with intermediate tree cover (50-75%) were rare, indicating unstable states.

There was a presence of livestock and small numbers of blesbok that fed on grasses on the farm (mostly in open sites). Sites kept open may have been kept open deliberately by the farmer for grazing purposes or could be a result of abiotic factors (soils moisture and nutrients) as fire has not been used as a management tool on the farm in the decades covered by this study. The highest increases in tree cover were observed between the years 2002 and 2013 and this period also had the highest mean annual rainfall and the highest Foley's indices (and highest mean annual rainfall in the previous decade). It can be concluded that rainfall may have played some role in the high absolute tree cover change between those years. There may be other reasons such as changes in land management practices, that may have enhanced the influence of drought on tree recruitment. Grazing, browsing and fire are integral components of savanna systems as they maintain both tree and grass biomass in the system (Staver & Bond, 2014; Staver *et al.*, 2017). Droughts may have exacerbated the growth of vegetation when there were additions of grazing animals on the farm. Intense grazing may suppress grass biomass and productivity during dry periods (Swemmer *et al.*, 2018), creating space for the establishment of tree seedlings. Bush encroachment is also thought to be caused by prolonged seasons of drought which are interrupted by heavy rains (Dean *et al.* 1995; O'Connor 1995; O'Connor & Crow 1999; Kraaij & Ward 2006; Joubert *et al.*, 2008). There were seasons of prolonged drought between the years, which caused an increase in tree cover as the historical data suggests. In this study's case, there were two drought periods, followed by high rainfall before the period between 2002 and 2013 and the trees that recruited during those periods of high rainfall may have only been visible in aerial photographs between 2002 and 2013.

5.1.2. Increasing tree cover changing canopy characteristics

There were distinct states of tree canopy cover that were characterized by a dominance of thicket or savanna tree species (Chapter 3). The tree species most abundant on the farm was *V. karroo* and it is suspected to facilitate the encroachment of other evergreen shrubs and trees—through bush clump succession. *Scutia myrtina* often accompanied *V. karroo* in most of the

open-moderate sites where they dominated the tree canopy composition. An increasing density of tree species was associated with an increase in the dominance of thicket adapted tree species. There have been many studies indicating that an increase in tree density results in shifts from grassland to scrub forest (Bowman *et al.*, 2010; Wigley *et al.*, 2010). Although the sites here represented patches in the landscape, where the process taking place was proposed to be thicket clump formation facilitated by *V. karroo*, most of the sites had very few trees in 1949, and the patches of trees grew in subsequent years. The trend of increasing clump size will over time transform the open savanna system to a system dominated by thicket trees. It was evident that the process of bush encroachment changed the composition of tree species. Increasing tree density resulted in an increase in canopy volume, canopy area, density of trees, maximum height, density of tall trees (trees >3m). Results from the SEM suggested that light transmittance was significantly influenced by canopy cover and woody vegetation structure—with woody vegetation structure having the strongest influence. *Vachellia karroo* and *S. myrtina* trees were dominant in sites with a light transmittance of <50% and became scarce beyond that level. Other trees that featured in high light transmittance sites were *Gymnosporia buxifolia*, *Olea europaea* subsp. *africana* and *Ehretia rigida*. Low light transmittance (high canopy cover) sites featured less of *V. karroo* and *S. myrtina* and were characterised by the presence of a diverse set of tree species (*Afrocanthium mundianum*, *Ziziphus mucronata*, *Dovyalis zeyheri*).

5.1.3. Response of the herbaceous layer to increasing canopy cover

There was a change in the composition of forb and grass species below 50% light transmittance range (~ 70 canopy cover). In literature, C₄ grasses are absent from the forest understory (Ratnam *et al.*, 2011). In this study, it was also shown that C₄ grasses were accompanied by a particular assemblage of forb species that were rare in thicket floors. There were instances where C₃ grasses (e.g., *Panicum maximum* and *Helictorichon turgidulum*) and C₄ (*Sporobolus fimbriatus*, *Setaria sphacelata*, *Themeda triandra*, *Eragrostis chloromelas*, *Eragrostis obtusa*, *Cymbopogon popischilii*) grasses occupied the same low canopy cover areas when there were fewer trees. However, this was a result of the shade that the few trees in those landscapes provided. Forbs were expected to increase with an increase in canopy cover because they were more likely to dominate beneath tree canopies (Linstädter *et al.*, 2016). This study only showed that forb species dominant in high light environments, became less prominent in low lit environments. There was a decline in the basal cover of both forb and grass species with

increasing canopy cover. It was evident that the forb and grass species composition were similar at open, low and moderate canopy covers and only became different at high canopy cover (< 50% light transmittance). The resilience of a savanna system through changing environmental conditions is strengthened by forb species that are functionally diverse and possess drought-tolerant traits (Turner & Knapp, 1996). Traits such as prostrate growth form, that forb species have, allow them to survive heavy grazing. The decline of forb species dominant in the open-moderate canopy cover sites with increasing canopy cover (declining light transmittance) suggests a weakening of resilience in the savanna system that will be susceptible to disturbances when they occur in the future.

The underlying theory of savanna and thicket occurring as alternative stable state explains how both savanna and thickets are maintained. The grass layer is important for fire incitement and suppression of tree seedling recruitment. Changes in tree cover were predicted to result in changes in the herbaceous layer composition. An increase in tree cover, resulted in the depletion of the herbaceous layer (abundance, richness and diversity) in this study. This study showed that most grasses had an optimum light transmittance (their maximum abundance) at >80%, which is open canopy with few trees. This point can be described as the point where species begin to decline from their peaks.

The process of bush encroachment is re-enforced through positive feedback systems by altering fire regimes (Staver *et al.*, 2011a), tree-grass mechanisms (light, water, competition) (Scholes & Archer, 1997) and further tilts the system in favour of woody cover closure, to a point where the initial savanna state is lost, and closed canopies are formed. This study showed that herbaceous species diversity, richness and abundance declined beyond an LAI ~ 0.5 (~ 38% canopy cover and 75% light transmittance). Sites that were moderate-open were similar in their species abundances, with significant difference being found between high tree cover sites and moderate-open sites. The same was observed with light transmittance classes. Sites with light transmittance levels below 50% were significantly different from sites with a light transmittance above 50%. The 50% light transmittance point can be interpreted as the threshold point for the maintenance of savanna- herbaceous diversity. Beyond this threshold point, the diversity of herbaceous species decreased drastically.

5.1.4. Conclusions: Implications of this study to land managers

An increase in tree cover over the years, had resulted in changes in both the herbaceous cover and its composition. An increase in canopy cover (tree density) also impacted the tree

composition- increasing more broad-leafed, evergreen species. While some have hypothesized that bush encroachment is an inevitable process, characteristic of semi-arid and arid environments (Wiegand *et al.*, 2005), it remains a management concern in South Africa where farmland and open savanna landscapes contribute to the overall productivity of land and the tourism economy. Axelsson & Hanan (2017) highlighted that savannas will tend to increase in woody cover towards a state of its climatic potential, and in cases where actual woody cover is substantially below potential cover, this process is likely to happen most rapidly. Endwell has high rainfall suitable for the thicket vegetation type and the areas of sub-escarpment thicket in the valleys and south facing slopes indicate the potential for this vegetation type to occur, and also representing a source of propagules. Therefore, patches of grassland are likely to increase in tree cover, further changing the composition of tree and herbaceous species with time.

Veldman (2015b) proposed that the term “old-growth” be extended to grasslands as well- a term initially used to describe forests. This would ensure that they are given the same level of conservation attention. Savannas that have been present for millennia do pose valuable plant species and are characterized by high species richness, high endemism, and unique species compositions. In this study, the outcome of an increasing tree cover was a decline in herbaceous species diversity and abundance. This suggests that an increase in tree cover over the seven decades had been detrimental to the function of the savanna system and led to a biome shift to functionally distinct thicket vegetation. This process was indicated with the gradual clump size increase. The sites that had transformed into thicket were rare in the study selected for sampling, and most sites were more advanced in their transformation into thicket than others. Land managers ought to seek methods of monitoring fire regimes, native herbivores, and livestock so that the system remains at a balance. Other concerns could be that of climate change (drought and increased rainfall) and rising CO₂ levels. The impact of climate change and rising CO₂ levels will greatly rely on the management of these systems.

Frequent fires and herbivory are presented as essential to the persistence of old-growth savannas, when rainfall and soil nutrients also allow for forest or thicket states to develop (Bond and Keeley, 2005). According to the farmer, fire had been minimized in most of the farm, and its exclusion could have resulted in the rapid transition, described in Chapter 2, from open grasslands to high density woodlands in some sites. The increase in density allowed more

shade-loving tree species to invade, further transforming the area past its threshold point leading it to transform into thicket vegetation.

The presence of trees in grasslands may be beneficial to the herbaceous layer, as there were some grasses, sedges and herbs that preferred growing in the shade. This implies that the decision of tree removal should be based on the outcome that maximizes herbaceous layer productivity. At open canopy cover sites, there was an abundance of C₄ grasses and other forb species. At low *V. karroo* and *S. myrtina* densities there was a mixture of C₄ sun loving grasses and C₃ grasses found underneath the canopies of trees. There were certain forb species that were common in dense sites that could be found in sites with moderate canopy cover. As the densities of trees increased, there was a decline in the species richness and diversity of the herbaceous species (both grasses and forb species grouped together). There were sites that had a moderate cover of *V. karroo* and *S. myrtina* with the same herbaceous species composition as low canopy cover sites. They indicated an early stage of encroachment that could still be reversed. The later stages of encroachment had fewer *V. karroo* species or none and these sites were dominated by other thicket species (*Afrocanthium mundianum*, *Ziziphus mucronata* and *Dovyalis zeyheri*) and there was little to no C₄ grass species in the understory. The forb and grass species in the high canopy cover sites had lower basal cover, indicating an irreversible vegetation state that would not be susceptible to fire. The state at which grass, and forb species were at their highest abundance was at the lower canopy covers (LAI < 0.5, which was estimated to represent ~75% light transmittance and ~38% canopy cover), indicating that trees are beneficial to C₄ grasses and the forbs that accompany them. The thinning of tree species by fire and mechanical methods would have to be implemented at moderate canopy covers (~39-50% aerial canopy cover). Therefore, further studies testing the resilience of the savanna system at the various encroachment stages would have to be conducted on the farm. Fire could be used to test the fire-suppression threshold points identified in chapter 3 and chapter 4 (< 50% light transmittance, ~ 75 % aerial cover). The study would test the points at which fire continues spreading, from an open site to a higher canopy site and the point (canopy cover, light transmittance and LAI) where fire causes significant topkill of *V. karroo* and the thicket species.

When thicket species begin to encroach in savannas, they change the herbaceous vegetation through their impact on the light, soil and nutrient environment (Belsky, 1994; Dent *et al.*, 2013; Jamison-Daniels *et al.*, 2021). In some rangelands, encroached areas are being cleared to make way for the herbaceous vegetation. The removal of some woody plants-preferably at

an early stage, may help restore the herbaceous layer (Dirbaba *et al.*,2014). In this study, there were points that indicated a switch in communities of savanna tree and herb species composition to those of thicket communities. The land managers would have to control the bush encroachment by burning sites that still have C₄ grasses intact (at aerial canopy ~ 70 %, 50% light transmittance) on a scheduled basis. Farmers would have to burn these sites before the savanna/thicket threshold is reached. However, the response of the system to tree thinning may be different depending on the system. The clearing of trees opens the landscape which leads to grasses and forb species establishing, shifting the vegetation type from thicket to grassland/savanna. There are however few tree removal processes that have been considered successful due to the high costs involved in the process and the loss of beneficial of woody plants and the re-establishment of the plants (Smit, 2004). While the Conservation of Agricultural Resources Act advocates for the control of bush encroachment, the Natural Environmental Management Act (NEMA) declares protection over virgin vegetation that cannot be cleared without permit. It becomes a challenge to decipher “bush encroachment” and “proper thicket”. Areas that have experienced encroachment in recent years will be evident from aerial photographs. In this way, old-growth savanna or thicket vegetation may be maintained by land managers.

Chapter 6

References

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Appendix A

The changes in canopy cover class from 1949-1968, 1968-1985, 1985-2002, 2002-2013 and 2013-2020

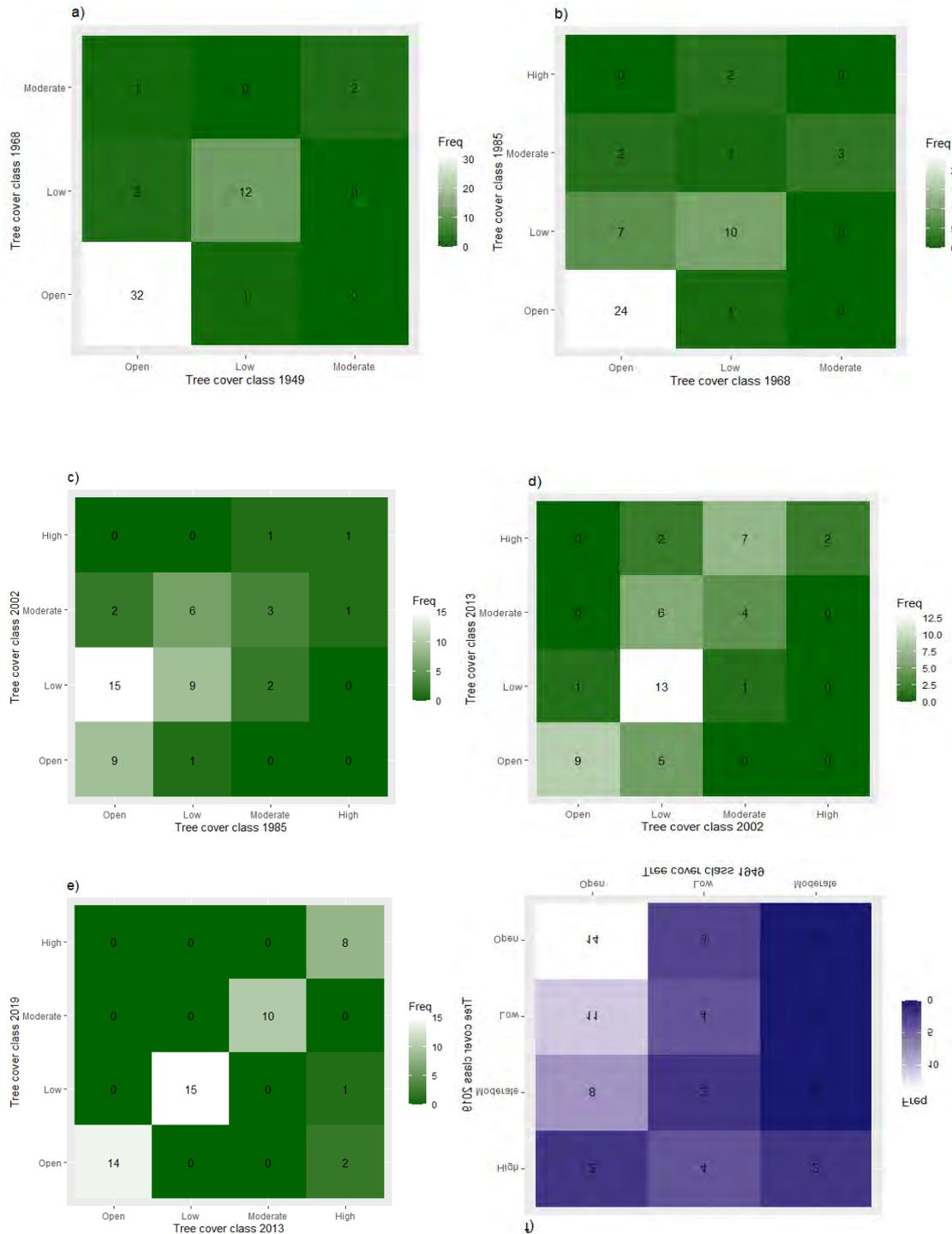
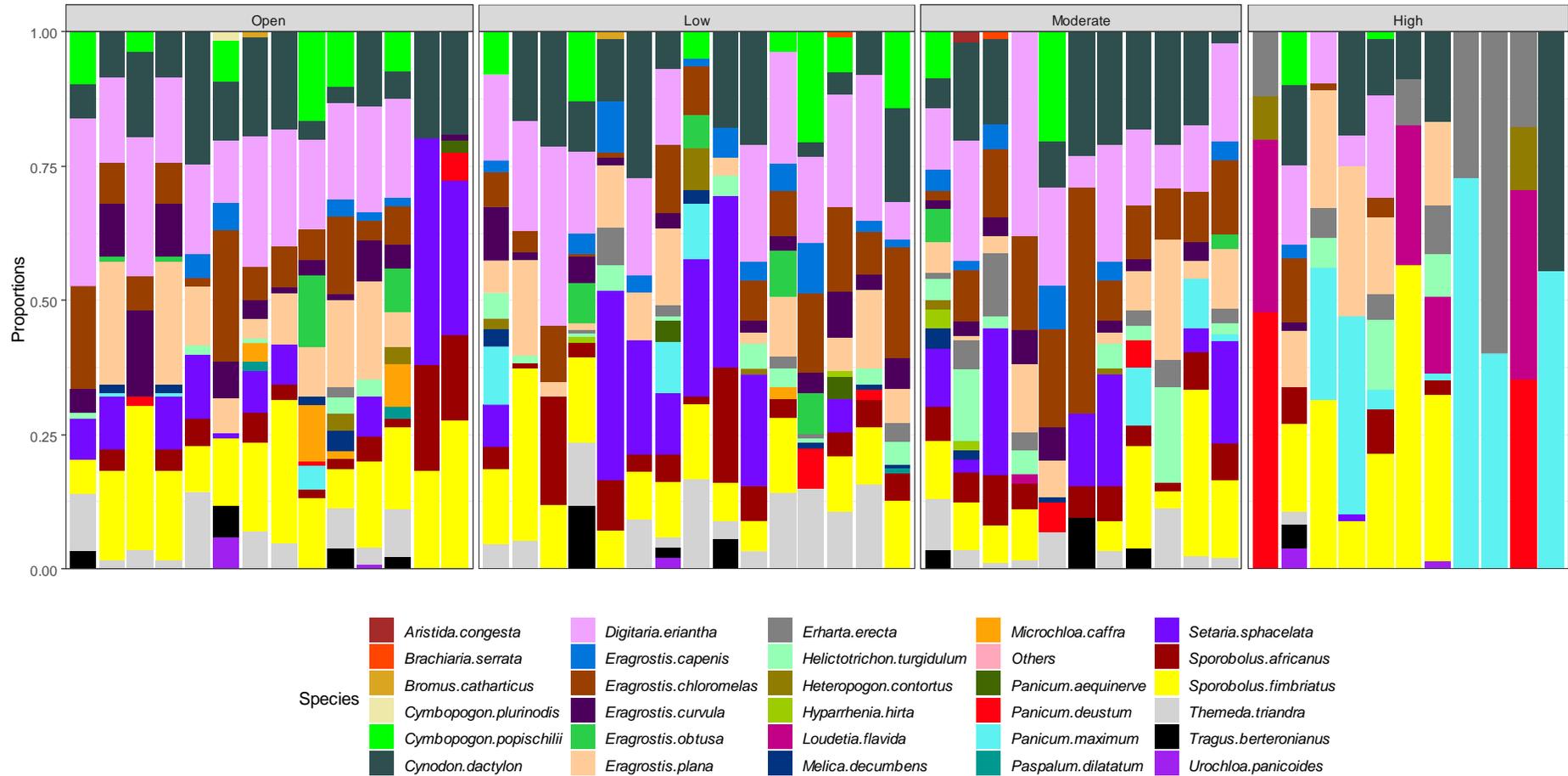


Figure A.1: The changes in canopy cover class from a) 1949-1968, b)1968-1985, c) 1985-2002, d) 2002-2013, e)2013-2020 and f) 1949-2020 (in blue).

Appendix B

a) Grass species composition plots at open (0%-15%), low (16%-30%), moderate (31%-50%) and high (51%- 100%) canopy cover



b) Forb species composition plots at open (0%-15%), low (16%-30%), moderate (31%-50%) and high (51%- 100%) canopy cover

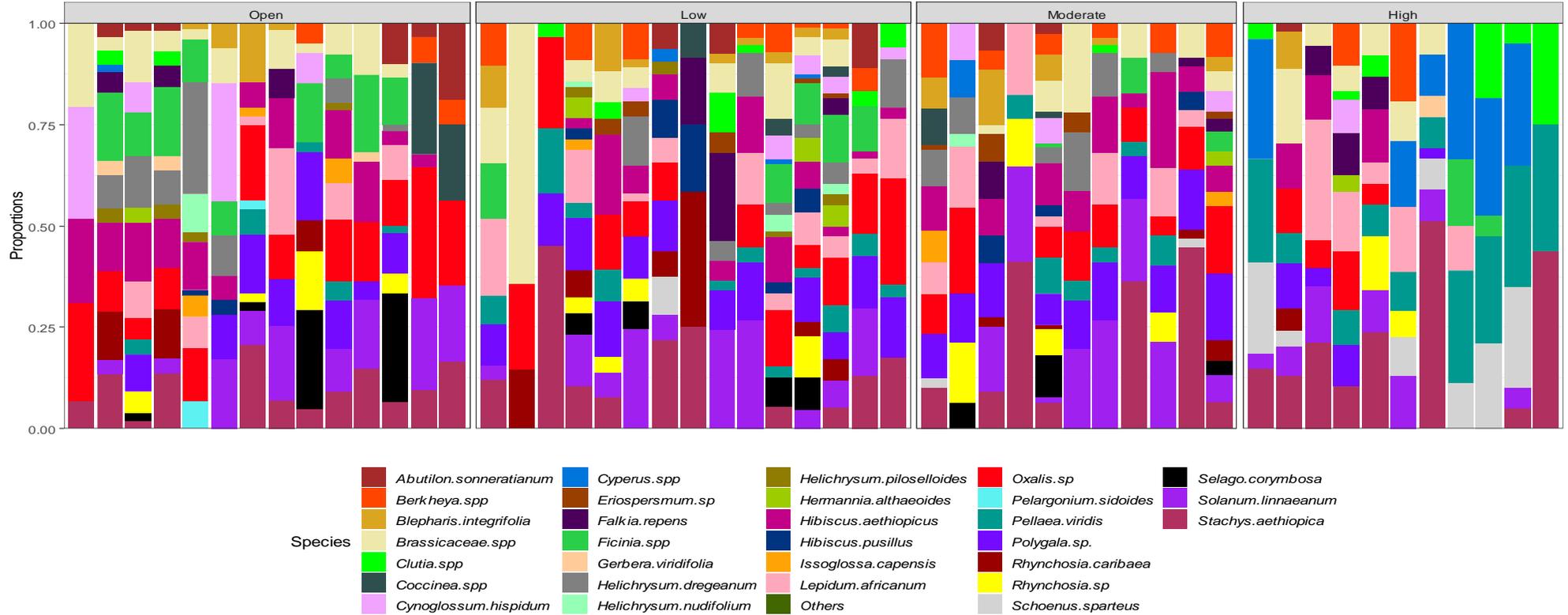


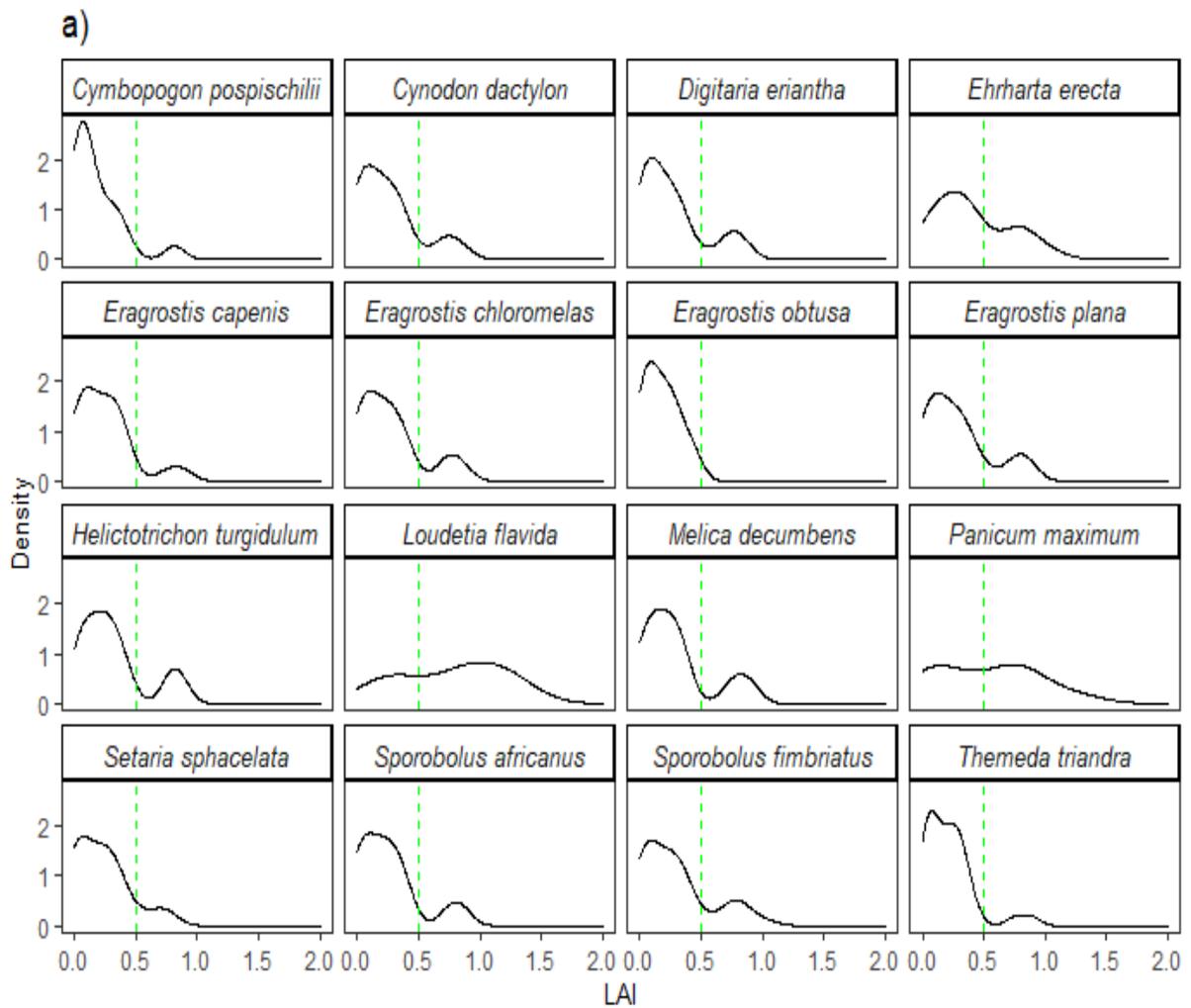
Figure B.1: Species composition plots showing the proportion each of the 30 a) grass and b) forb species and other herbaceous species contributing to the tree composition in the site. a) The groups are divided according to aerial canopy cover classes: Open (0-15%), Low (16-30%), Moderate (31-50%), High (51-100%).

Appendix C

Table C.1: Summary of linear regression correlations between key grass species and LAI, light transmittance and %canopy cover

Species	LAI			Light transmittance (%)			Canopy cover (%)		
	y=mx +c	R	p	y=mx +c	R	p	y=mx +c	R	p
<i>Cymbopogon pospischilii</i>	y=8.3-9.5x	-0.36	0.012	y=-3.5+0.11x	0.23	0.11	y=8.5-0.11x	-0.26	0.072
<i>Cynodon dactylon</i>	y=13-8.6x	0.31	0.033	y=-2.8+17x	0.27	0.061	y=15-0.14x	-0.35	0.014
<i>Digitaria eriantha</i>	y=20-12x	-0.26	0.012	y=-2.8+23x	0.27	0.061	y=22-0.2x	-0.31	0.029
<i>Ehrharta erecta</i>	y=1.1+2.5x	0.42	0.053	y=6.1-0.052x	-0.46	<1×10 ⁻⁴	y=0.74+0.038x	0.34	0.017
<i>Eragrostiscapensis</i>	y=2.6-1.6x	-0.083	0.24	y=-0.59+0.033x	0.21	0.14	y=2.9-0.026x	-0.19	0.19
<i>Eragrostis chloromelas</i>	y=9.7-5.9x	-0.13	0.098	y=-0.12+0.097x	0.14	0.34	y=11-0.11x	-0.27	0.063
<i>Eragrostis obtusa</i>	y=2.1-2.3x	-0.17	0.23	y=1.8-0.0053x	0.0056	0.97	y=2.4-0.035x	-0.22	0.14
<i>Eragrostis plana</i>	y=9.9-3.4x	-0.061	0.35	y=3.3+0.067x	0.029	0.31	y=10-0.054x	-0.14	0.35
<i>Helictotrichon turgidulum</i>	y=1.9+2.2x	0.22	0.16	y=4.7-0.026x	-0.14	0.35	y=2+0.02x	0.064	0.66
<i>Loudetia flavida</i>	y=-0.17+1.7x	0.24	0.037	y=6-0.066x	-0.36	0.01	y=-0.83+0.047x	0.37	0.0046
<i>Melica decumbens</i>	y=0.84-0.67x	-0.031	0.35	y=-0.28+0.011x	0.0042	0.96	y=0.96-0.012x	-0.15	0.30
<i>Panicum maximum</i>	y=0.32+11x	0.37	0.0095	y=21-0.21x	-0.46	<1×10 ⁻⁴	y=-1.7+0.19x	0.47	0.00059
<i>Setaria sphacelata</i>	y=12-11x	-0.34	0.019	y=-10+0.22x	0.35	0.015	y=13-0.17x	0.4	0.048
<i>Sporobolus africanus</i>	y=6.2-3.3x	-0.098	0.11	y=-1.1+0.077x	0.19	0.02	y=7-0.062x	-0.25	0.0088
<i>Sporobolus fimbriatus</i>	y=17-6.9x	-0.27	0.076	y=5.4+0.12x	0.22	0.12	y=18-0.12x	-0.33	0.019
<i>Themeda triandra</i>	y=7.5-5.9x	-0.34	0.019	y=-4.4+0.12x	0.39	0.005	y=8.8-0.11x	-0.37	0.008

Grass species response along gradients of increasing LAI, light transmittance, and canopy cover (%)



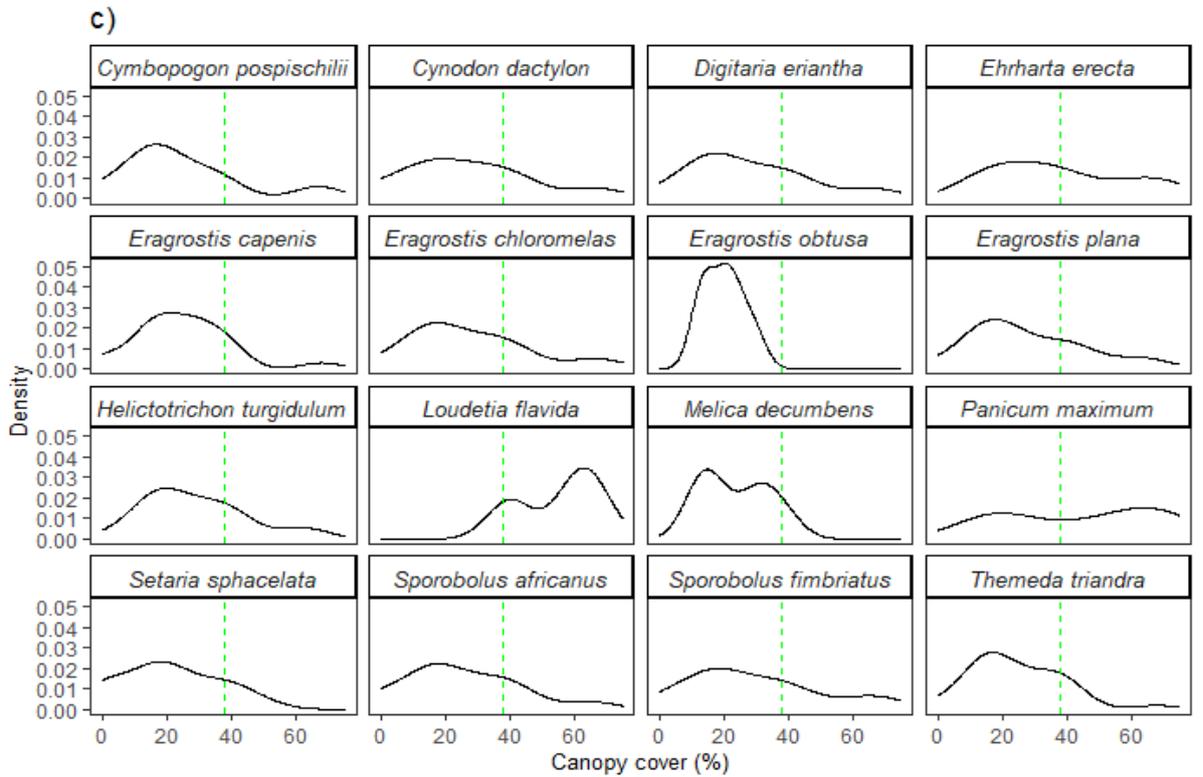
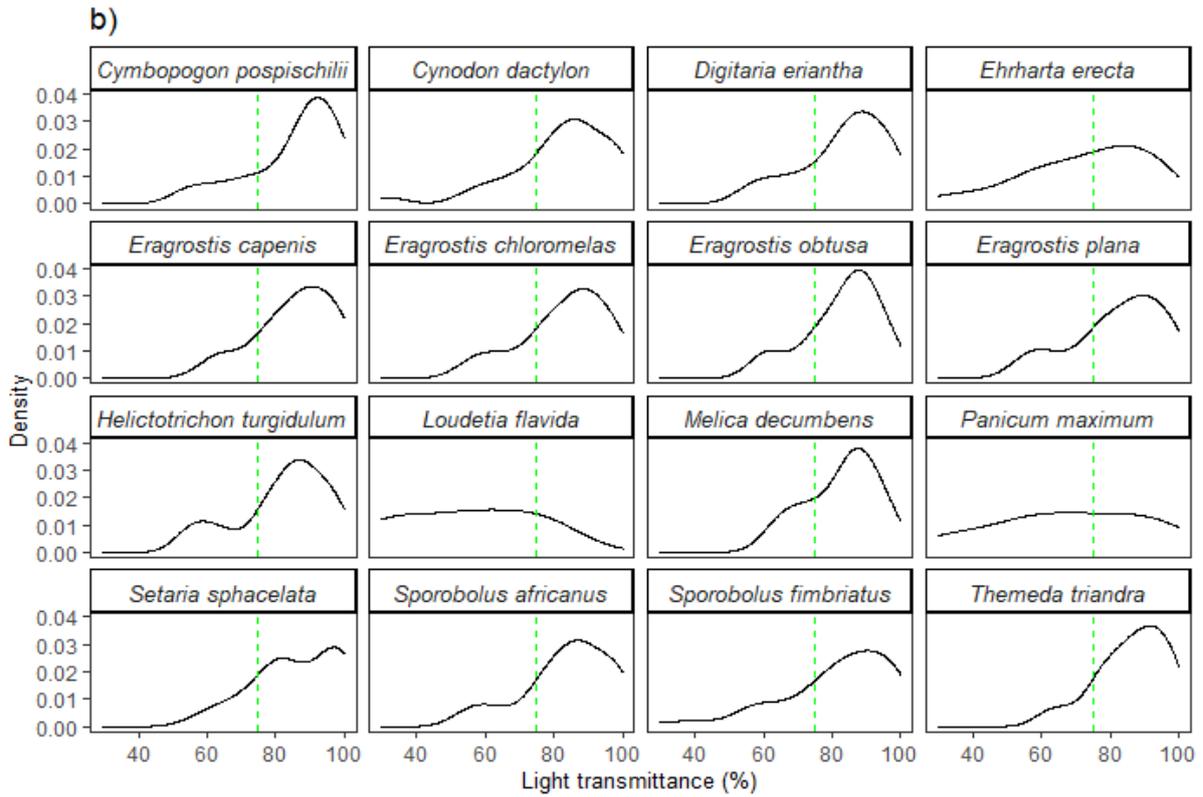


Figure C.1: The probability of herbaceous species occurring in increasing a) LAI b) Light transmittance (%) and c) Canopy cover. Presence and absence data was generated to model the density plot. The vertical lines are deduced threshold points from LAI= 0.5 and regression equations calculated in pair plots (figure 3.3).

Appendix D

The evolution of grass family's photosynthetic pathways

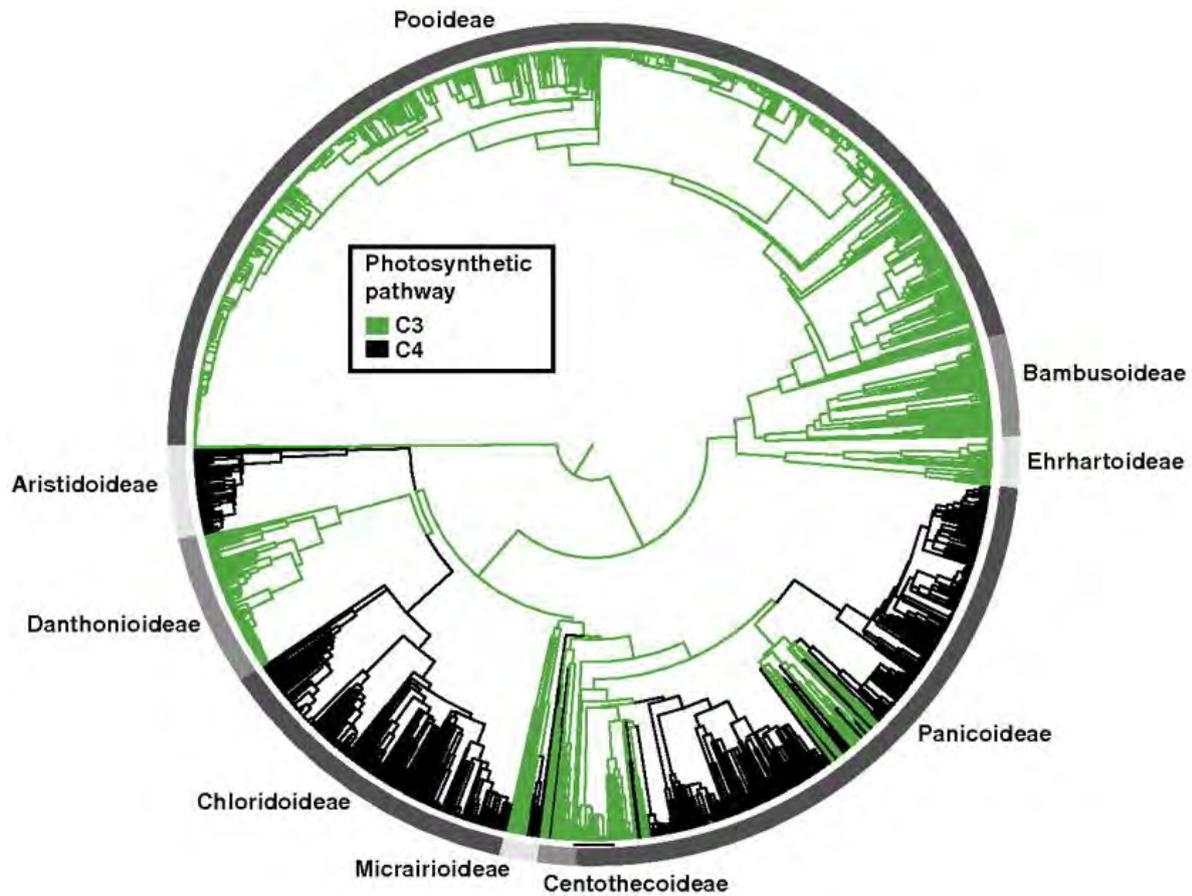


Figure D.1: A representation of the photosynthetic pathway in grass subfamilies (Image from Edwards and Smith, 2010). The green line indicates C3 photosynthesis, while black lines indicate C4 photosynthesis.

Table D.1: Grass species sub-families, tribes, and their photosynthetic pathways

Species	Subfamily	Tribe	Photosynthetic pathway
<i>Cymbopogon popischilii</i>	Panicoideae	Andropogoneae	C4
<i>Cynadon dactolon</i>	Chloridoideae	Cynodonteae	C4
<i>Digitaria eriantha</i>	Panicoideae	Paniceae	C4
<i>Ehrharta erecta</i>	Oryzoideae	Ehrharteae	C3
<i>Eragrostis capensis</i>	Chloridoideae	Eragrostideae	C4
<i>Eragrostis chloromelas</i>	Chloridoideae	Eragrostideae	C4
<i>Eragrostis obtusa</i>	Chloridoideae	Eragrostideae	C4
<i>Eragrostis plana</i>	Chloridoideae	Eragrostideae	C4
<i>Helictotrichon turgidulum</i>	Pooideae	Poeae	C3
<i>Loudetia flavida</i>	Panicoideae	Tristachyideae	C4
<i>Melica decumbens</i>	Pooideae	Meliceae	C3
<i>Panicum maximum</i>	Panicoideae	Paniceae	C3
<i>Setaria sphacelata</i>	Panicoideae	Paniceae	C4
<i>Sporobolus africanus</i>	Chloridoideae	Zoysieae	C4
<i>Themeda triandra</i>	Panicoideae	Andropogoneae	C4
<i>Sporobolus fimbriatus</i>	Chloridoideae	Zoysieae	C4

Appendix E

Average species abundance, richness and diversity with increasing light transmittance, and canopy cover (%)

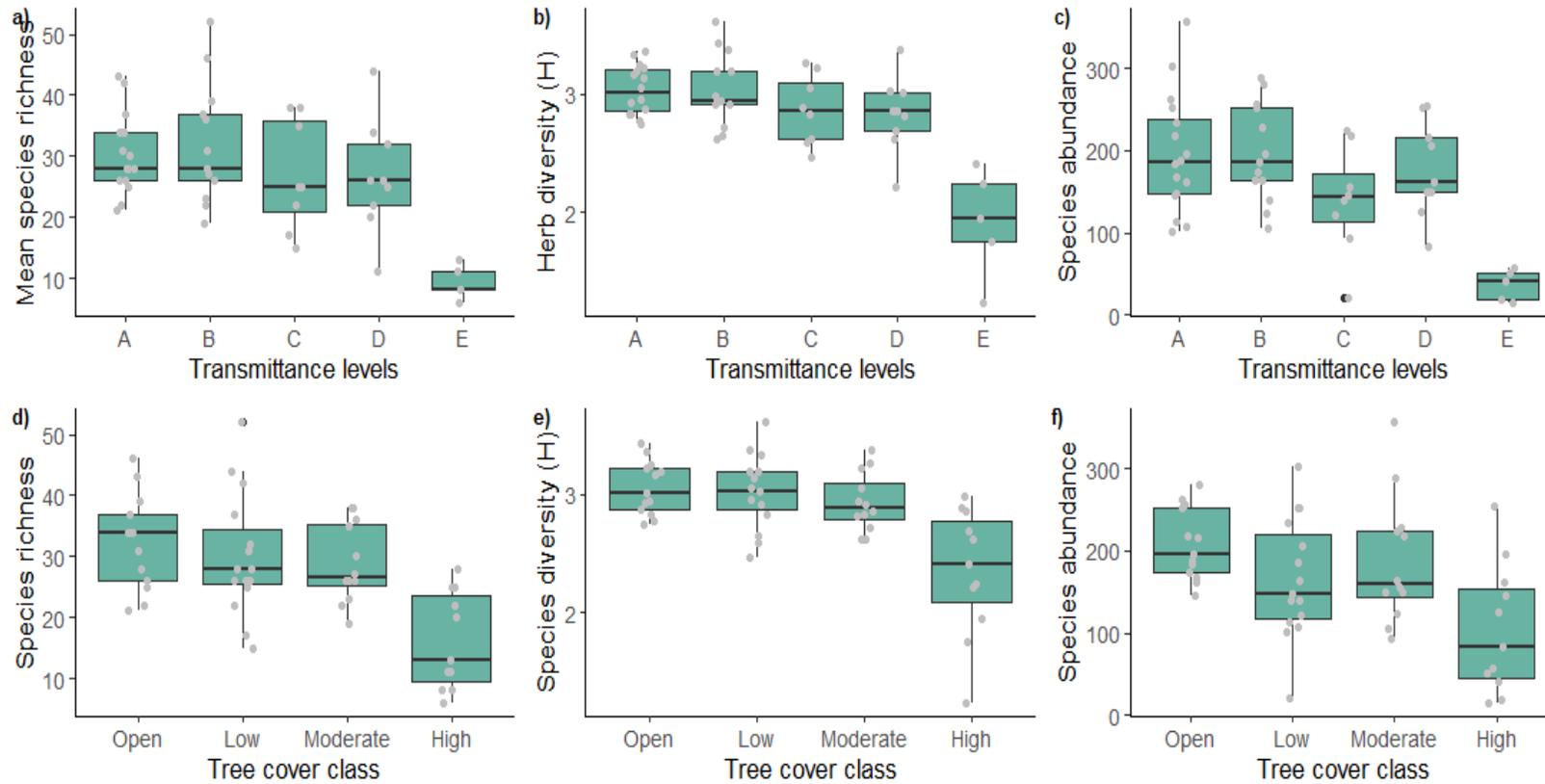


Figure E.1: The species richness, diversity and abundance at light transmittance classes: A (20-50%),B(50-70%),C(71-80%),D(81-90%),E (91-100%) and % tree cover classes high (51-100%), moderate (31-50%), low (16-30%), open (0-15%).

Table G.1: Pairwise Wilcox test for significant differences between A (20-50%), B (50-70%), C (70-80%), D (80-90%), E (90-100%) light transmittance classes .

Species richness		A	B	C	D
	B		0.937	-	-
C		0.407	0.381	-	-
D		0.381	0.381	1	
E		0.008	0.008	0.014	0.015

Species diversity		A	B	C	D
	B		0.913	-	-
C		0.291	0.291	-	-
D		0.190	0.285	0.913	-
E		0.008	0.008	0.014	0.019

Species abundance		A	B	C	D
	B		0.878	-	-
C		0.164	0.119	-	-
D		0.723	0.553	0.384	-
E		0.008	0.008	0.039	0.011

Table G.2: Wilcox test for significant differences between high (51-100%), moderate (31-50%), low (16-30%), open (0-15%) light transmittance classes

Species richness		Open	Low	Moderate
	Low		0.54	-
Moderate		0.54	0.86	-
High		0.0029	0.34	0.0041

Species diversity		Open	Low	Moderate
	Low		0.016	-
Moderate		0.0039	0.52	-
High		0.009	0.36	0.82

Species abundance		Open	Low	Moderate
	Low		0.074	-
Moderate		0.12	0.56	-
High		0.013	0.35	0.12

Appendix F

List of identified herbaceous species found in this study

Abutilon sonneratianum
Acanthaceae spp.
Achyranthes sp.
Amaranthus spp.
Aristida congesta

Berkheya spp.
Blepharis integrifolia
Brachiaria serrata
Brassicaceae sp.
Bromus catharticus
Bulbine frutescens
Chloris gayana
Chloris virgata
Cissampelos torulosa
Clusia alaternoides
Coccinea sp.
Commelina capensis
Crotalaria capensis
Crotalaria sp.
Cymbopogon plurinodis
Cymbopogon caesius
Cymbopogon popischilii
Cynadon dactylon
Cynoglossum hispidum
Cyperus albostriatus
Cyperus rotundus
Digitaria eriantha
Ehrharta erecta
Eragrostis capensis
Eragrostis chloromelas
Eragrostis curvula
Eragrostis obtusa
Eragrostis plana
Eriosepium sp.
Euphorbia prostrata
Eustachys paspaloides
Falkia repens
Felicia filifolia
Gerbera viridifolia
Gerbera piloselloides
Gnaphalium sp.
Helichrysum dregeanum
Helichrysum nudifolium
Helictotrichon turgidulum
Hermania althaeoides
Hermania spp.
Hermannia coccocarpa
Heteropogon contortus
Hibiscus aethiopicus
Hibiscus pusillus
Hippobromus pauciflorus
Hyparrhenia hirta
Hypochoeris radicata
Hypoestes aristata
Hypoestes forskalii

Hypoxis argentea
Hypoxis hemerocallidea
Hypoxis setosa
Indigofera sp.
Iridaceae sp.
Isoglossa sp.
Issoglossa capensis
Jamesbritternia spp
Kedrostis nana
Laportea peduncularis
Ledebouria ovatifolia
Lepidium africanum
Lepidium dictyotum
Leucas capensis
Loudetia flavida
Lycium cinereum
Malvaceae sp.
Melica decumbens
Microchloa caffra
Myosotis sp.
Nidorella sp.
Oxalis sp.
Panicum aequinerve
Panicum deustum
Panicum maximum
Paspalum dilatatum
Pavonia praemorsa
Pelargonium sidoides
Pellea viridis
Pelogonium alchemilloides
Plantago macrocarpa
Plantago major
Polygala sp.
Psoralea affinis
Raphionacme sp.
Rhynchosia caribaea
Rhynchosia totta
Richardia spp.
Rubiaceae sp.
Schizoglossum linifolium
Schoenus sparteus
Senecio rhomboideus
Senecio crassiusculus
Senecio deltoideus
Setaria sphacelata
Solanum linnaeanum
Solanum nigrum
Sporobolus africanus
Sporobolus fimbriatus
Stachys aethiopica
Sutera campanulata

Taraxicum officinale
Tephrosia capensis
Teucrium trifidum
Themeda triandra
Thunbergia capensis
Trachyandra affinis
Tragus berteronianus
Tulbaghia cernua
Urochloa panicoides
Vigna vexillate

List of identified tree species found in this study

Afrocanthium mundianum
Brachylaena elliptica
Buddleja dysophylla
Canthium ciliatum
Carissa macrocarpa
Diospyros dichrophylla
Dovyalis rotundifolia
Dovyalis zeyheri
Ehretia rigida
Grewia occidentalis
Gymnosporia buxifolia
Lycium cinereum
Lycium ferocissimum
Maytenus buxifolia
Olea europaea subsp.africana
Pavetta capensis
Putterlickia pyracantha
Scolopia mundii
Scutia myrtina
Searsia longispina
Searsia pterota
Searsia refracta
Searsia crenata
Vachellia karroo,
Zanthoxylum capense
Ziziphus mucronata

