Composition and structure of woody vegetation in thickened and controlled bushveld savanna in the Molopo, South Africa

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Abstract

A large portion of South Africa’s semi-arid Molopo Bushveld savanna is thickened (encroached) by indigenous increaser shrubs and trees (also known as bush encroachment), mainly as a result of poor grazing management practices and suppression of fires. A common approach to restore a balanced and productive woody:grass ratio in this savanna is the use of systemic, soil-applied arboricides, containing the active chemical ingredient Tebuthiuron, which can either be applied selectively by hand or non-selectively by aeroplane. Land owners also use non-chemical bush control (thinning) methods, such as stem burning. All bush-thinning practices create a highly dynamic and competitive post-controlled environment for different vegetation components.

In this dissertation, the impact of selective and non-selective bush-control technologies on the composition and structure of the woody vegetation is compared to non-controlled sites in four commercially managed areas in the Molopo Bushveld savanna, with emphasis on the response patterns of selected key woody species, namely Grewia flava, Senegalia mellifera subsp. detinens, Vachellia luederitzii var. luederitzii, V. erioloba and Boscia albitrunca. The study design included four bush control treatments, namely (1) selective chemical control by hand, (2) selective chemical control by hand with re-application, (3) non-selective chemical control by aircraft and (4) selective control by stem burning with re-application, which were located on three commercial cattle farms and one game farm. Three benchmark sites were also identified, forming part of the study design, including bush-thickened sites (BT), partially thickened sites (PT) and sustainably managed open rangelands (SM).

The results showed relatively low species richness per study area, with selected species dominating the Molopo Bushveld study area, as they outcompete other vegetation layers and woody individuals for available soil moisture and nutrients. These species include G. flava, which revealed the highest mean density, V. erioloba, B. albitrunca and the encroacher species S. mellifera subsp. detinens. The threat of savanna re-thickening following non-selective bush control, which is attributed to initial low grass densities and extensive loss of larger, mature woodies such as V. erioloba, accompanied by a change in inter- and intra-lifeform competition is predicted. The non-selective bush control sites revealed a poorly structured woody vegetation layer dominated by woody recruits, with scattered mature B. albitrunca individuals. This counteracts progressive development of vegetation towards a stable and productive grassy state, as is the case with a well-balanced woody:grass ratio. Thus, to avoid vegetation retrogression, a selective follow-up and maintenance programme of controlling woody recruits, in particular those of S. mellifera
subsp. *detinens* and *V. luederitzii var. luederitzii*, is mandatory within the first years after arboricide application.

The best practice towards a sustainable woody:grass ratio is the selective chemical application approach. The resulting post-control environment is complemented by a better-structured, species-rich woody layer, with higher tree equivalents/ha and mean height of favourable woody species compared to that in non-selective chemical control sites. Mature woody individuals, in combination with a well-established graminoid layer, prevent the re-thickening of a regenerative recruitment layer of thickening woody species such as *S. mellifera* subsp. *detinens* and *V. luederitzii var. luederitzii*. As a result, a lower relative abundance of these thickening woody species was recorded in selective chemical control sites compared to non-selective control sites.

**Key Words:** Bush thickening; encroachment; arboricides; tree-equivalents; ecosystems; environment; co-existence.
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CHAPTER 1

INTRODUCTION & LITERATURE REVIEW

1.1 The phenomenon of bush thickening

The encroachment of woody vegetation in grasslands and the shift from more open savannas to shrublands has been a phenomenon attracting the attention of scientists worldwide (Eldridge et al., 2011). This phenomenon, where the abundance of native trees and shrubs and bushes has increased in savannas and grasslands, is known as woody encroachment (Archer, 1995; Scholes & Archer, 1997; Roques et al., 2001; Briggs et al., 2005). The term ‘encroachment’ is synonymous with other wide-ranging terminologies such as woody or bush thickening (Van Auken, 2000), commonly used in southern Africa. Bush thickening has a suppressing effect on the herbaceous layer, which leads to a decreasing effect on agricultural production caused by the imbalance of the woody:grass ratio (Smit, 2004; Ward, 2005; Wigley et al., 2009). Since bush thickening negatively affects the biomass of climax, palatable herbaceous species, it is regarded as a type of rangeland deterioration (Smit & Rethman, 1999).

Globally, savanna ecosystems are threatened by bush thickening, which leads to major effects on both ecological and economic aspects (Archer et al., 1988; Dougill et al., 1999; Silva et al., 2001; Asner et al., 2003; Fensham et al., 2005). Ratajczak et al. (2012) discovered that grassland and savanna communities in North America experiences a decrease in plant species richness with an increase in bush densities. In Australia, the thickening of woody increaser species tends to spread out over extensive areas of semi-arid woodland as a result of the European settlement (Noble, 1997).

The first record of bush thickening in South Africa was in the 1920s and 1930s, especially in the provinces of KwaZulu-Natal and Limpopo. In the 1940s it was recorded in the savanna region found in the Kalahari basin, which includes the North-West province and the northern parts of the Northern Cape province (Hoffman & Ashwell, 2001). By 2001 an estimation on national scale revealed that out of 38 million ha of South African rangelands, 42% were heavily thickened, 24% moderately thickened and 19% vulnerable to bush thickening (Hoffman &

O’Connor et al. (2014) identified six increaser woody species responsible for bush thickening and invasion throughout southern Africa, namely Dichrostachys cinerea, Senegalia mellifera Vachellia karroo, V. hebeclada, V. nilotica, and V. tortilis, as well as Rhigozum trichotomum and Tarchonanthus camphoratus in the Northern Cape (Hoffman & O’Connor, 1999). One of the main increaser species in southern African savannas – receiving 400 mm of rainfall or less on average per year – is S. mellifera subsp. detinens (O’Connor et al., 2014; Hoffman & O’Connor, 1999). Although chemical and/or mechanical mitigation practices are implemented to reduce bush thickening, S. mellifera subsp. detinens produces a seed that is able to germinate with very little precipitation and grows in the open spaces created by bush-thinning practices (Joubert et al., 2013).

Ward (2005) suggested that semi-arid environments are exposed to a more serious threat of bush thickening because of the variability of rainfall patterns combined with the absence of enough herbaceous fuel loads for natural fires to control the woody vegetation. This situation is particularly true for the semi-arid Kalahari since it receives on average less than 400 mm of annual rainfall (Scholes, 2009; Ward & Esler, 2011; Kgosikoma et al., 2012). Britz and Ward (2007) also stated that sandy soils found in the Kalahari increase water infiltration, which enhances the rate of bush thickening.

Bush thickening caused by the S. mellifera in the southern Kalahari was first recorded during the early 1860s and 1870s along stock transport roads north of Kuruman (Fritsch, 1868, and Gillmore, 1882, as cited by Jacobs, 2000). A study by Moleele et al. (2002) concluded that 37 000 km² of bush thickening in the south-eastern parts of Botswana’s Kalahari had already occurred in 1994. During the 1960s, more than 856700ha of the semi-arid Molopo savanna had been affected by the thickening of S. mellifera (Donaldson, 1967). This includes the study area covering the Kuruman, Vryburg and Mafikeng districts in South Africa.

1.2 Tree-grass coexistence and bush thickening dynamics in savannas

Savanna ecosystems are mainly constructed out of two basic plant life forms that are constantly in competition for dominance, namely grasses and shrubs and trees (Scholes & Archer, 1997; Sankaran et al., 2004). The woody:grass ratio varies over a range of different savanna types.
because of local to regional differences in climate, herbivory, fire and human impacts. Therefore, the drivers that cause the changes over time, including bush thickening (Graz, 2008; Dougill et al., 1999), are still under discussion due to a lack of understanding and disagreements between scientists working in savannas (Scholes & Archer, 1997; Sankaran et al., 2004). Several models describe the coexistence between woody species and grass species, often trying to show whether a savanna ecosystem is ‘stable’ or ‘unstable’ and what the causes of change in the woody:grass ratio over time are (Scholes & Archer, 1997). Sankaran et al. (2004) reviewed different models describing grass-tree coexistence in savannas, which can be grouped into two categories: competition-based models and demographic-bottleneck models.

Competition-based models describe the competition among grass and woody vegetation for limiting resources, such as moisture, resulting in niche separation (Van Langevelde et al., 2003; Sankaran et al., 2004). These models include the phenological niche separation model, the root niche separation model, the balanced competition model and the hydrologically driven hierarchical competition-colonization model as described by Sankaran et al. (2004). The phenological niche separation model proposes that woody vegetation has the ability to store nutrients and water for unfavourable periods. This allows for an extended leaf expansion period before the rains of the following growing season, making these woody species superior competitors over the herbaceous layer, which does not have these storage abilities (Sankaran et al., 2004; Scholes & Archer, 1997). This model is not favoured in describing the dynamics in the woody:grass ratio, due to the length of the rainy season and total rainfall varies each season (Sankaran et al., 2004; Scholes & Archer, 1997).

The ‘balanced competition’ model assumes that water availability determines the dominance between the grass and woody vegetation (Sankaran et al., 2004). On the wetter end of the rainfall gradient (sub-humid savannas), the woody layer would be the superior competitor as the growth rate is supported by enough water. Woody vegetation root volumes are smaller as the demand for water is less, which leads to the thickening of woody vegetation as the tree-on-tree competition decreases. In contrast, woody vegetation occurring on the drier end of the rainfall gradient (arid savannas) tends to be self-thinning, as water levels are insufficient to support woody vegetation growth, creating gaps for the herbaceous layer to become superior competitors for soil moisture (Sankaran et al., 2004; Scholes & Archer, 1997). This model describes an enclosed woodland as being in a state of equilibrium and an open savanna in a state of disequilibrium maintained by fire and herbivory (Sankaran et al., 2004).
The hydrologically driven hierarchical competition-colonization model predicts a long-term coexistence between the herbaceous and woody vegetation layers, determined by the variability of inter-annual rainfall fluctuations (Sankaran et al., 2004). This model has the same prediction as the root niche separation model by Walter (1970) (Sankaran et al., 2004), which states that tree density increases with increasing volumes of rainfall (Walter, 1970). Ward et al. (2013) stated that the woody:grass ratio is in a stable equilibrium when referring to the well-known Walter’s (1939, 1970) two-layer soil water model (root niche separation model). Soil moisture is regarded as the most limiting factor regulating the intensity of competition between vegetation types. This model assumes that inter-life form competition is limited, as the roots of grasses and woody species occupy their own vertical niche in the soil, where each life form has exclusive access to water and nutrient resources. The herbaceous species are known to be superior competitors for soil moisture occurring at shallow depths in an arid savanna where the mean annual precipitation (MAP) is less than 250 mm (Ward et al., 2013). The woody vegetation has the ability to persist because their root system grants them exclusive access to water occurring in deeper soil layers (Ward et al., 2013; O’Connor et al., 2014). For a semi-arid and mesic savanna (>250 mm MAP), the grass layer is unable to absorb all of the water in the top soil layer, causing water to penetrate into deeper sub-soil layers, thus making more water available for woody vegetation (Ward, 2005). This leads to woody plants becoming the superior competitor of the vegetation layers (De Klerk, 2004; Ward, 2005; Ward et al., 2012).

On the other hand, Kumbatuku et al. (2013) showed that Walter’s two-layer soil water model could not be used in describing root niche separation in shallow soil profiles with underlying rock formations, although woody vegetation tends to grow around the rocks and through the cracks in order to obtain soil moisture from deeper soil layers. A study by Wiegand et al. (2005) supports this statement, as vertical niche separation is not possible in shallow soils. Kulmatiski and Beard (2012) indicated that herbaceous and woody vegetation simultaneously extracted moisture out of the shallowest soil layer (5 cm) during the beginning of the rainy season, but woody vegetation extracts more water out of deeper soil layers (30–60 cm) closer to the end of the rainy season as water becomes scarcer. In fact, the Walter’s two-layer soil water is only applicable in certain savannas ranging from very arid savannas to sub-tropical savannas (Brown & Archer, 1990; Kumbatuku et al., 2013). In humid regions, enough water is available and competition therefore is not necessary (Belsky, 1994; Kumbatuku et al., 2013). Several other studies (e.g. Davis et al., 1999; Dougill et al., 1999; Kraaij & Ward, 2006) reject the hypothesis
of Walter’s two-layer soil water model, as phosphorus (P) and nitrogen (N) have also been identified as limiting factors to vegetation growth.

Contrary to competition-based models, demographic-bottleneck models are focussed on the recruitment limitations of woody vegetation, which are driven by disturbances, such as fire, herbivory and variable climatic conditions, directly affecting the success of seed germination, establishment and plant growth rates (Scholes & Archer, 1997; Wiegand et al., 2006; Higgins et al., 2010; Sankaran et al., 2004). There are two main viewpoints (Sankaran et al., 2004): (1) interpreting savannas as systems in ‘disequilibrium’, where disturbances such as fire and herbivory are seen as ‘modifiers’ and ‘maintainers’ of the savanna state, hindering transitions into grassland or woodland equilibrium states, and (2) differentiating between arid and mesic savannas distinguishes between non-equilibrium dynamics with high rainfall variability and disequilibrium dynamics determined by fire intensity (Sankaran et al., 2004).

In arid savannas, the frequency and amount of rainfall is decisive for demographic dynamics, which is determined by the recruitment windows in time (Sankaran et al., 2004). The ‘storage effect’ designed by Higgins et al. (2000) explains how woody vegetation has the ability to ‘store’ their reproductive potential during unfavourable periods, such as drought, in combination with low adult woody mortality, so that woody seedling recruitment can be enhanced during favourable climatic periods. This phenomenon is applicable in arid savannas like the Kalahari, with variable rainfall patterns (Higgins et al., 2000; Sankaran et al., 2004). In mesic savannas, fire controls the ability of tree seedlings and saplings to grow into later life stages (Trollope, 2011); woody vegetation higher than 2–3 m is rarely affected by fire (Hoffmann & Solbrig, 2003).

The impact of browsing also contributes to the removal of bottlenecks of woody recruitments in arid savannas (Staver & Bond, 2014). A ‘browsing trap’ as described by Staver and Bond (2014) could be similar to a ‘fire trap’, as it controls woody seedling and sapling establishment. It also maintains a relatively open savanna as browsing ungulates hinder the growth of woody species through the removal of buds, foliage and twigs (Staver & Bond, 2014). The impact of browsing on woody vegetation can still be used in describing the structure of semi-arid savannas in the Kalahari region, as high densities of browsing ungulates occur on commercial game farms and conservation areas (O’Connor et al., 2014; Smit, 2004).

The modern demographic-bottleneck models are favoured over the traditional competition-based models (Sankaran et al., 2004), as the latter, focussing on competition for resources,
provide insufficient explanations for long-term woody-grass coexistence and are appropriate only in certain savanna types (Ward et al., 2013; Sankaran et al., 2004).

1.3 General causes of bush thickening

Bush thickening (encroachment) involves an imbalance of the woody:grass ratio because of changes in the competitive interactions between lifeforms (i.e. trees and grasses). When the balance triggered by competitive mechanisms and/or bottleneck mechanisms is disturbed, woody species start to dominate the system at the cost of herbaceous vegetation (Eldridge et al., 2011; Graz, 2008; Moleele et al., 2002; Sankaran et al., 2004).

Although much attention has been paid to the history, vegetation characteristics and environmental context in earlier studies on bush thickening, a universal explanation for bush thickening across southern Africa still does not exist (O'Connor et al., 2014). The theory that only the exclusion of fire and heavy grazing by domestic livestock leads to bush thickening can be rejected (Ward, 2005; Wiegand et al., 2005). According to Smit (2004), there are two basic processes leading to the increase in woody plant density. The first is reproduction (i.e. increase in tree density by means of seed germination and seedling establishment) and the second is vegetative growth (established plants increasing in biomass) (Smit, 2004). The determinants responsible for the imbalance in woody:grass ratio could either be primary (climate and soil) and/or secondary (fire and herbivory) (Teague and Smit, 1992; Smit, 2004). Smit (2004) suggested that man should be held responsible for modifying the determinants.

Primary determinants of bush thickening relate to climate change posing a tremendous threat to dryland regions especially (O'Connor et al., 2014). A decrease in precipitation combined with an increase in the rate of evaporation may lead to lower herbaceous biomass production, which could trigger the densification of woody species (Safriel, 2009; Archer & Tadross, 2009). The woody vegetation layer mostly has a much better adapted root system occurring in a wide spectrum of soil layers, ensuring their survival during drier and warmer periods at the expense of the herbaceous layer (Joubert et al., 2013). Smeins (1983) predicted that the drier and warmer climatic conditions of the past 100 years may favour woody growth and therefore lead to the densification of woody vegetation. This relates to the competition-based models for soil moisture between the woody and herbaceous layers in arid savannas, which will ultimately determine the success of woody and grass species establishment (Grundy et al., 1994; Jurena & Archer, 2003).
Fixation of atmospheric carbon ($CO_2$) by means of photosynthesis impaired by lower soil moisture content is known to be the general limiting resource of primary productivity in drylands (Safriel, 2009; Cowie et al., 2011). It is predicted that approximately 34.6% of grasslands in southern Africa will be lost and replaced by savanna due to elevated atmospheric $CO_2$ during the past few decades (Scheiter & Higgins, 2009; Archer et al., 1995). With increased atmospheric $CO_2$, bush thickening is enhanced (Scheiter & Higgins, 2009), following the loss of herbaceous biomass production to disturbances, because elevated $CO_2$ levels favour the growth rate and nutrient storage capacity of woody vegetation ($C_3$ plants) (Bond 2008; Kgope et al., 2010). Transpiration in both $C_3$ and $C_4$ grasses is negatively correlated with an increase in $CO_2$ levels (Kgope et al., 2010). This results in more available soil moisture, which leads to an increase in aboveground productivity of $C_3$ woody vegetation, causing patchiness and higher densities in the savanna system (Scholes & Archer, 1997; Bond & Midgley, 2000; Kgope et al., 2010; Tietjen et al., 2010).

The patchy distribution of vegetation in most savannas can also be correlated with the patchiness of precipitation distributed over time and space (Ward, 2005). Seedling recruitment only occurs during higher rainfall years in semi-arid savannas because of inter-annual rainfall variability (O’Connor et al., 2014). Individual plant species have adapted to withstand long periods of dormancy in order to bridge dry conditions (O’Connor et al., 2014). This means that woody vegetation would increase in abundance as wetter periods become more frequent (Wiegand et al., 2005). Seymour (2008) concluded that *V. erioloba* and *S. mellifera* form seedlings into a ‘sapling’ bank that occurs within the grass sward and can persist until released during a high rainfall period combined with a reduction in grass competition.

Secondary determinants of bush thickening include rangeland management systems, which lead to the exclusion of fire, the limiting of grazing and browsing pressures (Silva et al., 2001; Van Langevelde et al., 2003; Müller et al., 2007; Wigley et al., 2010) and the introduction of additional watering points (Smit & Retham, 1999), resulting in changes in savanna composition and structure. Smit (2004) stated that through the replacement of browsing ungulates responsible for suppressing the woody vegetation (Staver & Bond, 2014) by commercial livestock, a disequilibrium in the woody:grass ratio will result, as a bottleneck of woody recruitment will be favoured (Smit et al., 1999; Sankaran et al., 2004; Blaum et al., 2009). The reason for this is that commercial livestock graze the herbaceous layer, removing the competitive pressure of this layer (Smit, 2004; Smit & Rethman, 1992). This leads to the creation of open patches with more nutrients and soil moisture available for woody seedlings to
establish (Smit, 2004). Van Vegten (1983) found that overgrazing of grasses, especially climax grasses, was the main cause of bush thickening in eastern Botswana. On the other hand, Wigley et al. (2010) noticed an increase in woody vegetation abundance over a period of years regardless of the different land use systems implemented with varying grazing intensities. Skarpe (1990) noticed that shallow-rooted species, such as *S. mellifera* and *Grewia flava* increased in abundance as a result of overgrazing in western Botswana, as more water is available in the upper and deeper soil layers of this arid savanna region.

Several studies have shown that fire also plays an important role in the shaping of moist savanna ecosystems (Trollope et al., 2002; Van Langevelde et al., 2003; Wiegand et al., 2006; Higgins et al., 2007). Fire intensity is controlled by the available grass biomass and woody production and controls the regeneration of vegetation (Wiegand et al., 2006; Trollope et al., 2002; Higgins et al., 2007). The grass biomass production, on the other hand, is regulated by MAP and herbivore behaviour (Wiegand et al., 2006; Scholes, 2009). In African savannas, fire has a tremendous effect on the ability of herbivores to control woody cover (Staver et al., 2009). Browsing ungulates have a direct impact on the tree layer, but the effect of grazing ungulates on the woody layer is intertwined with fire (Staver et al., 2009; Higgins et al., 2000). The essential amount of herbaceous fuel to control woody vegetation is reduced through heavy grazing, which causes less intense and less frequent fires (Scholes & Archer 1997; Van Langevelde et al., 2003). This is particularly true in arid savannas where incorrect burning practices lead to the removal of the herbaceous layer without killing the woody vegetation, which will ultimately result in bush thickening (Higgins et al., 2000; Briggs et al., 2005; Wigley et al., 2010).

Bush thickening can be demonstrated by state-and-transition models such as described by Smit (2004). The stability, domain and resilience of attractions are three main principles that determine the dynamics of a specific ecosystem (Smit, 2004; Walker, 1980). The stability of an ecosystem is described by the tolerance of disturbances it can withstand before changing into another state (Smit, 2004). A certain threshold of potential concern (the intensity of disturbances) is assigned to each ecosystem, which will cause the system to either become extinct or change into another state if the threshold is exceeded (Smit, 2004; Joubert et al., 2014). The domain of attractions determines the ability of a disturbed ecosystem to return to the central point of equilibrium, i.e. the ecosystem is still resilient (Smit, 2004). Joubert et al. (2008) identified frost, fire and extreme rainfall events as the main drivers causing transitions between the different stable states (open savannas and woodlands) within the Highland semi-arid savanna of Namibia.
1.4 Causes of bush thickening in the Kalahari

Looking at the Kalahari environment, centred within western and central Botswana and continuing into neighbouring countries, scientists find it difficult to construct a suitable description of this vast area (Thomas & Shaw, 1991). A semi-arid and open savanna with scattered woody vegetation is typical to this environment (Dougill et al., 2010; Smit, 2004; Ward, 2005). Deep Kalahari sands with very limited relief cover the basin underneath, which is filled with nutrient-deficient aeolian sediments (Thomas & Shaw, 1990; Dougill et al., 2010). Dougill et al. (2010) stated that several scientists describe the Kalahari sands as being structureless and fine, with a lack of nutrients leaching out into deeper soil layers.

The root niche separation model (Walter, 1939) would be a semi-applicable model describing tree-grass coexistence in this deep and red sandy Kalahari environment. This model suggests that the competition for soil moisture among woody and herbaceous vegetation would be minimal, as they rely on soil moisture occurring at different soil depths, which allows niche separation to take place (Ward et al., 2013; Walter, 1939; O’Connor et al., 2014; Kombatuku et al., 2013).

Anthropogenic disturbances (discussed in section 1.1.2.1) leads to an imbalance in the woody:grass ratio, with woody vegetation outcompeting herbaceous vegetation, ultimately resulting in bush thickening (Ward et al., 2013; Walter, 1939). This phenomenon of woody vegetation increasing in density and abundance has been reported in Botswana (Van Vegten, 1981; Moleele et al., 2013; Archer, 1990), more specifically in south-eastern Botswana near settlements (Moleele et al., 2013; Jeltsch et al., 1997).

As an example from the Kalahari, O’Connor et al. (2014) looked at historical events in the Molopo region in South Africa that may have locally caused bush thickening and identified two possible explanations. The first concerns the development of human settlements from 1945 onwards, which resulted in more livestock being held in the area (O’Connor et al., 2014). Fencing of farms, rangeland overutilisation, reduction of veld fires and sinking of additional boreholes for more water supply because of the higher number of livestock are the factors assumed to have caused bush thickening over a period of 20 years (Donaldson, 1969, as cited by O’Conner et al., 2014). The second explanation involves the occurrence of woody increaser species, such as S. mellifera, by the 1960s, along stock-transport roads in the communal livestock regions of the Kalahari in the Northern Cape (Donaldson, 1969, as cited by O’Conner
et al., 2014). More recently, Richter et al. (2001) indicated that *S. mellifera* is not the only species responsible for bush thickening in the Kalahari region, but species such as *V. luederitzii*, *Dichrostachys cinerea* and *G. flava* are also contributing to woody thickening, especially in the Molopo farming areas. Moore et al. (1985) estimated that already 2.5 million ha of the grass biomass in the Northern Cape had been reduced, with an increasing problem occurring in the Molopo ranching area due to the effect of bush thickening.

Donaldson (1966, 1967, as cited by O’Connor et al., 2014) described several important ecological changes due to global warming. Some of these changes involve an increase in the woody vegetation because the mortality factor of fire has been removed. This led to an increase in seed production, the dispersal of which was aided by livestock. Through the replacement of indigenous game with commercial livestock, all of the perennial grasses have nearly been depleted by means of selective grazing, thus removing the suppressive factor over the woody seedlings and adult plants. Walter’s two-layer soil water model is in line with the water use and root distribution of the grasses and occurrence of *S. mellifera* across a range of soil types (Donaldson, 1969, as cited by O’Conner et al., 2014). Certain areas where the density of woody species has thickened over the threshold value (where all herbaceous species are absent) have been controlled, causing a significant increase in grass biomass production, even in periods of drought (e.g. during the 1965–1966 drought) (Donaldson & Kelk, 1970).

**1.5 Effects of bush thickening**

Globally, 73% of rangelands have lost 25% of their grazing capacity as a result of degradation (Harrison et al., 2000; UNEP, 2006). According to Eldridge et al. (2011) this has a detrimental effect on the economic status of more than two billion people worldwide, as ecosystem goods and services are lost (Van Auken, 2009; Silva et al., 2001; Asner et al., 2003; Fensham et al., 2005). Bush thickening contributes to rangeland degradation because of its negative socioecological effect on land users in arid savannas (Moleele et al., 2002), since they are forced to apply expensive restoration techniques to combat bush thickening (De Klerk, 2004; UNEP, 2006; Kellner, 2008). These techniques would result in an increased herbaceous yield, but the effectiveness thereof will depend on the restoration technique used and the MAP (Teague & Smit, 1992).

It is estimated that 10–20 million hectares of southern Africa rangelands are affected by bush thickening, resulting in the loss of grazing capacity and biodiversity (Ward, 2005; Eldridge et
Moore et al. (1985) discovered that 80% of the grass sward in semi-arid savannas has been removed through competition with increasing woody vegetation.

Woody vegetation plays an important role in savanna ecosystems by creating 'fertile islands' (Dean et al., 1999). These islands of fertility include an increased concentration of nutrients, soil organic matter (Schlesinger et al., 1990; Pugnaire et al., 2011; Scholes & Archer, 1997) and shade, which enhances the establishment and growth of other plant species (Dean et al., 1999). The roots, branches, leaves and fruit in some cases contribute to the enrichment of nutrients under the woody canopy (Eldridge et al., 2011; Vetaas, 1992; Schlesinger et al., 1990). The amount of nutrients released into the soil depends on the nutrient content of leaves and fruit of the woody species (Vetaas, 1992). Woody vegetation is also known to be geomorphological obstacles, especially for material transported by wind and water (Vetaas, 1992; Virginia, 1986). Debris and seeds transported by wind or water can be trapped beneath bush canopies (Bernhard-Reversat, 1982; Escudero et al., 1985), which causes a higher infiltration capacity of nutrients into the soil, making it available for root uptake (Bhark & Small, 2003; Eldridge et al., 2011).

Vetaas (1992) also indicated that woody vegetation has a positive effect on the nutrient status of surrounding soil, which increases the establishment of more woody seedlings. He noted that similar effects were observed in savannas of eastern and southern Africa. Looking at studies that measured nitrogen (N), carbon (C) and phosphorus (P) concentrations in the soil, a horizontal pattern was identified in the top soil, with increasing concentrations closer to the base of the shrub/tree (Vetaas, 1992). Significantly higher concentrations of these nutrients were recognised in the sub-canopy soil compared to open and exposed soils in woody-thickened areas (Eldridge et al., 2011). A meta-analysis conducted by Eldridge et al. (2011) revealed that an increase in total and organic carbon (C), potential soil nitrogen (N) mineralisation, exchangeable soil calcium (Ca) and available soil phosphorus P were associated with bush thickening. Similar results were obtained by Belsky et al. (1989) in a semi-arid savanna ecosystem of Kenya, where N, P, K, total C and soil-water availability were more abundant under the sub-canopy of V. tortilis trees than in open, bare areas. The nature of the ecological processes involved in this shift is controversial and the direction of change remains unpredictable (Hibbard et al., 2001).

In drylands, the nutrients that accumulate at the soil surface under bush-thickened areas could also be ascribed to the occurrence of biological soil crusts growing in the top few millimetres of
the soil layer (Tongway & Ludwig, 1994; Dougill et al., 1998; Dougill & Thomas, 2004). These can be considered a living community constructed out of algae, microfungi, bryophytes, lichens and cyanobacteria (Dougill & Thomas, 2004), which varies between different soil types, vegetation structure, climatic variability and disturbances (Dougill & Thomas, 2004).

According to Dougill and Thomas (2004), the relationship between biological soil crusts and vegetation remains complex, but competition among them for soil moisture, light and nutrients do occur (Thomas & Dougill, 2006). On the other hand, Dougill and Thomas (2004) discovered an increased crust formation in thickened *S. mellifera* stands in the Kalahari environment, as it provides shade and protection from disturbances such as livestock trampling (Thomas & Dougill, 2006). This leads to the enrichment of soil occurring in bush-thickened areas (Hagos & Smit, 2005) as an increase in the nutrient status and total nitrogen (N) percentage were recorded under the canopy of *S. mellifera* stands (Dougill & Thomas, 2004; Thomas & Dougill, 2006). Biological soil crusts not only have the ability to fix atmospheric nitrogen (N) and sequester carbon (C) (Evans & Lange, 2003), but can also enhance soil surface stability and retrench soil moisture, thus reducing the threat of erosion (Dougill & Thomas, 2004; Thomas & Dougill, 2006). In contrast, other studies found lower soil water availability under tree thickets due to a higher tree water uptake (Amundson et al., 1995; Anderson et al., 2001).

Carbon sequestration is one of the main biochemical ecosystem functions of savannas (Archer et al., 2001) and is described as the process of capturing and storing CO₂ and other forms of carbon in order to mitigate global warming (Harrison et al., 1993; Fisher et al., 1994; Townsend et al., 1992). Hudak et al. (2003) identified several studies that conclude that land-use changes over time have an effect on the soil organic carbon (C) storage, but remain complex in savanna ecosystems. The levels of carbon accumulating in the soil are controlled by the litter input of vegetation and the rates of decomposition (Hudak et al., 2003). With an increase in woody vegetation in bush-thickened areas, the rates at which soil carbon (C) sequestration occurs is increased (Hudak et al., 2003) due to more litter depositions under bush canopies (Eldridge et al., 2011). Research done by Hibbard et al. (2001) supports the previous findings, as they discovered higher %carbon (C) and %nitrogen (N) under the canopy of thickening woody vegetation in comparison to that of non-encroached areas between woody stands.

With the increase in woody vegetation density, a decrease in herbaceous vegetation occurs as they are outcompeted for limiting resources (Ward et al., 2013). This results in the creation of bare inter-patches between woody stands, especially in arid savannas with deep sandy soils (Ward et al., 2013; Ludwig et al., 2004; O’Connor et al., 2014; Kumbatuku et al., 2013). High
evapotranspiration rates in these bare inter-patches cause increased temperatures, resulting in the denitrification of organic nitrogen (N) incorporation and ammonia volatilisation as well as a decrease in soil pH and grass cover (Schlesinger et al., 1990; Eldridge et al., 2011). As there is no protection against the impact of raindrops on the bare inter-patches between woody individuals (Mills & Fey, 2004), depressions of clay within the soil are increased, blocking the surface pores, which results in a decreased infiltrability of the soil (Shainberg, 1992; Mills & Fey, 2004). Sandy soils with a very low clay content found in semi-arid and arid savannas also experience this phenomenon (Mills & Fey, 2004).

Not only does woody vegetation trap nutrients and organic material (Vetaas, 1992; Bernhard-Reversat, 1982; Escudero et al., 1985), but it also provides ecosystem goods and services to different organisms, such as mammals, birds, insects and other vegetation (Eldridge et al., 2011; Blaum et al., 2007; Sirami et al., 2009). As woody species increase in density and abundance, the population dynamics of other species relying on the woody species are affected (Eldridge et al., 2011; Sirami et al., 2009). The direct effects of bush thickening on other organisms are highly variable, with few studies concentrating on this relationship (Eldridge et al., 2011; Sirami et al., 2009). However, it has been shown that bush thickening affects the species distribution and structure of lizards (Meik et al., 2002), insects, especially ants (Ayres et al., 2001), tortoises (Ayres et al., 2001), mammals including carnivores and several rodent species (Blaum et al., 2007) and other arthropods (Blaum et al., 2009); whether the effect of bush thickening is positive or negative is variable and species-specific (Sirami et al., 2009; Eldridge et al., 2011). Bird species, on the other hand, tend to differ between contrasting environments such as an open savanna with several scattered trees versus woodland (Skowno & Bond, 2003; Sirami et al., 2009). The density of woody species could also be correlated to the abundance of selected bird species (Ayres et al., 2001; Eldridge et al., 2011; Kaphengst & Ward, 2008).

1.6 Mitigation and combat of bush thickening

The main objective of ecological restoration in general is to accelerate and assist in the recovery process of damaged, degraded or destroyed ecosystems (SER, 2004). One of the main goals of ecological restoration is to restore a degraded habitat to being self-sustaining and more resilient, resulting in the recovery of lost ecosystem goods and services and enhancing the livelihoods of people (Bullock et al., 2011; SER, 2004; Cortina et al., 2011).
Two types of restoration can be implemented, namely passive and active interventions (Kellner, 2008). Passive restoration interventions are less expensive and include the implementation of improved long-term management systems, such as rotational grazing followed by extensive resting periods, or simply the removal of the stress factor degrading the ecosystem, such as grazing animals (Milton & Dean, 1996; Scholes, 2009; Kellner, 2008). Passive interventions can be implemented in semi-arid savanna systems with limited functional damage and with a high resilience (Visser et al., 2007; Kellner, 2008). Active restoration, on the other hand, is much more expensive and requires active interventions, such as breaking the soil crust with an agricultural implement, re-seeding if the seed bank has been depleted, building water catchment areas to improve the soil moisture, cover with woody branches, veld burning, cultivation and/or fertilisation practices (Teague et al., 2010; Visser et al., 2007; Scholes, 2009). The implementation of bush thinning practices that lead to the removal or thinning of overpopulated woody species in an area by means of chemical and/or mechanical technologies, is a type of active restoration, which will typically be implemented in savanna ecosystems that have a low resilience and herbaceous cover and which lost their structure and function because of bush thickening (Aronson et al., 1993; Kellner, 2008).

From an agricultural perspective, bush thinning and control practices are often implemented to stimulate the herbaceous biomass production, which may lead to increased forage production available for grazing animals (livestock and/or game animals) (Smit, 2004; Smit et al., 1999). After bush-thinning practices were implemented in several areas in the semi-arid savanna of the Molopo, an increase in herbaceous biomass was recorded, even during the drought of 1965 (Donaldson & Kelk, 1970).

1.7 Bush control methods used in the Molopo region

The overall objectives for bush thinning in semi-arid savannas are to (1) increase visibility for hunters, (2) increase grazing capacity and herbaceous forage production for grazers and (3) improve accessibility for animals and humans (Bezuidenhout et al., 2014). The most commonly used methods for bush thinning include both mechanical and chemical measures (Smit, 2005).

Bush control by means of applying chemical arboricides in a granular or fluid form is commonly used in woody-thickened areas of the semi-arid savanna regions in South Africa, such as the Kalahari bushveld (Hagos & Smit, 2005). Smit (2004) suggested two aspects that need to be considered when applying chemical control methods to restore the herbaceous layer (to
improve the production for grazers), namely control measures need to be (1) economically justifiable and (2) ecologically sustainable and stable (Smit, 2004).

The different land tenure and management types, such as commercial, communal or conservation land, will influence the type of chemical bush control technique applied, as the aim and economic input required will differ between the types of land management (Smit, 2004). For example, in nature reserves bush-thinning practices are implemented to conserve biodiversity, whereas commercial farmers implement bush thinning to increase the herbaceous biomass production for livestock grazing (Bezuidenhout et al., 2014).

There are many arboricides manufactured in South Africa (Dow AgroSciences, 2003) that are used to control bush thickening, such as Bushwacker, Molopo and Savanna, which contain the active ingredient tebuthiuron (Smit, 2005). Tebuthiuron is a thiadiazole urea arboricide with excellent herbicidal action on a wide range of woody vegetation, including species such as *S. mellifera*, *V. erioloba*, *V. haematoxylon*, *V. hebeclada* and *V. luederitzii*, which tend to become thickened in arid savannas (Bezuidenhout et al., 2014). Tebuthiuron is applied within the Molopo region at rates of 2.5–3 kg/ha (Dow AgroSciences, 2009). Two common methods that have been identified for applying arboricides, are namely by hand and/or aeroplane (Hagos & Smit, 2005; Donaldson, 1966). Rain plays an essential part in the success of this arboricide as it leads to tebuthiuron infiltrating up to 600 mm into the soil (Dow AgroSciences, 2009). This non-selective arboricide is absorbed by the roots of woody plants and is transported to the leaves, where it inhibits photosynthesis, causing mortality (Dow AgroSciences, 2009).

Tebuthiuron-based products are favoured in Molopo savannas because the arboricide breaks down faster under increased soil moisture and higher temperatures (Chang & Stritzke, 1977). The Molopo area experiences low summer rainfall, which allows the arboricide to accumulate longer in the soil (Dow AgroSciences, 2009). The persistence of tebuthiuron in the soil is also influenced by the application rates of the arboricide and the soil type (Dow AgroSciences, 2009). This arboricide is mainly used in sandy, neutral or alkaline soils.

There are several important factors (including soil clay content, soil pH, organic matter content, target species and its size and the selected season of application) that need to be considered when calculating the dosage for successful arboricide application (Moore et al., 1985; Smit et al., 1999; Dube et al., 2011). The success of the chemical follow-up management plan will ultimately be determined by the recovery of the vegetation, especially the herbaceous species, after the chemical application (Snyman, 2003).
Because of the non-selective nature of the active ingredients of the arboricides, namely tebuthiuron, mechanical measures are often implemented together with the chemical application (Donaldson, 1966). These measures include the cutting of woody species by hand or with heavy machinery (Donaldson, 1966). The cut stumps (rooted in the soil) are then treated with arboricides, containing for example picloram as the active ingredient (Smit, 2005), because of the strong regrowth ability of woody plants. Fire is also often used as a follow up treatment, controlling the regrowth of the woody vegetation layer (Smit, 2004; Donaldson, 1966). This will, however, depend on the rainfall, soil conditions and available biomass in the area (Smit et al., 1999; Smit, 2004; Donaldson, 1966).

In the semi-arid Kalahari regions, fire cannot effectively be used as a management technique for bush thinning due to a lack of enough herbaceous material (which should be about 4 000 kg/ha or higher) caused by increased grazing pressure (Trollope, 2011; Joubert et al., 2012). Stem burning or fire girdling, on the other hand, is a well-known method for controlling bush-thickened areas as described by Donaldson (1966). Stem burning is carried out by packing the basal area of selected woody species with enough dry vegetation (e.g. woody branches), to create fuel loads to ring-bark the tree/shrub when burnt (Donaldson, 1966; De Klerk, 2004). This method is labour intensive and slow but inexpensive when carried out in the veld and does not imply chemical application (De Klerk, 2004).

The recruitment of *S. mellifera* depends on the current season’s seed production, as the seeds of this woody species are short-lived and do not remain viable in the seed bank for longer than one to two seasons (Donaldson, 1969, as cited by O’Conner et al., 2014). In addition, good rainfall events and the complete removal of competition are needed to enable the seeds to germinate and grow (Joubert et al., 2008). When a demographic bottleneck of woody seedlings occurs because of favourable environmental conditions, the control of these seedlings using browsing pressure would be insufficient (Bezuidenhout et al., 2014). To prevent such a bottleneck from becoming problematic, aftercare is needed (De Klerk, 2004). With chemical control measures, aftercare includes follow-up treatments and controlling the regeneration of woody vegetation every 5 to 7 years thereafter (Van Niekerk, 1990; Dahl & Nepembe, 2001, as cited by De Klerk, 2004). Several other techniques described by De Klerk (2004) could also be used as aftercare methods, which include the introduction of goats, game or cattle as browsing ungulates, combined with a rotational grazing system, manual removal of seedlings and saplings and occasional burning of the veld.
1.8 Changes in woody structure after bush-thinning practices

In open semi-arid savannas, like those found in the Molopo region, species composition and diversity could be substantially changed through anthropogenic disturbances such as bush-thinning practices, potentially affecting ecosystem resilience and function (Berhane et al., 2015). This also contributes to structural changes of the woody layer, which in turn influence the distribution of resources, e.g. soil moisture and nutrients, and the microclimate (Ludwig et al., 2004). These changes have cascading effects on biodiversity, with some organisms responding directly to changes in woody structure, while others are influenced by resource availability and microclimate (Berhane et al., 2015; Williams et al., 2002; Ripple & Beschta 2004).

Large individuals and keystone woody species, responsible for the regulation of fundamental ecosystem processes, are also removed through woody clearing processes, which could have severe effects on ecosystem stability, causing an imbalance in the woody:grass ratio (Berhane et al., 2015; Smit, 2004). Burrascano et al. (2008) suggested that the availability of seeds are influenced by the selective removal of mature trees, causing a change in plant community structure as plant species succession and regeneration are influenced. Gaps in the savanna are created by the harvesting of woody vegetation affecting the availability of light, nutrients and soil moisture, which can potentially further alter species composition (Brokaw & Busing, 2000). If the herbaceous seed bank is depleted, gaps created by bush-thinning practices could also lead to the establishment of new woody individuals or an increased growth of neighbouring woody species (Teague & Smit, 1992).

According to Smit and Rethman (2000), a complex inter-relationship between soil water, the soil type and vegetation occurs in semi-arid savannas of southern Africa. These authors emphasised the significant positive effect that bush control has on the soil water status of an area, which enhances the establishment of herbaceous plants (Smit & Rethman, 2000). As mentioned before, in semi-arid savannas higher grass biomass, known as dry-matter (DM) production is recorded at low tree densities and the complete removal of the woody layer results in a substantial increase in grass production (Donaldson and Kelk, 1970; Richter, 1991; Smit, 2005; Moleele et al., 2002).

Tree-on-tree competition is an important factor determining the success of seedling recruitment and regeneration (Smith & Goodman, 1986). Several scientists discovered that certain species respond differently to competition from neighbouring woody species, where some species use
the canopy of other species as a ‘safe site’ for establishment, others tend to appear only in the opening between canopy environments (Smith & Goodman, 1986; Grundy et al., 1994). Focusing on *Senegalia* and *Vachellia* species recruitment, Smit and Goodman (1986) also stated that several of these species struggle to establish under the canopies of mature trees because of competition for nutrients and soil moisture. Many studies have concluded that the post control environment bush thickening became worse after bush control were implemented due to coppicing (Smit, 2004), thus reducing the effective time span of restoration measures.

Some of the few studies describing structural changes of the woody layer after bush-thinning practices have been implemented identified an increase in abundance (plants per hectare) in the Mopane layer (Smit, 2014) as well as an increase of 10% in mean seasonal dry matter leaf production (Smit, 1994) in low tree-density plots, compared to a decline in abundance in the high tree-density plots. Interestingly, Smit (1994) noticed an increase in canopy diameter of remaining trees in the thinned plots, due to competition being removed as the tree density and abundance declines. In contrast, self-thinning occurred in the dense plots, caused by competition between the overpopulated woody vegetation, leading to equilibrium (Smit, 2014). Coe (1991) also discovered an increase of 1.2–3.9% in tree height and an 11–21% increase in stem basal area for *Colophospermum mopane* trees in thinned plots located in Botswana. Similar results were obtained by Smith and Goodman (1986) as they identified a significant increase in both shoot extension and stem diameter increment for the remaining *V. nilotica* trees where competing trees have been removed within a 5 m radius. Gaugris and Van Rooyen (2010) identified a change in stem diameter size class distribution in both the sand and woodland forests of Maputaland because of the utilisation regime, while the height structure remained unchanged (Smit, 2014). The general conclusion was that the smallest diameter woody plants combined with the largest woody plants occurred in conserved land under animal utilisation, whereas in the absence of utilisation an intermediate abundance of small diameter woody plants were found in combination with low densities of large trees (Gaugris & Van Rooyen, 2010).

It has been observed that the loss of large trees from savanna ecosystems because of the unselective nature of arboricides applied is one of the major reasons why long-term solutions for bush control were not achieved (Smit, 2004). Smit (2014) suggested the option of tree thinning rather than tree clearing to implement a sustainable woody:grass ratio. This can be achieved by tree thinning to a predetermined density (primary operation), after which post-thinning operations (aftercare), including low-level stocking rates with the control of re-sprouting woody
vegetation (Sankaran & Anderson, 2009; Higgins et al., 2007), follows to keep the woody:grass ratio in equilibrium (Smit et al., 1999). As previously mentioned farmers need to note that effective restoration of bush-thickened areas should not be considered a once-off event, but rather a long-term commitment (Smit, 2004). With tree-thinning techniques implemented, the remaining trees will benefit from the reduced competition, which will lead to an increased growth combined with a suppressing effect eventually outcompeting the newly establishing seedlings (Smit, 2004).

In order to have the minimal ecological and economic damage, rangeland degradation caused by bush thickening needs to be addressed in its early stages to prevent the loss of ecosystem goods and services (Von Maltitz, 2009). Integrative studies making use of site-specific indicators most affected by rangeland degradation, identified by local land users, should be undertaken to involve the land users in processes combating the degradation of rangelands by means of bush thickening (Kellner, 2008).

1.9 Problem identification and study aims

Smit et al. (1996) stated that there is a general lack of detailed research on the effect of different management practices on the woody vegetation. To help address this gap, this dissertation concentrated on the structure and composition of woody vegetation in relation to bush-thinning practices. Many studies have focussed on the effect of tree thinning/clearing on savannas and how the herbaceous layer reacts to reduced competition from woody plants (Moore & Odendaal, 1987; Harrington & Johns, 1990; Richter, 1991), but the reproductive, re-establishment and growth dynamics of the remaining woody individuals have rarely been investigated (Smit et al., 1996). Smit (2014) and Smith and Goodman (1986) mentioned that there is still a lack of scientific information regarding the long-term ecological impacts of tree-thinning practices conducted by man or caused by herbivory and fire in savanna ecosystems.

There are several reasons why scientists and farmers consider the reproduction, browse production and vegetative growth of woody vegetation that remains after clearing operations important (Smit et al., 1996). These reasons include the estimation of the effective time span for tree-thinning operations with regards to the rate of re-establishment, reproduction and vegetative growth of woody individuals (Scifres, 1987; Scholes, 1990). Smit (1994) suggested that the main source of feed for browsers is trees and that this source is reduced during the post-thinning periods. This phenomenon is of special interest to the game farming and
commercial cattle farming industries in savannas, as both game and cattle utilise a significant proportion of browse material, especially during the dry seasons (Kelly, 1977; Donaldson, 1979; Bayer, 1990). The consequences of altering this feed source should be addressed (Snyman, 1991).

Eldridge et al. (2011) concluded that there have been no attempts to their knowledge to formulate a global synthesis of the outcomes of bush thickening/densification from ecosystem-functional, utilitarian and community-structure perspectives, despite a few demonstrations regarding the comprehensiveness of the bush-thickening phenomenon.

In this study, the effect of different bush control techniques on the composition, diversity and structure of the woody savanna component was analysed by means of case studies in farming systems of the semi-arid savanna in the Molopo area of the North-West province in South Africa. The focus was on demographic patterns in order to identify species-specific response patterns and evaluate the need for post-control management and its effectiveness. This largely descriptive study served to get a better overview of the structural impacts of bush control, which is crucial for sustainable rangeland management decision-making. The specific aims of the study included the following:

- A description of general patterns in woody community composition and structure after bush control methods implemented.
- A description of short term response patterns of the woody vegetation layer to selective and non-selective chemical bush control with particular reference of selected key species.

1. 10 Hypotheses

The following hypotheses were formulated to address the study aims:

- Different bush control techniques result in differently structured post-control environments characterized by distinct and species-specific recruitment patterns.
- The threat of bush re-thickening is highest following non-selective bush control.
1.11 Dissertation structure

The dissertation consists of seven chapters. The present chapter provides a general introduction and simultaneously outlines problems associated with bush thickening. Also discussed in Chapter 1 are different methods for combating bush thickening in semi-arid savannas and the importance of assessing the woody vegetation.

Chapter 2 provides a description of the study area in terms of its location, land use, climate and vegetation. The materials and methods used in this study are outlined in Chapter 3. In Chapter 4, different response patterns in woody community composition and structure are evaluated, contrasting different bush-control techniques (selective and non-selective) used in the Molopo Bushveld vegetation. Chapter 5 describes the short-term responses of woody vegetation to selective and non-selective chemical bush control, where selected key species are emphasised.

Chapter 6 provides a synthesis of the dissertation, which includes a conclusion, followed by recommendations for future studies. Complete lists of references are given in chapter seven, and appendix is included at the end of the dissertation. Note that although raw data is not listed in the appendix, it is available on request.
CHAPTER 2
THE STUDY AREA

2.1 Location and land use

The study was conducted in the Molopo Bushveld vegetation type in the North-West and Northern Cape provinces of South Africa close to the border with Botswana. Exactly the same study area was also examined by another masters student of the NWU-Potchefstroom campus, with the title: “Landscape function in bush thickened and –controlled areas of the semi–arid savannah in the Molopo region, South Africa” (Fouche, 2016) during the same time period. Thus a similar description of the study area is given.

The study area falls within the Kagisano-Molopo local municipality (Figure 1), which in turn falls under the Dr Ruth Segomotsi Mompati District Municipality; formerly known as the Bophirima District Municipality (Dr. Ruth Segomotsi Mompati District Municipality, 2009). The study area forms part of the south-eastern edge of the Kalahari sand basin, which stretches over an area of approximately 2 million km² (Thomas & Dougill, 2006), and is 1000–1300 m above sea level (Mucina & Rutherford, 2006).

According to Tews et al. (2006), cattle farming and commercial game farming are practised in the area, with some of the largest cattle herds in the world found within this district. This high concentration of cattle led to the district becoming one of the largest beef-producing districts in South Africa (earning it the name of ‘the Texas of South Africa’). Most of the commercial farmers in the region make use of rotational grazing regimes, where their pasture is divided into various smaller camps (paddocks). These smaller camps are then grazed more intensively for shorter time periods to give other enough time to rest and recover before being grazed again (Tews et al., 2004).

The approximate long-term grazing capacity for the Molopo study area is 10–12 ha/LSU (Hectares per Large Stock Units) (Mostert et al., 1971, as cited by Richter et al., 2001; Tews et al., 2004). Communal areas are dominated by goats and donkeys with the occasional herd of cattle. Cattle herds in the communal areas were dealt a serious blow by the rinderpest that
moved through the area in the 1930s (Jacobs, 2000). The government forced the farmers in the areas affected by rinderpest to cull all the affected animals. This lead to a shift of goat and sheep farming. Donkey numbers also increased exponentially in the late 1930s after the rinderpest (Jacobs, 2000). Up till the 2015 Commercial farmers focussed more on cattle and sheep farming (Jacobs, 2000), while commercial game ranching only became popular during the mid 2000’s (Tews et al., 2006).

Good management of the pastures in the Molopo region can lead to promising net gains for farmers. However, extensive areas in the Molopo study area are affected by bush thickening as a result of several factors, including mismanagement, climate and environmental factors (Jeltsch et al., 1997; Harmse, 2013; Smit et al., 1999; Richter et al., 2001; Barac, 2003).

Figure 1: Location of the four study sites (1-4) in the Molopo study area situated in the North-West and Northern Cape provinces of South Africa.
2.2 Climate

The Molopo study area receives a summer rainfall with an MAP of 250–400 mm (Mucina & Rutherford, 2006). The precipitation is received predominantly between the months of November and March, also known as the summer-wet season in most parts of South Africa (Figure 2) (Thomas et al., 2002; South African Weather Service, 2014). The precipitation of the Molopo study area varies between extreme dry spells and occasional wet years (Thomas & Shaw, 1991; Nash & Endfield, 2002, South African Weather Service, 2014 www.weathersa.co.za).

Figure 2: The mean monthly precipitation (± standard deviation) recorded at Bray (weather station 0541297 5) and Severn (weather station 0428635 1) in the Molopo study area from 1985 to 2014.

The last 30 years of rain data were summarised and grouped into three groups of ten years each to show comparisons in the rainfall data between the three decades. The average annual precipitation for the Bray area (Figure 1) [weather station 0541297 5] shows high variability over the last thirty years. The average precipitation showed an increase from an average of 316 mm between the years of 1985 and 1994 to a very wet decade with an average of 419 mm for the years 1995 to 2004, followed by a drier decade with an average of 241 mm from 2005 to 2014 (Figure 3) (South African Weather Service, 2014). Severn (Figure 1) [weather station 0428635
1] showed less variability in its average precipitation between the three decades. The average precipitation for the first decade (1985–1994) was 275 mm, followed by a slightly wetter decade (1995–2004) with an average of 317 mm. The last decade (2005–2014) was the driest and an average of 241 mm was documented (Figure 3) (South African Weather Service, 2014).

![Figure 3: The mean annual precipitation (± standard deviation) recorded at Bray (weather station 0541297 5) and Severn (weather station 0428635 1) in the Molopo study area from 1985 to 2014.](image)

These comparisons in the rainfall data for the last three decades from the two weather stations coincide with the statements made by Thomas and Shaw (1991) and Nash and Endfield (2002) in that the precipitation of the Molopo area can vary from very dry spells to occasional wet years (Figure 3) (South African Weather Service, 2014). The Bray area suited this description best with its high variability in precipitation between the three decades: there was an increase of 102 mm from the first (1985–1994) to the second decade (1995–2004) and a decrease of 165 mm from the second to the third decade (2005–2014) (Figure 3) (South African Weather Service, 2014). The Severn area followed the same trend with the second decade (1995–2004) being the wetter decade followed by the driest decade (2005–2014), only with smaller differences (Figure 3) (South African Weather Service, 2014). The average precipitation for the Severn area increased with 42 mm from the first decade to the second and then decreased from the second to the third decade with an average of 76 mm (Figure 3) (South African Weather Service, 2014).
As a result of the drought experienced in the country, very little precipitation was received prior to the field surveys (end of February until beginning of March 2015) (Figure 4) (South African Weather Service, 2014). This led to poor herbaceous production, which made vegetation sampling difficult. The long-term average rainfall (1985–2014) for the Bray and Severn areas from November to February are 222 mm and 173 mm, respectively (South African Weather Service, 2014). These rainfall values decreased dramatically for the four months prior to the field surveys at the end of February 2015 (Figure 4) (South African Weather Service, 2014). The Bray area received only 65 mm from the end of 2014 until the beginning of 2015 compared to the long-term average of 222 mm. Severn also experienced a decline in the amount of rainfall received in these months, where 134 mm was received compared to the long-term average of 174 mm for the same time period (Figure 4) (South African Weather Service, 2014).

The rainfall data from the Bray and Severn areas were used in the description owing to their close proximity to most of the sampling sites.

![Figure 4: Monthly precipitation prior to the field surveys from the end of February until the beginning of March 2015 recorded at Bray (weather station 0541297 5) and Severn (weather station 0428635 1) in the Molopo study area.](image-url)
2.3 Geology and soils

In southern Africa, one of the largest sand-covered areas occurring globally, is known as the Kalahari, occupying a 2.5 million km$^2$ area located between 29° south of the equator and 14°–28° east (Scholes et al., 2002). Within this area, Walker et al. (2010) described the Molopo Farm Complex (MFC), previously known as the Bushveld Complex. The Molopo study area is largely situated within the MFC, which is approximately 13 000 km$^2$ in size, layered with ultramafic-mafic intrusions known as the Kaapvaal Craton (Walker et al., 2010). The Kalahari sands (Cenozoic Kalahari Group sediments) and Karoo strata occurring in the northern parts of the North-West province in South Africa and south-western parts of Botswana are presently overlying this complex (Reichhardt, 1994; Anhaeusser, 2006; Scholes et al., 2002). The thickness of these layers varies between 100 m in the west and south of the MFC, to approximately 200 m in the proto-Molopo palaeo-valleys (Walker et al., 2010).

Flat to sinuate sandy plains occurs in the Molopo, with the topography varying between 1 000 m and 1 300 m above sea level (Donaldson & Kelk, 1970; Rutherford et al., 2006). Closer to the drainage valley areas such as the Molopo River, sand dunes occur more frequently (Van Niekerk, 2011). This sand is known as the Cordonian Formation and is a red, deep Aeolian sand with a surface containing silcrete, calcrete and ferricrete (Low & Rebelo, 1996; Rutherford et al., 2006). The study area has red and yellow sandy soils that are well-drained and has a high base status (Rutherford et al., 2006). The Kalahari sand is characterised by a high infiltration rate and relatively level topography, which causes little to no water runoff in this area (Donaldson & Kelk, 1970). The deep sandy soils (>1.2 m) (Rutherford et al., 2006), characterised by coarse soil texture and low clay content, allow water, air and roots to easily penetrate, which results in a decreased water and nutrients retention capacity (Sims, 1981; Gebremeskel & Pieterse, 2006). Kalahari sand is not seen as a suitable growth medium for vegetation to establish in because of its low moisture retention, but the sand does manage to retain some moisture during rainfall episodes (Thomas & Shaw, 1991). The establishment of some vegetation is improved by moisture captured in the top six meters of soil and specialised roots with the ability to penetrate into underlying water tables (Thomas & Shaw, 1991).

2.4 Vegetation

Rutherford et al. (2006) described the study area as the Molopo Bushveld vegetation type with the scattered tree layer characterised by selected woody species, such as *Vachellia erioloba*
and *Boscia albitrunca*, and less common species like *Terminalia sericea* and *V. luederitzii* var. *luederitzii* (Rutherford et al., 2006). The shrub layer has a moderate development with common species such as *Grewia flava*, *Lycium hirsutum*, *Senegalia mellifera* subsp. *detinens*, *V. haematoxylon* and *V. hebeclada* subsp. *hebeclada*. Common perennial grass species include *Aristida meridionalis*, *A. stipitata*, *Eragrostis lehmanniana* *E. pallens*, *Schmidtia pappophoroides*, *Stipagrostis uniplumis* and *Urochloa mosambicensis*. Annual grasses include species such as *Enneapogon desvauxii* and *Schmidtia kalahariensis* (Richter et al., 2001; Harmse et al., 2014). This vegetation type is known to be the least threatened for conservation, as only 16% of the Molopo Bushveld needs to be conserved and 1% of that target is captured in the Molopo Nature Reserve (Rutherford et al., 2006).

In this dissertation, emphasis is placed on the diversity and structure of the woody layer of the Molopo Bushveld vegetation type. A previous study conducted by O’Brien (1993) aimed in describing the diversity of the woody vegetation within southern Africa. A strong positive correlation was drawn between woody species richness and MAP, with increasing species richness towards the eastern escarpment of the Kalahari Basin (O’Brien, 1993). Structural attributes of woody vegetation along an aridity gradient were also considered by Scholes et al. (2002) as they discovered a strong correlation between MAP, basal area, plant height and biomass of woody vegetation in the Kalahari.
3.1 Selection and description of study sites

The study design included four bush control treatments, namely (1) selective chemical control by hand (HC), (2) selective chemical control by hand with re-application (HC2), (3) non-selective chemical control by aircraft (AC) and (4) selective control by stem burning with re-application (SB) (Table 1). The respective sampling sites were located on three commercial cattle farms and one game farm (Table 1). At farm scale, site selection occurred with the help of the land owner, who was asked to indicate appropriate bush-thickened (BT) benchmarks, against which the treatment effect could be measured. As a control, bush-thickened areas corresponded to the initial level of bush thickening of the treated sites were selected. At one farm, however, only sites with a tendency towards bush thickening were found, identified as partially thickened (PT) (Table 1) and were accordingly referred to as such in the study. In another case, sustainably managed open rangelands (SM) that have not been thickened before were selected as another control (Table 1). For each site, qualitative data such as camp size, grazing regime, stocking rate, grass layer condition and soil condition were noted. Farmers and their local workers implemented the treatments.
Table 1: General background information of the selected study sites within the Molopo Bushveld vegetation type. All study sites were selected to be comparable with respect to climate, substrate (sandy) and topography (level).

<table>
<thead>
<tr>
<th>Study site</th>
<th>Farm: Omega</th>
<th>Farm: Wilzenau</th>
<th>Farm: Lafras</th>
<th>Farm: Jones &amp; De Klerk</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Type of control and number of sampling sites</strong>¹</td>
<td>ACG: 4 BTG: 4</td>
<td>ACK: 4 BTK: 4 HCK: 4</td>
<td>SB2B: 3 BTB: 3 SMB: 3</td>
<td>HC2O: 4 PTO: 4 HCO: 4</td>
</tr>
<tr>
<td><strong>Land tenure type</strong></td>
<td>Commercial game farm</td>
<td>Commercial cattle farm</td>
<td>Commercial cattle farm</td>
<td>Commercial cattle farm</td>
</tr>
<tr>
<td><strong>Stock composition</strong></td>
<td>Game Giraffe (browser) Oryx (grazer) Impala (grazer and browser) Kudu (browser) Blue wildebeest (grazer) Eland (mixed browser) Blesbok (grazer) Springbok (mixed grazer) Buffalo (grazer)</td>
<td>Cattle and horses</td>
<td>Cattle</td>
<td>Cattle</td>
</tr>
<tr>
<td></td>
<td>Sable (grazer)</td>
<td>Zebra (grazer)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>------------------------------</td>
<td>----------------</td>
<td>----------------</td>
<td>----------------------</td>
<td>----------------------</td>
</tr>
<tr>
<td><strong>Stocking rate</strong></td>
<td>10 LSU/ha</td>
<td>10 LSU/ha</td>
<td>12 LSU/ha</td>
<td>10 LSU/ha</td>
</tr>
<tr>
<td><strong>Grazing system</strong></td>
<td>Open system</td>
<td>Four-camp rotational grazing system. Rotating every two weeks.</td>
<td>Eight-camp rotational grazing for nine days, with a resting period of 63 days per camp.</td>
<td>Six-camp rotational grazing with two camps resting for a whole growing season.</td>
</tr>
</tbody>
</table>

*Total sampling sites: AC: non-selectively chemically controlled by aircraft; HC: selectively chemically controlled by hand once; HC2: selectively chemically controlled by hand with reapplication; SB2: selectively controlled by stem burning with re-application; SM: sustainably managed; PT: partially bush thickened; BT: bush thickened.
3.2 General sampling approach

The basic sampling design consisted of two belt transects of either 4 x 80 m or 4 x 100 m per replicated sampling site, because of the limited size of the bush-thickened areas (100 x 100 m) within the commercial game farm. The belts were laid in a representative and homogeneous area of vegetation, with the starting point of the middle-line determined at random. The replicated sampling sites per farm were a minimum distance of approximately 500 m apart and the two transects within the sampling site were approximately 30–40 m apart, laid in the same direction. All data were extrapolated to hectare spatial scale to make them comparable.

The following data for all woody species rooting within a belt were collected: (1) the species name and its abundance (ha), (2) the plant height, (3) two maximum, perpendicular canopy diameter and (4) the stem diameter at breast height (DBH) (i.e. 1.3 m; for multi-stemmed species the DBH of the thickest stem, for smaller plants just above the basal swelling). For woody species <0.5 m only the species name, height and DBH were recorded. As a qualitative measure, the condition of woody species was noted as dead, chemically affected with basal regrowth, affected with regrowth on branches, browsed, heavily browsed and/or unaffected.

Measurements of plant height and canopy diameters were done with two-metre plastic poles with markings every 10 cm. Based on the height measurements, plants were assigned the following height classes: ≤0.5 m (height class H1), >0.5–1 m (height class H2), >1–2 m (height class H3), >2–3 m (height class H4), >3–5 m (height class H5) and >5 m (height class H6).

3.3 General data analysis

An overview of applied statistics, e.g. analysis of variance (ANOVA), multivariate analyses and descriptive statistics, is provided below. A correspondence analysis (CA) was used in the CANOCO programme (Ter Braak, 1992) to identify any correspondence between the different treatments and structural parameters. Descriptive statistics (Microsoft Excel 2010) were used to describe the species composition and abundance patterns. The species-specific response patterns within each height class of the post-controlled environment were analysed in STATISTICA (version 10) (StatSoft, Inc., 2011).

The following calculations were used in processing the data, including formulas:
• Bush density (trees/ha): (no. of plants per 720 m² x 15.63) or (no. of plants per 800 m² x 12.5)

• Relative bush density (%): (total bush density/ha x 100/total density all height classes)/100

• Tree equivalents (TE)/ha: Phytomass = (bush density/ha x average height all plants)/1.5

• Species richness: (no. of species per 720 m² x 15.63) or (no. of species per 800 m² x 12.5)

• Shannon diversity: Diversity $H' = -\sum_{i=1}^{s} p_i \ln p_i$

• Shannon evenness: $E = \frac{H'}{H'_{\text{max}}} = -\frac{\sum_{i=1}^{s} p_i \ln p_i}{\ln s}$

Where: $s$: number of species

$p_i$: proportion of individuals or the abundance of the $i$th species expressed as a portion of the total cover

$\ln$: log base $e$

• Canopy area: $\frac{\pi (\text{canopy diameter 1} \times \text{canopy diameter 2})}{4}$

Detail regarding the statistical processing is provided in the research chapters below. Data analyses included descriptive statistics, parametric and non-parametric analyses of variance and randomisation t-tests, multivariate statistics (direct and indirect gradient analyses) and correlation analyses. Software used included PAST, SPSS, CANOCO and SigmaPlot (Kent, 2012).
CHAPTER 4

PATTERNS IN WOODY COMMUNITY COMPOSITION AND STRUCTURE AT REGIONAL SCALE

4.1 Objectives

The overall objective of this chapter is a description of general patterns in woody community composition and structure across all sampling sites (Table 1). This was done by (1) providing an overview of recorded species, their abundance distribution and measures of diversity, (2) describing the variability in a range of structural attributes of the woody layer and (3) analysing the distribution of sampling sites according to similarity in species composition and structural characteristics of the woody layer.

4.2 Statistical analysis

Descriptive statistics (SigmaPlot version 10.0) were used to summarise the variation in the data of the different attributes of the woody layer analysed. These included boxplots for identifying the mean, maximum and minimum values as well as histograms for summarising height class distribution (see Chapter 3) among all woody species and selected woody species. This was done to explain the growth form and population dynamics of the woody layer and the five most abundant species in the study area.

In order to analyse patterns in the vegetation samples based on woody species data, a Principal Components Analysis (PCA) was performed in PAST version 3.9, based on a variance-covariance matrix. Prior to analysis, rare species were omitted (occurrence in less than 10% of sampling sites) and species’ abundance values were normalised by fourth-root transformation. A second PCA of structural attributes of the woody vegetation layer (abundance of height classes/ha, bush density/ha, mean canopy area (m²), structural diversity, mean height, species richness, Shannon diversity and Shannon evenness) was performed based on a correlation
matrix, standardising the different data types. This was done to analyse the structural patterns of the woody layer sampled. Prior to analysis, input variables were tested for normal distribution and, if necessary, transformed; abundance data of height classes and bush density were square-root transformed and canopy area, structural diversity and bush density were log-transformed to create a normal distribution of the data matrix. The loadings between <0.3 and < 0.3 for each variable were considered in order to examine the relevance of a specific variable in describing the data distribution within in the PCA matrix.

4.3 Results

4.3.1 Woody species composition, diversity and distribution

In total, 19 woody species from 9 different families were recorded over 41 study sites (Table 2). The species richness over all the study sites ranged between 3 and 12 (Figure 5), with a median of 8 species. The data range in the Shannon evenness varied between 0 and 1 with a high median of 0.8, indicating an even species distribution across all the sampling sites (Figure 5). The Shannon diversity was fairly variable with a relatively high median of 1.66, which implies that a high abundance of a fair amount of woody species were recorded (Figure 5).

![Figure 5: Variability in species richness and Shannon indices. Boxplots refer to sampling sites (n = 41).](image)
The shrub *Grewia flava* was the most abundant and frequently observed species, followed by the major increaser species *Senegalia mellifera* subsp. *detinens* (Table 2). Two other frequently observed species were *Vachellia erioloba* and *Boscia albitrunca*, but at relatively low abundances (Table 2). All other species occurred with a mean density/ha below 60, including species commonly associated with sub-canopy habitats in denser vegetation, such as *Lycium* spp. and *Ziziphus mucronata* (Table 2).

The eigenvalue of the first ordination axis of 7.52 indicated that differences in the vegetation composition between the various plots of bush control and management actions were strongly correlated to the first axis (Figure 6).

The eastern study sites (ACG, BTG, ACK, HCK and BTK) formed a cluster on the right hand side of PC1 axis, separate from the western study sites (SBB, SB2B, BTB, PTO, HCO and HC2O), which formed a cluster on the left hand side of the PC1 axis of the Molopo study area (Figure 6). The bush-thickened (BT) sites clustered together in the top right-hand corner and chemically controlled sites (ACK, HCK and ACG) clustered in the bottom right-hand corner. The PCA revealed a gradual increase in abundance of the encroacher species *V. luederitzii* var. *luederitzii* (loading on PC1: 0.52113) in combination with a rapid increase in abundance of *G. flava* towards the bush-thickened sites (BTG). Encroacher species *Dichrostachys cinerea*, with the highest loading score (-0.64537) on PC2, and *S. mellifera* subsp. *detinens* increased in abundance within the study sites at HCK and ACK. The tree species *B. albitrunca* was strongly correlated to the non-selective controlled study sites in the eastern parts of the Molopo study area, whereas the tree species, *V. erioloba* was more strongly correlated to the selective bush controlled study sites in the western parts of the Molopo study area (Figure 6).
Table 2: Overview of woody species recorded across sampling sites (n = 41) and treatments. Species are listed in decreasing order of abundance (mean density/ha). Nomenclature follows Germishuizen and Meyer (2003).

<table>
<thead>
<tr>
<th>Species name</th>
<th>Growth form¹</th>
<th>Family name</th>
<th>Mean density/ha (±SE)</th>
<th>Relative frequency (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grewia flava</td>
<td>Shrub</td>
<td>Tiliaceae</td>
<td>225.96 ± 8.43</td>
<td>97.56</td>
</tr>
<tr>
<td>Senegalia mellifera subsp. detinens</td>
<td>Shrub</td>
<td>Fabaceae</td>
<td>179.77 ± 1.84</td>
<td>90.24</td>
</tr>
<tr>
<td>Vachellia luederitzii var. luederitzii</td>
<td>Tree</td>
<td>Fabaceae</td>
<td>62.29 ± 1.08</td>
<td>53.66</td>
</tr>
<tr>
<td>Vachellia erioloba</td>
<td>Tree</td>
<td>Fabaceae</td>
<td>57.32 ± 19.26</td>
<td>85.37</td>
</tr>
<tr>
<td>Boscia albitrunca</td>
<td>Tree</td>
<td>Capparaceae</td>
<td>51.31 ± 31.60</td>
<td>87.80</td>
</tr>
<tr>
<td>Dichrostachys cinerea</td>
<td>Shrub</td>
<td>Fabaceae</td>
<td>42.70 ± 7.33</td>
<td>31.71</td>
</tr>
<tr>
<td>Rhigozum brevispinosum</td>
<td>Shrub</td>
<td>Bignoniaceae</td>
<td>37.21 ± 1.09</td>
<td>17.07</td>
</tr>
<tr>
<td>Searsia tenuinervis</td>
<td>Shrub</td>
<td>Anacardiaceae</td>
<td>31.94 ± 19.23</td>
<td>39.02</td>
</tr>
<tr>
<td>Ehretia rigida</td>
<td>Shrub</td>
<td>Boraginaceae</td>
<td>31.79 ± 6.84</td>
<td>56.10</td>
</tr>
<tr>
<td>Lycium cinereum</td>
<td>Shrub</td>
<td>Solanaceae</td>
<td>29.05 ± 21.57</td>
<td>58.54</td>
</tr>
<tr>
<td>Grewia retinervis</td>
<td>Shrub</td>
<td>Tiliaceae</td>
<td>21.27 ± 6.22</td>
<td>39.02</td>
</tr>
<tr>
<td>Lycium hirsutum</td>
<td>Shrub</td>
<td>Solanaceae</td>
<td>10.59 ± 7.24</td>
<td>36.59</td>
</tr>
<tr>
<td>Ziziphus mucronata</td>
<td>Shrub</td>
<td>Rhamnaceae</td>
<td>6.63 ± 0.38</td>
<td>29.27</td>
</tr>
<tr>
<td>Cadaba aphylla</td>
<td>Shrub</td>
<td>Capparaceae</td>
<td>3.13 ± 2.68</td>
<td>19.51</td>
</tr>
<tr>
<td>Vachellia haematoxylon</td>
<td>Tree</td>
<td>Fabaceae</td>
<td>3.05 ± 26.52</td>
<td>7.32</td>
</tr>
<tr>
<td>Terminalia sericea</td>
<td>Tree</td>
<td>Combretaceae</td>
<td>2.21 ± 0.30</td>
<td>9.76</td>
</tr>
<tr>
<td>Vachellia hebeclada subsp. hebeclada</td>
<td>Shrub</td>
<td>Fabaceae</td>
<td>2.21 ± 13.31</td>
<td>12.20</td>
</tr>
<tr>
<td>Lycium echinatum</td>
<td>Shrub</td>
<td>Solanaceae</td>
<td>0.38 ± 1.15</td>
<td>2.44</td>
</tr>
<tr>
<td>Rhigozum trichotomum</td>
<td>Shrub</td>
<td>Bignoniaceae</td>
<td>0.30 ± 1.92</td>
<td>2.44</td>
</tr>
</tbody>
</table>

¹Growth form according to definition by Allen et al. (2011): shrub = woody plant having multiple stems arising at or near the base, mature height is generally <5–6 m; tree = woody plant characteristically with one primary stem from the base, mature height generally >5 m. Coppice growth on a tree may have multiple basal stems.
Figure 6: Principal Component Analysis (PCA) across all study sites based on a variance-covariance matrix with rare species omitted (occurrence in less than 10% of plots). Eigenvalues for PC1 = 7.52 and PC2 = 3.67; respectively % variance for PC1 = 33.14 and PC2 = 16.17. Non-selective chemically controlled by aircraft (light blue); selective chemically controlled by hand once (dark blue); selective hand chemically controlled by hand with reapplication (purple); selective control by stem burning with re-application (green); sustainably managed (black); partially bush thickened (light brown); bush thickened (dark brown).
Table 3: PC loadings of woody species. Bold loadings between <0.3 and <-0.3 are regarded as relevant in describing the variation in the principal component analysis (PCA) data matrix.

<table>
<thead>
<tr>
<th>Species</th>
<th>PC 1</th>
<th>PC 2</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Vachellia erioloba</em></td>
<td>-0.12421</td>
<td>0.0569</td>
</tr>
<tr>
<td><em>Vachellia hebeclada</em></td>
<td>-0.02179</td>
<td>0.11177</td>
</tr>
<tr>
<td><em>Vachellia luederitzii</em></td>
<td><strong>0.52113</strong></td>
<td>0.10547</td>
</tr>
<tr>
<td><em>Senegalia mellifera</em></td>
<td>0.18852</td>
<td>-0.13047</td>
</tr>
<tr>
<td><em>Boscia albitrunca</em></td>
<td>0.17279</td>
<td>-0.08722</td>
</tr>
<tr>
<td><em>Cadaba aphylla</em></td>
<td>-0.00896</td>
<td>-0.03264</td>
</tr>
<tr>
<td><em>Dichrostachys cinerea</em></td>
<td>0.22366</td>
<td><strong>-0.64537</strong></td>
</tr>
<tr>
<td><em>Ehretia rigida</em></td>
<td>0.36319</td>
<td>0.13721</td>
</tr>
<tr>
<td><em>Grewia flava</em></td>
<td>0.11091</td>
<td>0.085762</td>
</tr>
<tr>
<td><em>Grewia retinervis</em></td>
<td>0.29553</td>
<td><strong>-0.35942</strong></td>
</tr>
<tr>
<td><em>Lycium cinereum</em></td>
<td><strong>0.40362</strong></td>
<td>0.1081</td>
</tr>
<tr>
<td><em>Lycium hirsutum</em></td>
<td>-0.0824</td>
<td><strong>0.37924</strong></td>
</tr>
<tr>
<td><em>Rhigozum brevispinosum</em></td>
<td>0.19727</td>
<td>0.30042</td>
</tr>
<tr>
<td><em>Searsia tenuinervis</em></td>
<td><strong>0.32794</strong></td>
<td><strong>0.33029</strong></td>
</tr>
<tr>
<td><em>Ziziphus mucronata</em></td>
<td>0.20261</td>
<td>0.033297</td>
</tr>
</tbody>
</table>

4.3.2 Patterns in structural attributes of the woody layer

The mean height of the woody layer was 1.27 m, with the largest tree recorded at approximately 8 m (*V. erioloba*). The lower stratum of the woody layer (<2 m) appeared less variable in height (Figure 7a), indicating the presence of a regeneration layer in most of the sites. In contrast, there was much variation in the upper stratum (>2 m) as a consequence of chemically controlled larger woodies in some of the sites. Accordingly, the mean canopy area varied across study sites (Figure 7a), ranging between 1.99 m² and 14.57 m² on average. Structural diversity was found to have an average value of 1.28, with some sites showing very low values, corresponding to structurally poor, bush-controlled sites (Figure 7b). Bush density and tree equivalents (TE) were relatively variable, with an average abundance (per ha) of 825.80 and 634.47 respectively (Figure 8).
Figure 7: Variability in (a) the mean height of the woody layer for different height classes and mean canopy area and (b) structural diversity (Shannon diversity index) calculated based on the density of the height classes. Boxplots refer to sampling sites (n = 41).

Figure 8: Variability in bush density and tree equivalence (TE) per hectare across sampling sites (n = 41).

The overall height class distribution of sampled woody communities revealed a generally large number of small individuals, followed by medium-sized individuals, a typical reversed-J-shaped curve. Large individuals constituted a low proportion of the woody communities, particularly in the height classes >3 m (H5–6) (Figure 9).
Individuals of *G. flava* had the highest relative abundance within the height class >1–2 m (H3), with a low proportion of individuals reaching a height of 3 m (Figure 9). More than 50% of the recorded individuals of *S. mellifera* and *V. erioloba* were smaller than 0.5 m. With exception of *B. albitrunca* and *G. flava*, the most abundant species showed a relatively even proportional composition of height classes above 0.5 m.

A high relative abundance in bush density (per ha) of seedlings and saplings below 0.5 m created an J-shaped population structure (Figure 10). *Vachellia luederitzii* var. *luederitzii*, *V. erioloba* and *B. albitrunca* revealed a higher relative abundance in bush density (per ha) above the height of 3 m, with a reversed-J-shaped curve for *V. erioloba* population structure (Figure 10).
Figure 10: Height class distribution of the five most abundant woody species (compare to Table 2) across all study sites (n = 41).
Figure 11a: Principal component analysis (PCA) showing PC1 and PC2 of the structural attributes and height classes (height classes H1–6, bush density, canopy area, structural diversity, density, mean height, species richness, Shannon diversity and Shannon evenness), based on a correlation matrix. Eigenvalues for PC1 = 4.70 and PC2 = 3.10; % variance for PC1 = 36.17 and PC2 = 23.82. Non-selective chemically controlled by aircraft (light blue); selective chemically controlled by hand once (dark blue); selective hand chemically controlled by hand with reapplication (purple); selective control by stem burning with re-application (green); sustainably managed (black); partially bush thickened (light brown); bush thickened (dark brown).
Table 4: PC loadings of structural attributes and height classes. Bold loadings between <0.3 and <-0.3 are regarded as relevant in describing the variation in the principal component analysis (PCA) data matrix.

<table>
<thead>
<tr>
<th>Structural parameters</th>
<th>PC 1</th>
<th>PC 2</th>
<th>PC 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Height classes</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>H1 (≤0.5 m)</td>
<td>0.39137</td>
<td>-0.17078</td>
<td>0.15801</td>
</tr>
<tr>
<td>H2 (&gt;0.5–1 m)</td>
<td>0.41893</td>
<td>0.058881</td>
<td>-0.11977</td>
</tr>
<tr>
<td>H3 (&gt;1–2 m)</td>
<td>0.2247</td>
<td>0.32401</td>
<td>-0.36844</td>
</tr>
<tr>
<td>H4 (&gt;2–3 m)</td>
<td>0.068933</td>
<td>0.4564</td>
<td>-0.21078</td>
</tr>
<tr>
<td>H5 (&gt;3–5 m)</td>
<td>0.17319</td>
<td>0.26429</td>
<td>0.096001</td>
</tr>
<tr>
<td>H6 (&gt;5 m)</td>
<td>0.01109</td>
<td>0.13763</td>
<td>0.46801</td>
</tr>
<tr>
<td>Canopy area (m²; C-area)</td>
<td>-0.28843</td>
<td>0.23449</td>
<td>0.34469</td>
</tr>
<tr>
<td>Structural diversity (SDiv)</td>
<td>-0.06946</td>
<td>0.47922</td>
<td>-0.20232</td>
</tr>
<tr>
<td>Density (per ha)</td>
<td>0.43173</td>
<td>0.071686</td>
<td>-0.06987</td>
</tr>
<tr>
<td>Mean height (m; Height)</td>
<td>-0.26729</td>
<td>0.43085</td>
<td>-0.01106</td>
</tr>
<tr>
<td>Species richness (Richness)</td>
<td>0.39537</td>
<td>0.072029</td>
<td>0.16542</td>
</tr>
<tr>
<td>Shannon diversity (Shannon D)</td>
<td>0.28945</td>
<td>0.16668</td>
<td>0.39</td>
</tr>
<tr>
<td>Shannon evenness (Shannon E)</td>
<td>-0.00411</td>
<td>0.23857</td>
<td>0.45613</td>
</tr>
</tbody>
</table>

Figure 11a reveals a clear distinction between chemically control study sites (ACG, ACK, HC2O, HCO and HCK) and untreated study sites (BT, SM and PT) along PC1 axis, where BT sites were characterised by a high abundance of individuals from all height classes (H1–H6). In contrast, the non-selective chemically controlled by aircraft sites correlated to a high abundance of individual seedlings within height class H1 (Figure 11a). The sustainably managed (SMB) and partially thickened (PTO) sites grouped together because of high average height on the second PC (0.43085) and mean canopy diameter (Figure 11a).
Figure 11b: A principal component analysis (PCA) showing PC1 and PC2 of the structural attributes and height classes (Height classes 1–6, bush density, canopy area, structural diversity, density, mean height, species richness, Shannon diversity and Shannon evenness), based on a correlation matrix. Eigenvalues for PC1 = (4.70) and PC3 (2.21); % variance for PC = 36.17 and PC3 = 17.00. Non-selective chemically controlled by aircraft (light blue); selective chemically controlled by hand once (dark blue); selective hand chemically controlled by hand with reapplication (purple); selective control by stem burning with re-application (green); sustainably managed (black); partially bush thickened (light brown); bush thickened (dark brown).
Looking at the first and third PCs, a division could be made between non-selective aeroplane chemically controlled (ACG and ACK) and selective chemically controlled by hand sites (HC2O, HCO and HCK) in Figure 11b. Non-selective aeroplane chemically controlled sites group together because of a high Shannon diversity (0.39) and height class H6 (0.46801) on PC3 (Figure 11b). The cluster of selective chemically controlled by hand sites was strongly characterised by average height of the woody individuals and especially structural diversity (Figure 11b). The PCA revealed a positive correlation of bush density and species richness to the BT study sites. PTO and SMB sites were characterised by the greatest mean canopy area (m²) and average height (m) with a very weak correlation to woody individuals smaller than height class H3 (Figure 11b).

4.4 Discussion

4.4.1 Species composition and distribution

When comparing similar studies done in the semi-arid Kalahari region (e.g. Kgokosika et al., 2012), the average richness of shrubs and trees in this study was high, with 19 woody species recorded in all study sites. Sankaran et al. (2005) described the deep sandy soil in the Kalahari as favourable for woody vegetation establishment and growth, which lead to this high abundance of woody species recorded. A high Shannon evenness (0.8) implied that all of the species occurring within the selected study areas were fairly dominant and even in abundance. This means that lower species richness per study area was recorded with selected encroacher species dominating the system, as they outcompete other vegetation layers and woody individuals for available soil moisture and nutrients (Higgins et al., 2000; Sankaran et al., 2004). This is particularly true for arid savannas like in the Kalahari. These selected species included *Grewia flava, Senegalia mellifera, Vachellia erioloba and Boscia albitrunca* as they were the species with the highest relative abundance across all study sites.

Species richness and diversity indices were stronger related to BT sites due to a wide variety of species that were represented in all height classes (H1–6). Poorly structured controlled study sites resulted in the variability in species richness and diversity indices as certain height classes and selected species were removed. As the species richness and diversity indices varied across all study sites, the Shannon evenness remained stable, which implies that the species that did occur in that specific study area were equally dominant. This phenomenon is particularly present in both BT and controlled study areas.

*Grewia flava* had the highest mean density and was the most frequently observed. This species is not targeted by selective bush thinning practices, which explains its common
occurrence across sampling sites and treatments, respectively. Another increaser species that was also fairly frequently observed across all study sites was the tree species *V. erioloba*. According to the PCA ordination regarding species richness, this species was more strongly related to selective chemically control by hand (HC) and stem burning (SB) as it is a protected species, it was also not targeted through bush thinning practices.

On the other hand, *S. mellifera* subsp. *detinens* and *V. luederitzii* var. *luederitzii*, contributing significantly to the bush-thickening phenomenon (Smit, 2004; O’Connor et al., 2014; Hoffman & O’Connor, 1999), was fairly frequently observed in high abundances across all study sites, which means that these species recovered in abundance after bush control measures were implemented. *Senegalia mellifera* subsp. *detinens* and *V. luederitzii* var. *luederitzii* produce large amounts of seeds (Joubert et al., 2013; Donaldson, 1969), which increases their ability to establish in high abundances in open spaces. According to Smit (2004) and Joubert et al. (2013), this phenomenon happens seldom (Donaldson, 1969) as a minimum of two consecutive good rainfall seasons are needed for these woody seedlings to establish and grow. The competition for soil moisture from other vegetation layers also needs to be lowered for the abovementioned woody species to be superior competitors for available soil moisture. In this case, the non-selective control of woody vegetation, which created open gaps with less competition from other woody species, in combination with the prescribed conditions from Joubert et al. (2013) ultimately resulted in the formation of a demographic-bottleneck of both *S. mellifera* subsp. *detinens* and *V. luederitzii* var. *luederitzii*. The fact that some BT stands were mono-dominant, with *S. mellifera* subsp. *detinens* and *V. luederitzii* var. *luederitzii* being the same height, contributes to the assumption that a demographic-bottleneck occurred with these species. This also reduced the structural diversity of the study area as it was dominated by a dense stand of *S. mellifera* subsp. *detinens* of the same age and height.

Several selected species like *Cadaba aphylla*, *Lycium echinatum*, *Rhigozum brevispinosum*, *R. trichotomum*, *Terminalia sericea*, *Vachellia haematoxylon*, *V. hebeclada* subsp. *hebeclada*, and *Ziziphus mucronata* were observed less than 30% of the time spent on the field survey. They were also more strongly related to BT sites, which means that they were not able to recover after bush-thinning practices have been implemented as encroacher species outcompeted them for available soil moisture.

### 4.4.2 Structural parameters

The PCA ordination of the structural attributes of the woody layer revealed a clear distinction between the HC sites in the eastern regions and the AC sites in the western regions of the
Molopo study area according to species richness. This difference in species richness is management-related as the farmer in the east, who made use of selective hand control methods, re-treated the study area 12 years after the first chemical application, only treating the increaser woody species *S. mellifera* subsp. *detinens*, *Vachellia luederitzii* var. *luederitzii*, *D. cinerea* and *R. trichotomum*. This resulted in species-poor and open savanna area, decreasing the structural diversity in comparison with the area that was treated non-selectively with chemicals once in the west. Smit (2004) suggested that woody individuals in an open savanna, like the one artificially created in the east, outcompete the regrowth woody generation for available soil moisture. This showed that the selective bush control approach to be more sustainable than the non-selective approach, which leads to the regrowth of the woody layer that will ultimately lead to bush thickening.

Along the first component of the PCA regarding woody structural attributes, species richness, Shannon diversity and density increased towards the BT sites, i.e. the denser the sites, the more species were present. BT sites were mixed, not species poor and with no particular species dominating the area. This showed BT sites as not yet being impenetrable, but still remaining fairly open to the establishment of new woody individuals.

Cluster formation among different treatments occurred within the PCA ordination regarding structural attributes. HC and SB sites, where follow-up treatments were implemented, clustered as they were characterised by a low structural diversity and high average height and mean canopy diameter. Several untreated species that were dominant in these sites, like *V. erioloba* and *B. albitrunca*, were in their mature stages as they represent a large average canopy diameter and broad DBH. These sites were classified as open savannas due to the re-application of selective bush-control techniques.

AC sites were mainly characterised by woody seedlings falling within height class H1 (≤0.5 m). This non-selective bush control method resulted in poorly structured woodland as all height classes have been removed. The occurrence of only height class H1 can be ascribed to the removal of competition with all other height classes for available soil moisture. This formed open spaces (Kgosikoma et al., 2012; Trollope, 1980), which resulted in the appearance of a regeneration layer of thickening woody species.
CHAPTER 5
SHORT-TERM RESPONSES IN WOODY VEGETATION TO SELECTIVE AND NON-SELECTIVE CHEMICAL BUSH CONTROL WITH SPECIAL REFERENCE TO SELECTED KEY SPECIES

5.1 Introduction

As mentioned, bush thickening is a serious problem in semi-arid savannas as the herbaceous layer is outcompeted by the woody layer for available soil moisture and nutrients (Ward, 2005; Smit, 2004; Kgosikoma et al., 2012). In an attempt to restore the herbaceous layer, land owners implement different bush-thinning practices (Smit & Goodman, 1986), which include both selective bush control measures (where only selected woody species are treated by hand chemical application) and non-selective measures (where all woody species are treated by means of chemical application via aeroplane). These practices result in disturbed, open areas, altering ecosystem function, processes and resilience as well as the structure of the woody vegetation layer, as new ecosystems are created over time (Berhane et al., 2015).

In turn, woody vegetation responds differently after bush thinning practices were implemented, as the post-control environment is redesigned (Smit, 2004). Seed dispersal, seed dormancy, seed germination, establishment and competition from other vegetation layers for available nutrients are key aspects in the initial stages of the post-control environment (Midgley & Bond, 2001). Dispersed seeds away from the mother plant have a higher rate of establishment (Midgley & Bond, 2001) as they do not have to compete with the mother plant for light, soil moisture and nutrients. Predation activities on seeds are also concentrated under the mother plant, where resources are abundant. The dispersed seeds therefore have a higher chance of survival as they avoid predation (Wilson & Travest, 2000).
Ernst et al. (1990) elaborated on the difference between *Senegalia* and *Vachellia* mortality of <10% (*Senegalia mellifera*) and >60% (*Vachellia erioloba*) caused by predation of bruchid beetles on the seeds of these woody species because of their poor dispersal mechanisms. Seed dormancy of *Vachellia* and *Senegalia* species is transient as germination events are rarely observed in these semi-arid environments (Joubert et al., 2008, 2013). Research by Smit (2004), Kraaij and Ward (2006) and Joubert et al. (2008, 2013) stated that a minimum of two to three consecutive good rainfall seasons will encourage the successful establishment of *S. mellifera*.

Fire also contributes to the germination of several *Vachellia* and *Senegalia* species (Sabiti & Wein, 1987), but since fire is not a frequent event in semi-arid savannas, regular rainfall for at least seven weeks is necessary for seed germination followed by establishment (Wilson & Witkowski, 1998). Seed germination and establishment however occur very seldom in arid savannas because of the erratic rainfall pattern (Joubert et al., 2008). When favourable conditions occur, seed germination follows and woody plants develop vast root systems, which enable them to utilise moisture trapped in deeper soil layers (Ingrouille & Eddie, 2006; Ward et al., 2013). As soon as germination and establishment occur simultaneously, a dominant layer of evenly aged woody vegetation is created, which then outcompetes the herbaceous layer for available soil moisture and nutrients (Higgins et al., 2010; Sankaran et al., 2004). These findings describe the reason for woody vegetation layers being poorly structured after it has been disturbed in semi-arid savannas (Joubert et al., 2008, 2013; Smit, 2004; Midgley & Bond, 2001).

In this study, key woody species were selected as woody species with the highest abundance in the study area, which were also heavily affected by bush control measures. These species are also regarded as high in ecological value as it contributes to biodiversity. These include *Grewia flava*, *Boscia albitrunca*, *S. mellifera*, *V. erioloba* and *V. luederitzii*. *Senegalia mellifera* which produces large amounts of seeds, and after ripening and fall off underneath the canopy of mother plants during the middle of November and beginning of December (early rainy season in the study area) (Donaldson, 1969; Joubert et al., 2013).

The fleshy-fruited *G. flava* depends on biotic seed dispersal mechanisms including birds and mammals to ensure not only germination, but successful recruitment and survival of these individuals (Tews et al., 2004). Shrub thickening of *G. flava* in southern Kalahari savannas is mainly caused by larger ungulates like cattle that browse the seeds, contributing to the increased dispersal of the species through the dung (Tews et al., 2004). Sub-canopy environments of other woody individuals, especially *Vachellia* and *Senegalia* species, with sufficient precipitation and removal of competition from other vegetation layers contribute to
the successful long-term survival of these perennial shrubs (Dean et al., 1999; Twes et al., 2004).

The seedlings of *V. erioloba* have a slow growing rate above ground level for the first four to five years (Barnes, 2001). During this establishment phase, seedlings are threatened by browsing ungulates such as elephants, giraffe and impala (Belsky, 1984; Barnes, 2001) because they are favoured as a fodder resource. The successful establishment of *V. erioloba* seedlings lies in their ability to grow an extensive tap root system into deeper soil layers, where water is a permanent resource (Barnes, 2001). Timberlake (1980) recorded this root system to exceed 40 m in length. *Vachellia erioloba* and *S. mellifera* have another competitive advantage as these species use stored energy to produce new shoots, leaves and flowers during the dry season while other species remain dormant (Barnes, 2001).

Pendota et al. (2016) stated that seed germination of *B. albitrunca* happens fairly quickly in arid environments, but the establishment and survival of seedling is relatively unsuccessful, with only 27% of individuals achieving maturity (Briers, 1988, as cited by Pendota et al., 2016). Furthermore, because of this species’ palatability, seedlings are subjected to browsing, trampling and harvesting, which decrease the sustainable establishment and growth of *B. albitrunca* (Pendota et al., 2016).

Many studies have aimed to determine the effect of tree thinning or clearing on savannas and how herbaceous plants would react to reduced competition from woody plants (Moore & Odendaal, 1987; Harrington & Johns, 1990; Richter, 1991). The reproductive ability, re-establishment and growth dynamics of the remaining woody individuals have, however, rarely been investigated in any detail (Smit et al., 1996). Smit (2014) and Smith and Goodman (1986) suggested that there is still a lack of scientific information regarding the long-term ecological impacts of tree-thinning practices conducted by man or caused by herbivory and fire (Smith & Goodman, 1986) occurring in savanna ecosystems.

In this study, the following two main questions were asked: (1) How does the woody layer in a semi-arid savanna ecosystem respond to selective and non-selective chemical bush control? (2) What is the population structure and regeneration status of selected woody species in the post-control environments of selectively and non-selectively chemically controlled savanna rangelands? To answer these questions, the following data were gathered: (1) an overview of the composition, diversity and abundance patterns of selected key species and (2) the variability in a range of structural attributes of the woody layer, referring to these key species. The hypothesis is that the post-control environment of non-selective chemical bush control by aeroplane (AC) includes a mono-aged woody recruitment layer, dominated by seedlings of *S. mellifera*, *V. erioloba* and *V. luederitzii*, with scattered
mature individuals of *B. albitrunca*. No significant differences in structural diversity and species composition when comparing bush-thickened sites (BT) with selectively hand controlled (HC) sites are also predicted.

5.2 Materials and methods

Refer to Chapter 2 for general description of the study area, including the location, land use, climate, geology and soils and dominant vegetation of the Molopo Bushveld vegetation type. Chapter 3 provides a general background of the selected study sites (Table 1), as well as the sampling approach, general methods and data analysis.

5.2.1 Site selection

This study design included a total of eight AC sites, eight HC sites and eight BT sites (Table 5). All study sites are thoroughly discussed in Chapter 3 (Table 1). BT sites were included as they represent a benchmark of the pre-controlled environment. All of these BT sites fell within the same rainfall gradient and had not been influenced by specific management regimes implemented by the respective farmers. Thus their respective structural attributes and species compositions were homogenous.

Table 5: The number of sites selected within each treatment on respective farms.

<table>
<thead>
<tr>
<th>Non-selective bush control</th>
<th>Bush thickened</th>
<th>Selective bush control</th>
</tr>
</thead>
<tbody>
<tr>
<td>AC: Four sampling sites on Omega farm</td>
<td>BT: Four sampling sites on Omega farm</td>
<td>HC: Four sampling sites on Jones &amp; De Klerk farm</td>
</tr>
<tr>
<td>AC: Four sampling sites on Wilzenau farm</td>
<td>BT: Four sampling sites on Wilzenau farm</td>
<td>HC: Four sampling sites on Wilzenau farm</td>
</tr>
<tr>
<td>Total AC = 8</td>
<td>Total BT = 8</td>
<td>Total HC = 8</td>
</tr>
</tbody>
</table>

AC: non-selective chemically controlled by aircraft; HC: selectively chemically controlled by hand once; BT: bush thickened.

5.2.2 Statistical analysis

A Correspondence Analysis (CA) was used (the CANOCO programme; Ter Braak, 1992) to identify any correspondence between the different treatments and structural parameters (mean canopy area, mean height, structural diversity, TE/ha and density/ha). Descriptive statistics (Microsoft Excel 2010) were used to describe the species composition and abundance patterns of selected key species subjected to the AC, HC and BT treatments. The relative abundance of woody species for AC, HC and BT sites were compared in a bar chart in order to investigate structural differences in the post-controlled environment in each height class (H1–6) examined. The species-specific response patterns within each height
class of the post-controlled environment were analysed in Microsoft Excel 2010 and STATISTICA (version 10) (StatSoft, Inc., 2011), with the results shown in a bar chart. Woody structural parameters such as height class distribution were used to execute an ANOVA test in STATISTICA (version 10) (StatSoft, Inc., 2011) to indicate statistically significant differences (p<0.05) between AC, HC and BT sites, with special reference to five selected key species. Owing to a lack of adequate amounts of data, the non-parametric alternative of ANOVA, namely the Kruskal-Wallis test, was used to evaluate the structural diversity, mean height, TE and species richness in the different bush control sites.

5. 3 Results

5.3.1 Species composition, diversity and abundance patterns

According to the CA ordination, distinct groupings were recognised according to the species composition and structural data of HC, AC and BT sites. The CA ordination provided evidence that distinct groupings for the different treatments could be distinguished and that AC and BT sites were the least similar regarding structural parameters, especially according to axis 2 of the ordination shown in Figure 12.

5.3.2 Structure of woody vegetation layer

The ANOVA indicated significant differences in the height class distribution, when comparing AC, HC and BT sites. No significant differences were recorded in the ≤0.5 m (H1) and >5 m (H6) height classes between the different treatments (Table 6). All three treatments revealed significant differences in the height classes >0.5–1 m (H2), >1–2 m (H3), >2–3 m (H4) and >3–5m (H5) (Table 6).

Table 6: Analysis of variance comparing abundance of individuals in different height classes, indicating significant differences, with p <0.05, in red.

<table>
<thead>
<tr>
<th>Height classes</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>H1: ≤ 0.5 m</td>
<td>0.077</td>
</tr>
<tr>
<td>H2: &gt;0.5–1 m</td>
<td>0.001</td>
</tr>
<tr>
<td>H3: &gt;1–2 m</td>
<td>0.000</td>
</tr>
<tr>
<td>H4: &gt;2–3 m</td>
<td>0.000</td>
</tr>
<tr>
<td>H5: &gt;3–5 m</td>
<td>0.001</td>
</tr>
<tr>
<td>H6: &gt;5 m</td>
<td>0.082</td>
</tr>
</tbody>
</table>
The poorly structured woody layer of the AC sites encompassed the heights abundance of woody recruits (≤0.5m) (Figure 13). This was also supported by the low mean height of the woody species at the AC sites (Figure 13). The higher mean height of woody species identified in the HC sites (Figure 17) was a result of the high abundance of individuals of height class H3 (>1–2m) (Figure 13).

The abundance of woody individuals within each height class was compared between the two different controlled sites and the BT sites (Figure 13). BT and AC sites had the highest number of seedlings (height class H1, ≤0.5 m), whereas the dominant height of the woody species was found in height classes H3 (>1–2 m) for the HC treatment (Figure 13). Woody
species in height classes H4 and H5 (>2–3 m and >3–5 m) were the most abundant in the BT sites (Figure 13). Very few woody individuals occurred in the >5 m height class for both AC and BT sites and no such large individuals occurred in HC sites (Figure 13).

![Figure 13: Bar chart comparing the relative abundance of woody individuals in each height class. Tukey-HSD test *p <0.05 for BT vs. AC and HC sites in height class >0.5–1 m, >2–3 m and >3–5 m; *p <0.05 comparing AC and HC sites as well as the BT site for height class >1–2 m.](image)

ANOVA revealed significant differences (p <0.05) within the structural data of the woody vegetation layer when comparing AC, HC and BT sites (Table 7).

**Table 7**: Analysis of variance comparing structural parameters of different bush control treatments, indicating significant differences with p <0.05 in red.

<table>
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<td>TE/ha</td>
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<tr>
<td>Mean height</td>
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<tr>
<td>Structural diversity</td>
<td>0.000</td>
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<tr>
<td>Species richness</td>
<td>0.001</td>
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</table>
Figure 14: Comparison of mean species richness between bush-thickened (BT), non-selective control (AC) and selective control (HC) sites. Kruskal-Wallis test *p < 0.05 for HC and BT sites as well as for AC and BT sites.

Figure 15: Comparison of structural diversity bush-thickened (BT), non-selective control (AC) and selective control (HC) sites. Kruskal-Wallis test *p < 0.05 for HC and BT sites and *p < 0.1 for AC and HC sites.
Figure 16: Comparison of TE/ha between bush-thickened (BT), non-selective control (AC) and selective control (HC) sites. Kruskal-Wallis test *p <0.05 for HC and BT sites.

Figure 17: Comparison of mean height between bush-thickened (BT), non-selective control (AC) and selective control (HC) sites. Kruskal-Wallis test *p <0.05 for HC and BT sites and *p <0.1 for HC and AC sites.
BT sites had the highest species richness, structural diversity, TE/ha and mean height compared to both the AC and HC sites (Figures 14–17). There was no significant difference between AC and HC sites regarding species richness (Figure 14).

Significant differences in TE/ha, structural diversity, mean height and species richness (p<0.05) were observed, when comparing BT sites to AC sites (Figures 15, 16 and 17). The species richness differs significantly between HC sites compared to BT sites and also between AC sites compared to BT sites p<0.05 (Figure 14). Differences were observed between AC and HC sites with regards to structural diversity and mean height, at a p <0.1 significance level (Figures 15 & 17). HC sites represented a better structured woody layer supported by higher TE and mean height than AC sites (Figure 16, 17).

5.3.3 Species-specific response Patterns

Figure 18a: Bar chart comparing the abundance of *V. erioloba* individuals allocated in each height class. No significant differences according to Tukey-HSD test *p* <0.05.
**Figure 18b**: Bar chart comparing the abundance of *B. albitrunca* individuals allocated in each height class. Tukey-HSD test showed *p < 0.05 for BT vs. AC sites in height class >0.5 to 1 m.

**Figure 18c**: Bar chart comparing the abundance of *G. flava* individuals allocated in each height class. Tukey-HSD test *P < 0.05 for BT sites vs. HC sites in height class ≤0.5 m; *p < 0.05 comparing AC to BT and HC sites for height class >1 to 2 m; *p < 0.05 comparing AC and HC sites in height class >2 to 3 m.
Figure 18d: Bar chart comparing the abundance of *Senegalia mellifera* individuals allocated in each height class. Tukey-HSD test *P <0.05 for BT vs. AC sites in height class >1 to 2 m; "p <0.05 comparing AC and HC sites with the BT sites for height class >2 to 3 m.

Figure 18e: Bar chart comparing the abundance of *Vachellia luederitzii* individuals allocated in each height class. Tukey-HSD test "p <0.05 for BT vs. AC and HC sites in height classes >2 to 3 m and >3 to 5 m.
The species abundance patterns within different height classes for the five selected key species were assessed. Overall, *V. erioloba*, *B. albitrunca* and *S. mellifera* represented the height abundance of individuals in the height class ≤0.5 m across all three treatments (Figure 18a, 18b, 18d).

AC sites had a dominant layer of *V. luederitzii* and *S. mellifera* recruits (≤0.5 m) (Figures 21 & 22), whereas *V. erioloba* and *B. albitrunca* revealed a higher abundance of seedlings (≤0.5 m) in the HC site (Figures 18 & 19). A well-established structural diversity in the BT sites were developed by the selected species in the HC sites, i.e. *V. luederitzii* and *S. mellifera*. The regeneration layer of these two species differed in abundance between AC and HC sites (Figures 21 & 22).

*Grewia flava* showed a high abundance of mature shrubs in height class of >1–2 m, especially for HC and BT sites (Figure 20). No *G. flava* individuals were recorded in the 3–5 m height class, as the natural growth form does not exceed 3 m (Figure 20).

Significant variation in the height class distribution when comparing selected key woody species was recorded (p <0.05) (Table 8). These significant differences were identified with regards to height class distribution data, when *S. mellifera* was compared with *B. albitrunca* and when *G. flava* was compared with *B. albitrunca* (Table 8).

**Table 8**: Analysis of variance comparing abundance patterns of five selected species distributed over different height classes, indicating significant differences with p <0.05 in red.

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<th>(3)</th>
<th>(4)</th>
<th>(5)</th>
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<td>0.1551</td>
<td>0.2245</td>
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<td>0.9999</td>
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<td><em>Boscia albitrunca</em> (3)</td>
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<td></td>
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<tr>
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<td>0.9999</td>
<td>0.0285</td>
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<td><em>Vachellia erioloba</em> (5)</td>
<td>0.2245</td>
<td>0.9991</td>
<td>0.0876</td>
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</tr>
</tbody>
</table>

5.4 Discussion

5.4.1 Response patterns of the woody vegetation in a post chemically controlled environment

Non-selective chemical bush control by aeroplane application (AC) targets all woody species susceptible to the arboricide used, leaving bare ground patches with little vegetation (Smit et al., 1996). The woody vegetation layer responded after the non-selective application by the recruitment of a high number of woody seedlings (≤0.5m) after 12 years of application. This
resulted in a poorly structured woody layer with a low mean height in woody canopy cover. The regeneration layer was dominated by woody encroacher species, such as *S. mellifera* subsp. *detinens*, *V. luederitzii* var. *luederitzii* and the protected tree species, *V. erioloba*.

It therefore seems that mature woody individuals established a proper seed bank, which was kept dormant in the soil over a period of at least 2–4 years (Joubert et al., 2008), outcompeting the recruitment of seedlings (Smit, 2004; Joubert et al., 2013). When the competition was removed by AC treatment (Smith & Goodman, 1986), seeds were able to utilise resources such as soil moisture and nutrients in order to establish saplings contributing to the high recruitment ratio. As predicted, a dominant layer of woody saplings (≤0.5m) was the result of favourable conditions for the woody regeneration layer to establish (Smit, 2004; Donaldson, 1969; Moleele et al., 2002; Joubert et al., 2013).

Species richness results revealed significant differences between BT and AC sites, as the richness declined after bush-thinning practices were implemented. This indicated that not all woody species were able to recover, as their competitive ability was less than that of encroacher species. It seems that *Senegalia mellifera* subsp. *detinens* and *V. luederitzii* var. *luederitzii* were better competitors for soil moisture and available resources because of the mono-species dominated post-control environment of the AC sites (O’Connor et al., 2014; Hoffman & O’Connor, 1999). This finding supports the hypothesis of this chapter.

During selective chemical bush control by hand application (HC), mostly encroacher species such as *S. mellifera* subsp. *detinens*, *Rhigozum trichotomum*, *S. hebeclada* subsp. *hebeclada* and *V. luederitzii* var. *luederitzii* were targeted, decreasing their competitive ability and causing an increase in density of other, already established woody individuals that can utilise extra available soil moisture and nutrient resources. Pielou (1962, as cited by Smith & Goodman, 2001) discovered similar response patterns in that if one or two woody species are removed, the growth of the remaining species will be enhanced and the seed bank of the removed species will remain dormant. Pielou (1962) further concluded that the distance between two plants determines the intensity of competition for available soil moisture and nutrients. In this case, the remaining woody species that were not targeted by the HC treatment, was *G. flava*, especially in the height class >1 to 2 m.

The post-controlled environment in the HC sites revealed a better structured woody vegetation layer than for the AC sites, as a higher TE/ha and mean height were recorded in the HC sites. A recruitment layer containing *V. erioloba* and *B. albitruncata* individuals were also observed in abundance in the post HC treatment environments. These species are, however, not targeted
by bush-thinning practices, but are protected by the land user. Thus the second hypothesis of this chapter is therefore accepted, in that the structural attributes of the HC and BT sites remain similar.
CHAPTER 6

CONCLUSION AND RECOMMENDATIONS

6.1 Conclusion

Different bush control measures have different impacts on the structure and composition of the woody vegetation layers of savannas in the study sites of Molopo Bushveld vegetation type, as different response patterns were recognised in the post-controlled woody environments. Less intensively selective control measures (HC & SB) result in species-rich, better-structured and open savannas, as a variety of different height classes amongst woody species were recognised. More intensively non-selective control measures (AC), on the other hand, resulted in poorly structured open savanna with scattered individuals of Boscia albitrunca. After approximately 4 to 6 years of favourable conditions for woody germination and recruitment, the post-control environment transformed into a closed woodland dominated by a woody layer of increasing woody species saplings of lower height classes (<0.5 m), on account of initially losing large trees.

With the loss of large, mature trees, competition in the surrounding area is decreased, leaving bare patches with available soil moisture and nutrients. In semi-arid environments, such as the semi-arid Molopo bushveld, available soil moisture is the limiting factor for vegetation establishment and growth. The seeds of increaser woody species utilise this previously unavailable soil moisture and nutrients, which then leads to germination. Germination and establishment of increaser species including Senegalia mellifera subsp. detinens and Vachellia luederitzii var. luederitzii follows with favourable environmental conditions and outcompete other woody species, as well as the herbaceous layer, for available soil moisture and nutrients because of their ability to germinate quickly, complimented by a superior competitive growth regime.

The sustainability of a non-selective chemical control measure therefore relies on re-treatment of the regenerative increaser woody layer after several years in order to remove well-established, reproductive woody increaser species dominating the post-control environment. Several retreatments will ultimately result in open grasslands.
During selective chemical bush control (HC), certain encroacher tree and shrub species are removed. This post-control environment is complimented by a better-structured woody layer, with higher TE/ha and mean height of favourable woody species compared to that resulting from intensively non-selective bush control techniques (AC). Mature woody individuals such as V. erioloba and G. flava trees and shrubs are not removed, which prevents a sustainable well-structured, open savanna from transforming into a mono-species dominated, species-poor, closed woodland. These mature individuals also prevent the increaser woody species’ seed bank from establishing, as they outcompete seedlings for available soil moisture and nutrients. The increaser species S. mellifera subsp. detinens and V. luederitzii var. luederitzii seedlings’ relative abundance were much lower in the post-controlled environment of HC sites compared to that in BT and AC sites. After one selective chemical application, a stable, well-structured woody vegetation layer has been achieved, and thus does not require intensive follow-up treatment for the removal of a few remaining individual increaser woody species. A sustainable, stable, open savanna is achieved much faster following less intensively selective bush control techniques, compared to more intensively, non-selective bush control techniques.

Bush control measures are management-related, where the cattle farmer strives to construct an open savanna dominated by a grass layer with scattered mature woody individuals using selective chemical control measures (HC). The game farmer involved in the study design, on the other hand, aims to create open grassland patches with only scattered B. albitrunca individuals, complimented by closed woodland areas representing a species-diverse woody vegetation layer for a variety of browser species, using non-selective control measures (AC). Both of these management regimes strives to restore the herbaceous layer, but the selective control approach (HC) resulted in a restored, balanced and stable woody:grass ratio, whereas the non-selective approach (AC) resulted in an open grassland with minimal woody individuals. According to Smit (2004), the most sustainable approach is the selective bush control approach (HC & SB), as mature woody individuals within the open savanna will be superior competitors for available soil moisture, keeping the regeneration layer of selected increaser woody species such as S. mellifera subsp. detinens and V. luederitzii var. luederitzii from establishing and transforming the open savanna into a mono-species dominated woodland.

6.2 Recommendations for further studies

Several farmers do not favour chemical bush control measures, as they believe that these chemicals accumulate in deeper soil layers, which will later be utilised by larger trees susceptible to the arboricide. As an alternative, labour intensive stem burning measures are implemented in order to address the bush thickening phenomenon. Recommendations for future
studies include: (1) testing different depths of soil layers for active Tebuthiuron-based arboricides that could have leached into deeper soil layers, (2) measuring the effect on available nutrients and soil moisture utilised by woody species in the Molopo region at different soil depths; (3) carry out a comparative analysis between chemically treated areas and non-chemically treated areas outside the study area.

One particular species, *Grewia flava*, revealed significant response patterns in the HC sites in both a number and size increase in the post-controlled environment. Very few studies have been conducted on the growth response patterns of this particular species after different bush control measures have been implemented. Recommendations for future studies would be to assess the structural response patterns of *G. flava* after the implementation of different bush control measures. The ecological value of *G. flava* to both the environment and the farmer also needs to be assessed to determine the importance of this species.

During non-selective chemical bush control, the arboricide is applied to all woody species by means of an aeroplane. One particular protected tree species, *Boscia albitrunca*, occurs in abundance in the Molopo region and is also treated with arboricides during the non-selective application process. In the short term this species shows no side effects to the arboricides, but monitoring the response patterns of this species in the long term have not yet been attempted.

In conclusion, the first hypothesis of the study, stipulating that bush control techniques result in differently structured post-controlled environments is accepted, based on the results and study design. The second hypothesis of this study, stipulating that the non-selective bush control sites poses a greater threat of re-thickening than selective bush controlled sites is partially accepted, based on the findings captured in this thesis.
CHAPTER 7

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Table A 1: Structural data of the specific sampling sites on the farm Omega.

<table>
<thead>
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<td>Height <em>Dichrostachys cinerea</em></td>
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Table A 3: Structural data of the specific sampling sites on the farm Lafras.

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Table A 4: Structural data of the specific sampling sites on the farm Jones & De Klerk.

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Table A 5: Specific location of all sampled sites, as well as their respective bush density.

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<th>GPS-Belt 2</th>
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</table>
Figure A1: Basic sampling approach included a 100m measuring tape; 2m poles marked every 0.1m used for measuring the canopy diameter as well as height of the woody individual and a ruler to measure the DBH (diameter at breast height).
Figure A2: Illustration of the bush encroached sites (BE)

Figure A3: Illustration of the aeroplane chemical controlled sites (AC).
**Figure A4**: Illustration of the hand chemical controlled sites with a follow-up treatment (HC2).

**Figure A5**: Illustration of the hand chemical controlled sites with one application (HC).
**Figure A6**: Illustration of the stem burned controlled sites with a follow-up treatment (SB2).

**Figure A7**: Illustration of sustainably managed sites (SM).