EFFECTS OF VARIOUS MANAGEMENT CONTROL MEASURES ON SEASONAL LEAF QUALITY OF *COLOPHOSPERMUM MOPANE* AND *TRAGELAPHUS STREPSICEROS* BROWSE OF *C. MOPANE,* LIMPOPO PROVINCE, SOUTH AFRICA

by

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ABSTRACT

Colophospermum mopane (Benth.) J. Léonard, commonly known as mopane, is a dominant tree or shrub in the mopane woodland. It is distributed in the low-lying areas of southern Africa's savannas. Mopane maintains its foliage well into the dry season, and thus provides nutritional forage for browsers such as *Tragelaphus strepsiceros*, commonly known as the greater kudu. Despite its wide distribution and value as a source of forage for browsers, especially during the dry season, knowledge of the effect of browsers on mopane leaf quality is limited. There is also inadequate knowledge of the diet composition of the greater kudu during different seasons in the mopane woodland. Such information is important for proper management of browsers in the mopane woodland.

As a result, a field experiment was conducted at Musina Nature Reserve, Limpopo Province, South Africa to determine the effect of pruning on mopane leaf phenology, production, macronutrients, trace elements and secondary metabolites. Pruning was conducted to simulate the effect of browsing by large herbivores such as the greater kudu on mopane leaf quality. In addition, rumen content analysis of greater kudu was conducted in order to quantify the amount of mopane and other plants browsed during the dry and wet seasons. Collected datasets were analysed using descriptive and inferential statistics. A two-tailed Mann-Whitney U-test was used to test the effect of pruning on mopane leaf phenology and production. The effect of pruning on the monthly concentration of macronutrients, trace elements and secondary metabolites was tested using a two-tailed t-Test: Two-Sample Assuming Equal Variance. The seasonal and annual effect of pruning on the concentration of macronutrients, trace elements and secondary metabolites was tested using One-Way Anova. Rumen datasets were analysed using the Pearson Correlation Coefficient.

This study found that the rate of leaf phenology and production, including the concentration of certain macronutrients (Ca, K, N, P, S, Cl, Na, protein and fibre), trace elements (Fe, Mn, Mo, Cu, Zn and Se) and secondary metabolites (TP, CT and PPT) increased during leaf flush in October and then declined as the leaves

matured and aged. However, the concentration of selected macronutrients (Mg and NO_3) and trace elements (B, Co and F) increased when the leaves reached maturity in June, particularly during the leaf senescence stage, and declined thereafter. The concentration of macronutrients, trace elements and secondary metabolites between the control and pruned trees was statistically insignificant at $P>0.05$ for most samples.

This study further showed that *C. mopane* contributed most (47%) to the diet of the greater kudu during the dry season. Other important dry season browse plants were *Dichrostachys cinerea* (30%), *Commiphora edulis* (12%), *Grewia bicolor* (6%) and *Combretum apiculatum* (5%). However, when gender was considered, the diet of the female greater kudu during the dry season consisted mainly of *C. mopane* (71%) and *D. cinerea* (22%). The diet of the male greater kudu contained less *C. mopane* (33%), but similar proportions of *D. cinerea* (31%) and other browse species. However, during the wet season, the diet of the greater kudu was mainly composed of *C. apiculatum* (43%). Other wet season browse plant species were *Sclerocarya birrea* (24%), *C. mopane* (12%) and *Senegalia nigrescens* (8%), with the contribution of the remaining species to the diet being insignificant. The diet of the female greater kudu in the wet season consisted mainly of *C. apiculatum* (44%) and *C. mopane* (20%), while the diet of the male mostly contained *S. birrea* (38%) and *C. apiculatum* (34%).

It is concluded that the concentration of macronutrients, trace elements and secondary metabolites in mopane leaves is not dependent on <10% pruning, but seems to be associated with leaf growth stages. It is further concluded that the concentration of nutrients and chemical compound in mopane leaves has implications on the diet composition of browsers such as the greater kudu in the mopane woodland. The dependency of the greater kudu on species such as *C. mopane* and *C. apiculatum* as main sources of browse indicates the importance of these species to the diet of the greater kudu in the mopane woodland.

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To God be the Glory

DECLARATION

I declare that the thesis hereby submitted to the University of Limpopo, for the degree Doctor of Philosophy in Botany has not previously been submitted by me for a degree at this or any other university; that it is my work in design and in execution, and that all material contained herein has been been duly acknowledge.

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02 July 2020

DEDICATION

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LIST OF PUBLICATIONS

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2. Makhado, R., Potgieter, M., Luus-Powell, W., Cooper, S., Oppong, C., Kopij, G., Mutisi, C. & Makhabu, S. 2016. *Tragelaphus strepsiceros* browse during the dry season in the mopani veld of Limpopo Province, South Africa. ***Transactions of the Royal Society of South Africa*** 71(1):17–21.
3. Makhado, R.A., Potgieter, M.J. & Luus-Powell, W.J. 2016. Nutritional value of *Colophospermum mopane* as source of browse and its chemical defences against browsers: A review. ***Journal of Animal & Plant Sciences*** 26(3):569–576.
4. Makhado, R., Potgieter, M., Luus-Powell, W., Cooper, S. & Kopij, G. 2016. *Tragelaphus strepsiceros* browse during the wet season in the mopani veld of Limpopo Province, South Africa. ***Rangeland Ecology & Management*** 69(5):408–413.
5. Makhado, R.A., Potgieter, M.J., Luus-Powell, W.J. & Mapaure, I. 2017. Effects of pruning on the concentration of trace elements in *Colophospermum mopane* leaves. ***African Journal of Ecology*** 55(4):600–608.
6. Makhado, R.A., Potgieter, M.J. & Luus-Powell, W.J. 2018. *Colophospermum mopane* leaf production and phenology in southern Africa's savanna ecosystem - A review. ***Insights of Forest Research*** 2(1):84–90.
7. Makhado, R.A., Potgieter, M.J. & Luus-Powell, W.J. 2018. Effects of pruning on the concentration of secondary metabolites in *Colophospermum mopane* leaves. ***Southern Forests: A Journal of Forest Science*** 81(2):123–128.
8. Makhado, R.A., Potgieter, M.J. & Luus-Powell, W.J. 2019. Effects of pruning on the concentration of macronutrients in *Colophospermum mopane* leaves. ***African Journal of Ecology*** 57(2): 260–267.
9. Makhado, R.A., Potgieter, M.J. & Luus-Powell W.J. 2020. Effects of pruning on the concentration of *Colophospermum mopane* leaf phenology and production. ***African Journal of Ecology*** 58(1):145–148.

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CHAPTER 1
GENERAL BACKGROUND

1.1 INTRODUCTION

Colophospermum mopane (Benth.) J. Léonard, commonly known as mopane (Léonard 1949), is a dominant tree or shrub in the low-lying areas of the southern African savanna biome (Mapaure 1994). This biome is the most extensive vegetation type in Africa. It occupies about 20% of the land surface of the world (Scholes & Archer 1997), around 40% of the land area of Africa (Okitsu 2004), approximately 65% of southern Africa (Scholes 1997), and roughly 35% of South Africa (Scholes & Archer 1997).

In Africa, this biome is important for the wildlife it supports, which is of strategic importance for the tourism and hunting industries (Scholes & Walker 1993). The savanna is home to the greatest density and diversity of wild herbivores and carnivores of any ecosystem on earth (Sankaran & Anderson 2009). Most rangelands, livestock farms, game reserves and national parks are found in the savanna (Bonsma & Du Toit 2010). Wildlife viewing in nature reserves and national parks of the savanna makes a positive contribution to the economy of most African countries.

Savanna is one of the world's major tropical terrestrial biomes, characterised by a dynamic mixture of trees and grasses in the landscape (Sankaran *et al.* 2005). The balance between these vegetation strata influences both plant and livestock production, and has a profound impact on several aspects of ecosystem functioning, including carbon, nutrient and hydrological cycles (Scholes & Archer 1997). Tree-grass interactions can vary greatly, as influenced by rainfall, nutrients, fire and herbivory (Whitecross *et al*. 2017).

The availability of resources (water and nutrients) and disturbance regimes (fire and herbivory) are thought to be important in regulating woody cover in the savanna (Scholes & Archer 1997), but perceptions differ on which of these are the primary drivers of savanna structure (Sankaran *et al.* 2005). Skarpe (1992) has indicated that the dynamics in the African savanna are driven mainly by the effect of fire and large herbivores, rather than climate. Nevertheless, the availability of water and the occurrence of fire and herbivory limit woody cover and permit grasses to co-exist. This suggests that future changes in these controlling factors may affect the distribution and dynamics of the savanna (Sankaran *et al.* 2005).

The quality of forage, as influenced by dynamics in savanna ecosystem, influence the feeding patterns and distribution of wildlife and livestock (Muposhi *et al*. 2016). In addition, the concentrations of plant metabolites such as tannin and minerals, protein, sugar and starch influence the browsing of individual plants by herbivores (Ginane *et al.* 2005). However, insufficient research has been undertaken to determine variations in attractants and deterrents across an animal’s home range and where it forages selectively for a diet that is not only balanced, but also avoids accumulating levels of plant secondary metabolites that become toxic (Skidmore *et al.* 2010).

It is therefore important that the leaf quality of mopane as a dominant species in the mopane woodland (Werger & Coetzee 1978) should be clearly understood. Mopane woodland is widely distributed in the southern African savanna biome, and constitutes 30–35% of the 1.5 million km^2 of savanna in southern Africa (Mucina & Rutherford 2006). Mopane is highly browsed by *Tragelaphus strepsiceros* (Pallas 1766), commonly known as greater kudu (Ansell 1972), in the mopane woodland, especially during winter (Curlewis 2014). This necessitates the need to understand the attractants and deterrents in mopane leaves browsed by the greater kudu. This is because the greater kudu is highly adapted to survive in the mopane woodland and its diet, especially in winter, consists mainly of mopane forage (Makhado *et al*. 2016). Kudu also contribute to the economic growth through trophy hunting, dried meat industry and tourism (Taylor *et al*. 2016). Despite the value of mopane as a source of browse for the greater kudu and other ungulates, especially in winter, there is still insufficient information on the quality and parts browsed during different seasons, which made it necessary to undertake this study. Management of mopane woodland is important in order to provide the greater kudu with nutritional browse.

1.2 PROBLEM STATEMENT

Proactive park, game and reserve managers annually conduct surveys on the carrying capacity in a specified area in order to determine the quantity of forage. In addition, wild animals, especially in nature reserves and game farms, are culled annually in accordance with the available forage. However, as indicated by Walker *et al*. (1987), the basis for deciding whether to cull or not remains highly contentious, because of uncertainty on whether culling does avoid progressive deterioration in habitat condition, or whether episodes of apparent overgrazing or over-browsing are an intrinsic and readily reversible feature of vegetation-large herbivore interaction. Despite such interventions in most nature reserves in South Africa, wild animals such as the greater kudu die every year because of starvation (Curlewis 2014), especially during dry seasons and drought years.

Wessels *et al*. (2006), for instance, recorded severe game mortalities in the mopane woodland when game ranchers lost up to 70% of their greater kudu populations. It is clear that seasonal changes (dry and wet) determine the quantity and quality of forage available for browsers, thus influencing the survival of wild animals. Owen-Smith *et al*. (2005) indicated that rainfall triggers the production of forage, which influences the survival of greater kudu. Curlewis (2014) further pointed out that during a shortage of forage, as caused by low rainfall, mortality among mature male greater kudu is higher than among young males and females. This is due to the high demand for quality forage by mature males and loss of energy because of the long distances travelled in search of quality browse (Curlewis 2014). This implies that during the dry season mature males might be at greater risk of starvation than females.

The quantity of forage in any given area may be high, but that does not necessarily mean that the quality is also adequate, and will ensure the survival of wild animals such as the greater kudu. Despite a large quantity of forage, wild animals may still die if the quality of forage is low. An increase in secondary metabolites such as tannins and phenols makes the forage indigestible or stops the breakdown of protein, which may eventually result in the death of animals such as the greater kudu (Furstenburg 2010).

The difficulty in game management is that most of the focus is placed on forage quantity, with little emphasis on quality. The leaf quality of mopane, which is highly browsed by the greater kudu, has not been adequately researched. This knowledge gap makes it difficult for decision-makers and conservationists to implement effective plans and strategies for the management of mopane woodland and the wildlife it supports. In addition, culling based only on forage quantity is in most cases misleading, resulting in game being culled without good knowledge of forage quality. This requires a detailed assessment of forage quality to be conducted before a decision is taken on whether to cull or not. Such an assessment can enable park, reserve and game managers to take informed decisions.

It is thus critical that game ranchers in mopane woodland areas obtain relevant information on the diet requirements of the greater kudu, one of the most farmed wild species in that vegetation type. A few studies have attempted to determine the leaf quality of mopane (Bonsma 1942; Wessels *et al.* 2007; Kohi *et al.* 2010), but none of these studies have determined the effect of browsers on mopane leaf quality. In addition, there is old and limited information on the greater kudu diet composition during different seasons in the mopane woodland (Hooimeijer *et al.* 2005; Curlewis 2014). The knowledge generated by this study is thus essential to ensure that the best and most sustainable management practices for game ranching in the mopane woodland are developed.

1.3 GENERAL LITERATURE REVIEW

Most of the previous research on the savanna focused primarily on tree-grass-herbivore-fire relationships (Skarpe 1991, 1992; Scholes & Walker 1993; Scholes & Archer 1997; Jeltsch *et al.* 2000; Sankaran *et al.* 2004; Sankaran *et al.* 2005; Sankaran & Anderson 2009; Smit 2014; Whitecross *et al*. 2017). Mapaure (1994), Mucina and Rutherford (2006) and Siebert (2012) conducted studies on the extent and distribution of mopane woodland in southern Africa (see Chapter 2).

Other studies investigated the uses and management of mopane (Madzibane & Potgieter 1999; Mashabane *et al.* 2001; Makhado 2008; Makhado *et al*. 2009).

Thinning and coppicing were the two main management practices for mopane woodland (Tietema *et al.* 1988; Tietema *et al.* 1991; Mushove 1992; Mushove & Makoni 1993).

Few authors have conducted research on mopane leaf phenology (Guy *et al.* 1979; Styles & Skinner 1997; Kohi *et al.* 2010). The number of studies on mopane leaf production is also limited (Hrabar 2005; Wessels *et al*. 2006; Kohi *et al*. 2010). Dealing with the lack of knowledge on mopane leaf phenology and production requires the integration of available literature (see Chapters 3 & 6).

The nutritional value of mopane to browsers such as the greater kudu was researched in Africa by various authors (Bonsma 1942; Mosimanyana & Kiflewahid 1988; Macala *et al.* 1992; Wessels *et al.* 2007; Kohi *et al.* 2010). Hooimeijer *et al.* (2005) and Wessels *et al.* (2007) also identified chemicals that deter browsers from browsing mopane leaves (see Chapters 4, 7, 8 & 9).

Extensive studies on greater kudu browse selection were carried out across Africa by various researchers (Hofmann & Steward 1972; Pienaar 1974; Giesecke & Van Gylswyk 1975; Owen-Smith 1979; Cooper 1985; Boomker 1987; Kelso 1987; Du Toit 1988; Owen-Smith 1993; Owen-Smith 1994; Owen-Smith 2002; Hooimeijer *et al.* 2005; Owen-Smith *et al.* 2010; Furstenburg 2010; Curlewis 2014). In addition, various studies have tested the effect of forage quality on the greater kudu's feeding behaviour (Owen-Smith 1993; Hooimeijer *et al.* 2005; Wessels *et al.* 2007; Furstenburg 2010). The current study contributed to the body of knowledge by determining the proportion of mopane in the greater kudu's diet by conducting rumen content analysis during different seasons (see Chapters 10 & 11). The sections that follow provide reviews on mopane and the greater kudu's browsing selectivity in the mopane woodland.

1.3.1 *COLOPHOSPERMUM MOPANE*

Mopane is a widespread and important tree species, distributed in much of sub-tropical southern Africa (Siebert 2012). Villagers mainly use mopane wood and poles for fuelwood and construction purposes, and less commonly use the root, bark and leaves for medicinal purposes (Madzibane & Potgieter 1999; Mashabane *et al.* 2001). Mopane trees also host mopane worms. These are the larvae of *Imbrasia belina*, which are widely consumed by rural and increasingly also by urban populations across southern Africa. The outbreak of mopane worms occurs twice a year, from December to January and again from April to May (Makhado *et al*. 2009).

1.3.1.1 Taxonomic description of mopane

Colophospermum mopane is a monotypic genus in the sub-family Caesalpinioideae of the family Leguminosae (Léonard 1949), and is classified as belonging to the tribe Caesalpinieae Benth. (Ross 1977). The generic name of *C. mopane* comes from a Greek word, meaning “resinous seed”, an allusion to the numerous scattered resin glands that cover the seed (Ross 1977). The common name for *C. mopane* is mopane, but locally the Vhavenda people in the Limpopo Province call it “mutanari” or “mupani”. In this study, the scientific name, “*C. mopane”,* is interchangeably used with its common name “mopane”.

Mopane is a small to medium-sized tree, which can grow up to 20 m high, with an erect narrow crown, although it can sometimes be found as an irregular deciduous 1–3 m high shrub (Werger & Coetzee 1978; Timberlake *et al.* 1993; Figure 1.1A). The diameter of mature trees is normally around 50–80 cm, but some large mopane trees can reach a diameter of up to 1 m. The outer bark of mopane is dark grey or brown, but the inner bark is pink to red (Madams 1990). Mopane is a deciduous species and sheds its leaves from August to October (Henning 1976). The leaves are alternate, with a single pair of large triangular leaflets, often termed “butterfly-shaped” (Henning 1976; Sebego 1999; Figure 1.1B), and appear after the first rains (Sebego 1999), normally in October-November. The younger leaves are glossy and golden, changing to green as they mature (Sebego 1999). The flowers of mopane are small, pale yellowish-green in colour, and are borne on slender hanging racemes, which are 2–3 cm long. Mopane produces flowers in the early summer, from October-November, along with the new leaves (Madams 1990). The seeds are large reuniform and corrugated with numerous small, sticky, reddish glands (Jordaan & Wessels 1999).

Figure 1.1: *Colophospermum mopane* trees during the wet season. Images (A) mopane woodland © Rudzani Makhado, and (B) mopane leaflets © SA National Biodiversity Institute.

Thompson (1960) and Sebego (1999) indicated that the roots of mopane are generally shallow; around 30–120 cm in depth, but Timberlake and Calvert (1993) found that some roots can penetrate down to 2 m in deep soils. The lateral roots are well developed, but a taproot is sometimes present (Henning 1976). It was observed that the seedlings of mopane initially produce a well-developed taproot system, which grows vertically downwards (Madams 1990), but gradually disappears to leave most mature individuals with a relatively shallow root system (Henning 1976).

1.3.1.2 Distribution of mopane

Mopane is widely distributed in the tropical areas of southern Africa (Werger & Coetzee 1978), covering 555 000 km^2 (Mapaure 1994). The extent of mopane distribution in southern Africa and factors associated with its distribution in southern Africa are reviewed in detail at Chapter 2.

1.3.1.3 Mopane leaf production and phenology

Ghazoul (2006) indicated that there is a need to assess plant growth in response to various management controls. As a result, a field experiment was conducted in order to determine the effect of coppicing, pollarding and pruning regimes on subsequent leaf productivity of mopane. There were no significant differences between trees subjected to the various treatments and the control trees (Wessels *et al.* 2006). However, rainfall resulted in continued leaf production in the coppiced, pruned and pollarded trees, even during the dry months (Wessels *et al.* 2006).

Leaf phenology is a measure of the greenness of the leaves and a good indicator of tree health. Vegetation health can easily and quickly be determined by assessing leaf phenology (Fuller 1999). Various factors can influence variation in leaf phenology, but the availability of water and nutrients, and disturbances such as fire and browsing effects, seem to have the overriding influence (see Chapters 3 & 6).

1.3.1.4 Leaf quality

Leaf quality in the savanna varies seasonally (Schroeder & Malmer 1980), which means that a leaf can be preferred for browse in a specific season and then rejected in another season. Even though leaf quality may be high, the plant's physical defence (such as leaf texture, leaf size, spines and thorns) and plant chemical defences (for example, phenols and tannins) determine the extent to which an animal can browse it (see Chapters 4, 7, 8 & 9).

Plants with structural deterrents such as spines and thorns reduce bite sizes and biting rates to varying degrees, but greater kudu browse those plants during the wet season regardless of their structural defences (Owen-Smith & Cooper 1983). This is the period when the concentration of secondary metabolites is highest in thornless plants. This means that wild animals are likely to browse leaves with high concentrations of protein and minerals, and low concentrations of fibre, lignin and condensed tannins (Owen-Smith & Cooper 1987). However, Owen-Smith (2002) indicated that a plant with high protein content, but with a high content of secondary metabolites such as tannins, will be less preferred for browse than a plant with low protein content but without these chemical defences. Diet selection thus becomes a trade-off between nutritional benefits against various costs and rates of restriction (Owen-Smith 2002).

It is also important to consider that forage intake is due to various factors such as availability of forage, type of herbivore, forage quality and plant characteristics (leaf size or shape, spines or thorns and tree height). However, limited information is available on mopane leaf production and quality under various management regimes, which is a major limitation in the ability to use and manage mopane woodland effectively.

1.3.1.5 Mopane leaves as food source for browsers

Savanna trees are more important to mixed feeder herbivores than grass because they provide much-needed fodder during the dry season (Anderson & Walker 1974) and their nutritional value is generally higher than that of grass (Codron *et al*. 2007). Mosimanyana and Kiflewahid (1988) indicated that browsing of a particular plant is normally a function of, among other factors, relative palatability, growth form and availability. On the other hand, palatability is also a function of many components and seems to correlate positively with crude protein, mineral content and moisture content (Mosimanyana & Kiflewahid 1988).

Makhado *et al*. (2016) indicated that mopane leaves and twigs are a valuable source of browse for wildlife in the dry season. Mosimanyana and Kiflewahid (1988) as well as Macala *et al*. (1992) corroborate these findings by indicating that during the dry season and in drought years, mopane tree pods with seeds and dry leaves are essential source of browse to animals. The above studies therefore agrees with Bonsma’s (1942) sentiment that access to mopane browse can greatly reduce stock losses during the drought years.

Macala *et al*. (1992) further indicated that livestock prefer to browse mopane leaves during winter when the leaves are dry and reddish-brown in colour. The crude-protein content in the dry leaves averages around 11% (Bonsma 1942), while it is between 15–16% in mopane pods with seeds (Macala *et al.* 1992). Browsers prefer young mopane leaves, particularly at the end of the dry season, possibly because foliar chemical deterrents such as polyphenols are at a lower concentration (Styles & Skinner 1997).

Fresh green mopane leaves have a high crude-protein content of almost 13% (Macala *et al.* 1992). However, feeding on highly nutritious green mopane leaves is limited because of a high concentration of secondary metabolites such as tannins and phenols, which reduce the crude protein digestibility of browse (Wessels *et al.* 2007). The production of high secondary metabolites during summer also means that mix-feeders will mainly feed on grass that is abundant in summer (Macala *et al.* 1992), and then on dried leaves in winter when the grass is dry or dead. On the other hand, the effect of browsers reduce the shade effect of trees, which allow grass to emerge. As Sankaran and Anderson (2009) indicated, previous conceptual models suggested that both positive and negative feedback loops are important in determining savanna structure and function. These models further explained the tree-grass-animal interaction in the savanna.

Such dynamics are essential to understand or explain the so-called 'plant-animal' relationship theory in the savanna better. They can also be used to understand theories on how trees such as mopane survive in the savanna, despite the effect of browsing by megavores and other incidents such as fires. However, conservationists, game and reserve managers should take into account that a higher secondary metabolite concentration in plants that are used, translates to re-growth of lower nutritional value. In systems where mopane constitutes an important forage resource, this finding might therefore have negative repercussions for animal performance (Wessels *et al.* 2007).

1.3.1.6 Management control measures in mopane woodland

Various management control measures have been reported by different authors across southern African mopane woodland. These management practices include thinning, coppicing and pruning, and are discussed below.

1.3.1.6.1 Thinning

Coe (1991) explained that thinning of dense mopane has the potential to increase basal area growth of the remaining shoots by more than 11% after one year.

Furthermore, thinning increases regeneration of shoots (Mapaure 2013). However, thinning frequently has little effect on tree height, the main effect being in the redistribution of basal area increment among fewer stems. Although it results in loss of tree production per hectare, it yields desired pole size more quickly (Smit 1994). It implies that this type of management practice was primarily designed to increase pole production. Thinning also promotes the growth of grass owing to the availability of horizontal space. Regardless of promoting pole production, thinning can also be a good management practice to increase forage for mixed feeders.

1.3.1.6.2 Coppicing

Mopane coppices easily, and the diameter growth of coppice shoots is linear up to seven years (Tietema 1989). On the basis of regression equation, Tietema (1989) predicts 12 kg/tree for mopane of 7.5 cm basal diameter at a population density of 10 000 trees/ha after 15 years. The desired basal diameter class of between 5 cm and 25 cm can be obtained within a period of five to 10 years (Tietema *et al.* 1988). Scholes (1990) suggested that cleared mopane shrubland could revert to its original basal area after 14 years. About 20–80% of stumps had coppice shoots after three months of cutting, and those cut at a 1 m height produced more, and taller, coppice shoots than those cut at 10 cm height (Mushove 1992; Mushove & Makoni 1993). This implies that cutting promotes coppicing and increases grass growth, which is essential for mixed feeders. It is therefore suggested that coppicing could be an ideal management control measure to simulate the effects of wood harvesting (firewood and poles) within mopane tree.

1.3.1.6.3 Pruning

Pruning involves the trimming of twigs and leaves in order to promote growth of new shoots and long leaves. Pruning also yields high production and improves the quality of the leaves. As a result, pruning improves the quality of browse for ungulates (Du Toit *et al*. 1990). It is therefore suggested that pruning can be an ideal management control measure to simulate the effects of browsers on leaf quality.

1.3.1.6.4 Evaluation of thinning, coppicing and pruning

Thinning and coppicing management practices were primarily undertaken to promote mopane pole production, with little emphasis on improving leaf production and quality. Despite awareness that mopane leaves provide valuable browse for wild animals, especially during the dry season (when secondary metabolites such as phenols and tannins are low), few researchers have attempted to apply pruning management practices to improve leaf production and quality in the mopane area. Wessels *et al*. (2007) conducted an experiment at Musina Experimental Farm where mopane trees were subjected to coppicing, pollarding and pruning. The result of the experiment showed the order of magnitude of the response and was positively associated with the severity of the impact. The effects of canopy treatments on the concentration of secondary metabolites such as phenol and tannin were small compared to seasonal and inter-seasonal fluctuations. However, the amount of secondary metabolites in the leaves increased significantly in relation to the severity of impact (Wessels *et al.* 2007). Du Toit *et al*. (1990) also found that pruning improved the quality of browse for ungulates. It is deduced from this study that pruning and defoliation of leaves promote re-growth of new fresh mopane leaves, which is critical in sustainably supplying browsers with forage during different seasons.

Kohi *et al*. (2010) further found that defoliation intensity significantly influenced the condensed tannin concentration of mopane leaves, with an intermediate level of defoliation (50%) yielding the re-growth with the highest concentration of condensed tannins. However, the tannin concentration after 75% and 100% defoliation was not significantly different from the control treatment (Kohi *et al.* 2010). It is in this context that pruning can be used to simulate the effect of browsers, such as the greater kudu, on mopane leaf quality.

1.3.2 *TRAGELAPHUS STREPSICEROS*

The greater kudu (Figure 1.2) is highly adapted to mopane woodland. Curlewis (2014) indicated that the greater kudu has adapted to the availability of resources from the mopane woodland and changes its browsing pattern, in order to survive changes in food quantity and quality during different seasons.

Figure 1.2: *Tragelaphus strepsiceros* at Musina Nature Reserve. Bulls have spiralled horns. Photo: B.J. Curlewis.

1.3.2.1 Greater kudu taxonomy

The greater kudu belong to the Tragelaphus genus in the sub-family Bovinae of the family Bovidae. It belongs to the tribe Tragelaphini (Ansell 1972). There are various sub-species of greater kudu and their distribution areas determine their classification. These include the southern greater kudu (*Tragelaphus strepsiceros strepsiceros)*, the Eastern African greater kudu (*Tragelaphus strepsiceros bea*) and the northern greater kudu (*Tragelaphus strepsiceros cottoni*). The lesser greater kudu (*Tragelaphus imberbis*) occurs in north-east Africa and Arabia (Furstenburg 2005). The current study focuses on the southern greater kudu (*Tragelaphus strepsiceros strepsiceros*). Furstenburg (2005) indicated that the southern greater kudu occurs naturally in southern Africa. The name greater kudu originates from the Hottentot or Khoikhoi word ku:du (Furstenburg 2010).

Members of the Tragelaphini have a medium to large body size, twisted horns (mostly absent in females), no face or pedal glands, inguinal glands present or absent, two pairs of mammae, varied tail (long or tufted to medium and bushy), frontal tuft, mane, throat and ventral fringes variously developed, face and body pattern of white spots and stripes, variously developed, no preorbital fossa and ethmoid fissure present. Males are distinctly larger than females (Furstenburg 2005).

Male greater kudu are taller with a greater body mass than the female. According to Furstenburg (2005), adult males (bulls) from the Limpopo Province have a mean shoulder height of 1.42 m and a mean body mass of 235 kg, while adult females (cows) have a mean shoulder height of 1.34 m and a mean body mass of 155 kg. As the name indicates, the adult males of the lesser greater kudu (*T. imberbis*) are commonly 35% shorter in height and have less than half the body mass of the southern greater kudu (Furstenburg 2005).

1.3.2.2 Distribution of the greater kudu

The distribution of the greater kudu is predominantly in southern and eastern Africa (Skinner & Chimimba 2005; Figure 1.3). The environmental conditions of the area, especially vegetation and climate, influence the distribution of the greater kudu (Pienaar 1974). In this area, high temperature and low rainfall areas seem to be the natural distribution ranges of the greater kudu, while cold areas limit its distribution. Owen-Smith (2000) has shown that greater kudu are highly susceptible to death when cold and wet weather occurs near the end of the dry season. However, during winter, greater kudu move away from cold, lower-lying areas to warm uphill areas in order to survive cold conditions (Furstenburg 2010).

In addition, the ability of the greater kudu to survive arid to semi-arid environments is due to the fact that they can survive for long periods without drinking water or obtaining sufficient moisture from their food, but become water-dependent at times when the vegetation is very dry (IUCN SSC Antelope Specialist Group 2008).

The distribution of the greater kudu therefore covers moist to arid habitats, forest and moist savanna, mesic savanna, arid savanna, and sub-desert habitats. In those habitats they are highly distributed in areas such as woodland, shrubland and savanna and sparsely distributed in grassland, thickets and rocky outcrops (Pienaar 1974).

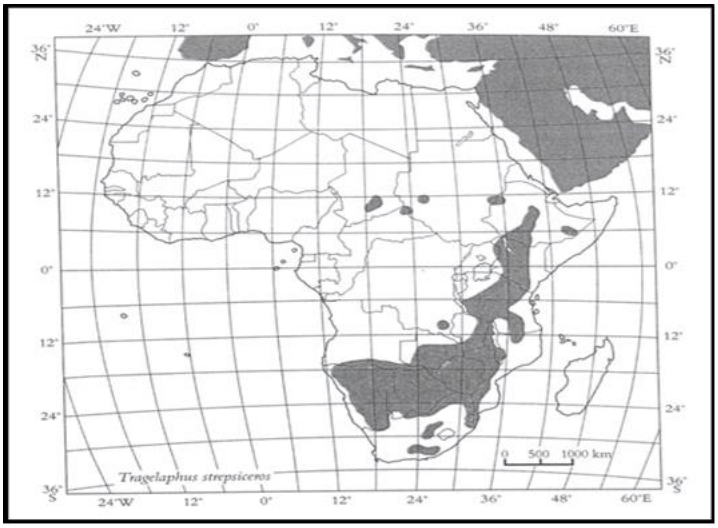

Figure 1.3: Distribution of *Tragelaphus strepsiceros* in Africa. Source: Skinner and Chimimba (2005).

The greater kudu is considered native to countries such as South Africa, Angola, Botswana, Malawi, Mozambique, Namibia, Swaziland, Tanzania, Zambia, Zimbabwe, Kenya, Ethiopia, the Central African Republic, Chad, Congo, Eritrea and Uganda (IUCN SSC Antelope Specialist Group 2008). The wide distribution of the greater kudu indicates how highly adaptable it is as a species (Pienaar 1974), capable of exploiting a diverse range of habitats (Ferrar & Walker 1974). Greater kudu still occur outside conservation areas in southern Africa (Skinner & Chimimba 2005). They occupy a wide range of habitats and prefer to live in small groups, occupying a small home range (Ansell 1972).

The recent International Union for Conservation of Nature (IUCN) assessment considers the species possibly extinct in Djibouti and Sudan and regionally extinct in Somalia. The total estimated population number of greater kudu is about 482 000, with about 15% occurring in protected areas, 61% on private land and 24% elsewhere (IUCN SSC Antelope Specialist Group 2008).

The greater kudu is one of the more valuable antelope species on privately owned game farms in the mopane woodland, Limpopo Province (Curlewis 2014), in view of its ability to survive in the hot and dry conditions in that vegetation type. The composition of the plant species eaten by greater kudu determines the diet quality, which has an impact on the kudu's condition and mortality levels (Hooimeijer *et al*. 2005).

1.3.2.3 Greater kudu browsing activity

Greater kudu have a relatively small rumen capacity (Hofmann & Steward 1972) and the rumen is adapted to a rapid rate of passage of food (Giesecke & Van Gylswyk 1975). Short *et al*. (1974) indicated that grass tends to be digested more slowly than browse, and grazers typically have a capacious rumen designed to retain the food longer. The digestive anatomy of the greater kudu is thus not conducive to grasses. This would limit them from accepting mature grass under normal circumstances (Hofmann & Stewart 1972), which justifies their sparsely distribution in the grassland habitat (Pienaar 1974). Greater kudu are largely regarded as non-selective browsers, feeding on leaves, shoots, pods or fruit of a wide range of shrubs, trees, dicot forbs and succulents; but generally only accepting small quantities of grass (Furstenburg 2010).

The food choice for greater kudu is between herbaceous and woody plant components (Owen-Smith 1993). Furstenburg (2010) also explained that the diet of the greater kudu in the Eastern Cape valley bushveld consists of 70–80% trees and shrubs, 15–18% herbaceous dicot forbs and 5–12% grass. Furthermore, in the northern savanna mixed bushveld of the Limpopo Province, the diet composition of the greater kudu consists of 61% trees and shrubs, 21% forbs and 18% grass (Furstenburg 2010). According to Curlewis (2014), the greater kudu prefer to browse forbs such as *Indigofera* species and trees without thorns in winter, while in summer they prefer to browse forbs such as *Leucas glabrata* var. *glabrata* and thornless trees. In winter, the greater kudu prefers to browse on mopane. Greater kudu were not recorded eating grass at the Musina Experimental Farm (Curlewis 2014). Various authors also confirm that the greater kudu prefers browsing to grazing (Hofmann & Stewart 1972; Short *et al.* 1974; Pienaar 1974; Giesecke & Van Gylswyk 1975; Owen-Smith & Cooper, 1987; Owen-Smith 1993; Furstenburg 2010; Curlewis 2014).

According to Owen-Smith (1993), the greater kudu spends 50–75% of its active time foraging during the late wet season. The consumption rate for herbs is between 4.4–7.1 g min^{-1}, while it is 3.4–8.5 g min^{-1} for woody species. The wet bulk digestive capacity for herbs and woody species is 2.02 kg^{-1} and 2.95 kg^{-1}, respectively. The mean food requirement for greater kudu between herbs and woody species is 2.12 and 2.78 kg^{-1}, respectively. The observed mean diet proportion for herbs and woody species was 52% and 48%, respectively (Owen-Smith 1993).

Browse activity of the greater kudu changes in accordance with the changes in environmental conditions. Browsing height also changes in response to the availability and accessibility of forage. Du Toit (1988) showed that the browse height of the greater kudu was between 1.2 and 1.7 m in the Kruger National Park, while in the Pilanesberg National Park it was found to be <1.5 m (Kelso 1987). According to Curlewis (2014), the browse height of greater kudu in Musina Nature Reserve was mainly 1.01–1.5 m during all seasons. However, the size and gender of greater kudu also determine the browsing height. The larger sized body of the male greater kudu enables it to browse at a higher stratum than the female (Curlewis 2014).

Boomker (1987) found that an adult greater kudu of 210 kg can consume 3.7 kg of dry material per day in winter and 5.4 kg in summer. The average bite sizes are between 3.7 and 4.5 cm pieces from both old and young twig ends. Greater kudu switch from foregut in summer to hindgut fermentation in winter in order to overcome the natural drop in nutrition quality. The hindgut has a greater ability to digest fibre (Boomker 1987). Habitat selection for greater kudu also influences the browsing pattern. Curlewis (2014) indicated that greater kudu prefer open savanna. The top five woody species browsed more than 2% by both male and female greater kudu in mopane woodland include; *C. mopane*, *Combretum apiculatum*, *Senegalia nigrescens*, *Vachellia* species, *Dichrostachys cinerea* and *Grewia* species (Hooimeijer *et al.* 2005; Curlewis 2014). Mopane was the plant browsed most often in mopane woodland, especially during dry season. Mopane constitutes on average 39.2% of the greater kudu's diet per month in the mopane woodland over a year (Hooimeijer *et al*. 2005).

1.3.2.4 Influence of forage quality on the greater kudu browse

Greater kudu prefer to browse nutritional forage and starts to reject forage when there is a gradual increase in tannins and phenols (Furstenburg 2010). Secondary metabolites reduce the digestible energy concentration of the food and may reduce apparent digestion of protein and possibly cell walls (Robbins *et al.* 1987). Tannins decrease the fermentation rate of the food and its digestibility. Even though food supply may increase, reduced digestibility due to a high concentration of tannins can cause a decline in the net energy intake (Gordon & Illius 1996).

The available protein concentration in the forbs, fruit and flower dry matter is 17%, while the available protein digestion rate is 0.33 g min^{-1}. The available protein concentration for dry matter of woody species such as *Grewia flavescens* is 13%, while the available protein digestion rate is 0.22 g min^{-1} (Owen-Smith 1993). Wessels *et al*. (2007) established that the total phenols and condensed tannins in mopane are lowest in August at 48.4 and 53.1 mg g^{-1}, respectively, but increases to a maximum in December, at 96.7 and 112.4 mg g^{-1}, respectively.

Hooimeijer *et al*. (2005) showed that crude protein content declines in the late dry season and reaches its minimum (6.2% dry weight) in October. In the late wet season, the maximum crude protein value recorded was 12.6% (dry weight), corresponding to the month with the highest number of species found in the diet. However, the average crude protein, tannin and phenol concentrations between the wet and dry season do not differ, probably because high levels of crude protein in the diet persisted quite long into the dry season. Condensed tannin content generally follows the same trend as crude protein levels, with low levels in the late wet and late dry seasons. The measured condensed tannin levels in mopane were lowest at 3.8% dry weight in October/November, but increased in December/January to 9.8% dry weight (Hooimeijer *et al*. 2005). Wessels *et al*. (2007) are of the view that a higher secondary metabolite concentration in plants browsed translates to re-growth of lower nutritional value. This implies that mopane will be highly browsed in winter and spring when the secondary metabolite concentrations are lower, rather than in the summer.

Hooimeijer *et al*. (2005) established that mopane was consumed irrespective of its high concentration of tannin and phenols. The percentage of mopane in the diet of greater kudu was highest during the late dry season (August–November), reaching a peak of 91% in September but dropping to 3% during March. Interestingly, crude protein concentrations were positively associated with high levels of tannins and phenols for mopane, but the diet of greater kudu in that period comprised significantly more species during the wet season compared to the dry season (Hooimeijer *et al*. 2005). Hooimeijer *et al*. (2005) further pointed out that diet diversification, instead of protein maximisation, seems to be the potential tool to satisfy protein requirements while reducing potential toxic effects associated with a high intake of secondary compounds. Browse selection by the greater kudu is detailed in Chapters 10 and 11.

1.4 PURPOSE OF THE STUDY

1.4.1 Aim

The aim of this study was to determine the effects of pruning on seasonal leaf quality of *Colophospermum mopane* and *Tragelaphus strepsiceros* browse in the mopane woodland of the Limpopo Province, South Africa.

1.4.2 Objectives

The objectives for this study were to determine the:

i. Effects of pruning on seasonal leaf production and phenology of *C. mopane*.
ii. Effects of pruning on seasonal leaf quality of *C. mopane*.
iii. Parts of and extent of *C. mopane* browsed through various seasons by *T. strepsiceros,* through conducting rumen analysis.

1.4.3 Hypotheses

The hypotheses for this study were as follows:

i. Pruning has no effect on seasonal leaf phenology and production of *C. mopane*.
ii. Pruning has no effect on seasonal leaf quality of *C. mopane*.

iii. Seasonal changes have an influence on the diet composition and browse selection of *T. strepsiceros* in the mopane woodland.

1.4.4 Research questions

The research questions for this study were as follows:

i. What is the effect of pruning on mopane leaf phenology and production?
ii. What is the effect of pruning on mopane leaf quality?
iii. Which parts of mopane (leaf, twigs, pods, flowers, fruit and bark) constitute the highest proportion of the diet of the greater kudu during the different seasons?
iv. What is the diet composition for greater kudu in different seasons?

1.5 MOTIVATION FOR THE STUDY

Colophospermum mopane is a widespread and important tree species in southern Africa (Werger & Coetzee 1978). *Tragelaphus strepsiceros*, commonly known as the greater kudu, is predominantly distributed in southern and eastern Africa (Skinner & Chimimba 2005). It is highly adapted to the savanna biome, especially in the mopane woodland (Hooimeijer *et al*. 2005). The greater kudu changes its feeding behaviour in order to survive changes in food quantity and quality (Curlewis 2014). This implies that while the greater kudu in mopane woodland depend on mopane forage throughout the year, it is mainly consumed during the dry season.

Mopane woodland is important for game farming in southern Africa and its existence contributes to tourism and economic development. Considerable parts of the largest and best-known national parks in southern Africa lie in the mopane belt. These include, most notably, the Limpopo Transfrontier Park between South Africa, Mozambique and Zimbabwe; the Mapungubwe-Tuli-Shashe Transfrontier Park between Botswana, South Africa and Zimbabwe; Chobe National Park in Botswana; and the Etosha Park in Namibia. Because of this significant economic value, there is a need to understand the relationship between plant and animal in the mopane woodland in order to develop sustainable conservation strategies that could translate into economic benefits for those located in the mopane woodland.

The lack of current information on the crucial role played by mopane as a source of browse for the greater kudu in mopane woodland, especially during the dry season, is undermining the effective management of mopane woodland and the wild animals it supports. This study is thus necessary because it could equip game farmers and conservationists with knowledge that they can utilised to adjust their management interventions effectively. The study is also important because it has provided researchers, conservationists and decision-makers with relevant information that can be used when developing conservation and management practices for mopane woodland and the wild animals it supports. Results from this study has further assisted in gaining better understanding of mopane as an important browse species for the greater kudu in the mopane woodland. This has ultimately contributed to better management of browse for the greater kudu in mopane woodland during different seasons.

1.6 ETHICAL CONSIDERATIONS

This study involved the collection of mopane leaves and kudu rumen content at Musina Nature Reserve. Greater kudu rumen content was collected from kudu that were culled as part of a culling programme or from animals that were hunted for trophy or venison purposes. Animal trials were not conducted in this study, and as a result no approval from an ethical committee was required. A permit to conduct this study at Musina Nature Reserve was approved by the Limpopo Department of Economic Development, Environment and Tourism (Ref: 1058944; see Appendix 1). Secondary data was collected through reviewing various sources from books, journals and conference proceedings. All ethics requirements related to research and copyright were adhered to and respected in line with the requirements of the University of Limpopo Research and Ethics Committee.

1.7 SCOPE AND LIMITATION OF THE STUDY

The scope for this study was to determine the effects of various management control measures on seasonal leaf quality of mopane and greater kudu browse in the mopane woodland of the Limpopo Province. During the study period, several limitations were encountered, as explained below:

- The researcher had to apply for a permit to access the Musina Nature Reserve. The permit approval process took longer than expected, which delayed the commencement of data collection.
- The cost of analysing leaf samples was high, which required the study to use a reasonable sample size.
- The initial plan was to design coppicing, pollarding and pruning experiments as management control measures, but only <10% pruning was approved by the reserve authorities. However, the decision did not disadvantage or jeopardise the study. It was realised that pruning is in fact the ideal control measure to simulate the browsing effect of the greater kudu on leaf quality, while coppicing and pollarding are ideal management control measures for simulating the browsing effect of large herbivores such as elephants on mopane leaf quality. The reserve does not have elephants, and pruning was consequently the ideal control measure for simulating the seasonal effects of pruning involving only the greater kudu on mopane leaf quality.
- There was limited treatments because only <10% pruning treatment was applied.
- During the study period, the greater kudu population was not culled at the study area, which made it difficult to obtain kudu rumen samples from Musina Nature Reserve. The samples were consequently obtained from the Sandown Game Farm, which is situated in the same vegetation type, and where culling programme was being conducted. The cost of the purchase of the kudu was also high, R8 000 for a bull and R5 000 for a cow.

1.8 THESIS OUTLINE

This thesis is organised into 12 independent, but interlinked chapters. The chapters were prepared concurrently for article publication and thesis. There is therefore a limited number of duplication between the various research chapters. Chapters 2-4 provides literature review, while the findings are presented in chapters 6-11. These chapters are briefly outlined in the following manner:

Chapter 1 provides the general background, statement of the research problem, brief literature review, aim and objectives, hypotheses, research assumptions and justification of the study.

Chapter 2 delivers a review of the distribution of mopane in southern Africa. The value of this chapter is that it explores the factors that determine the distribution of mopane in the hot, dry environment of southern Africa. This is important in order to understand the response of mopane to seasonal changes and disturbances such as fires and herbivory.

Chapter 3 is a review of mopane leaf production and phenology in southern Africa's savanna. The value of this chapter is that it explores the influence of mopane leaf production and phenology on browsers. This chapter form the foundation of Chapter 6.

Chapter 4 presents a review of mopane leaf quality in the southern African savanna. The value of the review is that it integrates scanty and old information on mopane leaf quality and its effect on browsers in the mopane woodland. This chapter form the basis of Chapters 7-9.

Chapter 5 provides the detailed description of the study area. It further presents the location, climate, geology, soil, fauna and flora of the study area. This chapter is important because it gives the insight into the conditions in play, which determine the interaction between the greater kudu and mopane.

Chapter 6 presents research findings on the effect of pruning on mopane leaf production and phenology. This chapter is important in determining the amount and availability of mopane forage and its implications for browsers in the mopane woodland.

Chapter 7 delivers research findings on the concentration of macronutrients in mopane leaf. This chapter is crucial in determining the effects of browsing on the amount of macronutrients in mopane leaves.

Chapter 8 provides research findings on the concentration of trace elements in mopane leaf. This chapter is important in determining the effects of browsing on the concentration of trace elements in mopane leaves.

Chapter 9 presents research findings on the amount of secondary metabolites in mopane leaf. This chapter is vital in determining the effects of browsing in the concentration of secondary metabolites in mopane leaves.

Chapter 10 provides research findings on the greater kudu’s browse during the dry season. This chapter is critical in determining the type and parts of plant species browsed by the greater kudu during the dry season. Diet selection by male and female greater kudu was also determined.

Chapter 11 delivers research findings on the greater kudu’s browse during the wet season. This chapter determined the type and parts of plant species browsed by the greater kudu during the wet season. Diet selection by male and female greater kudu was also determined.

Chapter 12 is the summary and general conclusion of the most significant research findings. The chapter also provides various recommendations in relation to future studies.

CHAPTER 2

ADAPTATION AND DISTRIBUTION OF *COLOPHOSPERMUM MOPANE* IN SOUTHERN AFRICA'S MOPANE SAVANNAS[1]

2.1 INTRODUCTION

Colophospermum mopane is a dominant tree or shrub in the mopane woodland in the sub-tropical areas of southern Africa's savanna ecosystems (Henning 1976), between latitudes 9ºS and 25ºS (Werger & Coetzee 1978). Estimates show that mopane woodland accounts for about 30–35% of the 1.5 million km^2 of savanna areas in southern Africa (White 1983), which represents more than a quarter of land area in the region. The total area covered by mopane woodland in the whole of southern Africa is 555 000 km^2 (Mapaure 1994; Table 2.1). Mopane is distributed in the hot, dry valley bottoms and adjacent plains of southern Africa (Timberlake *et al.* 2010; Siebert 2012). Its distribution ranges from southern Angola and northern Namibia across Botswana and Zimbabwe to central and southern Mozambique, and from the Luangwa valley in Zambia and central Malawi to northern South Africa (Mapaure 1994; Figure 2.1).

Previous studies have demonstrated that rainfall, altitude and soil types influence the distribution of mopane in southern Africa (Burke 2006). Mopane occurs in areas receiving low to moderate annual rainfall ranging from 400 to 800 mm (Madams 1990). These are normally areas at altitudes ranging from 200 to 600 m (White 1983), with variable soils, but usually fine-grained, having textures ranging from sandy through loamy to clayey. The species is known to occupy both shallow and deep soils, containing significant amounts of exchangeable sodium (Madams 1990).

Other factors influencing the distribution of mopane include minimum temperature and dry season day length (Stevens *et al.* 2014). Mopane is commonly distributed

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[1] Makhado, R.A., Mapaure, I., Potgieter, M.J., Luus-Powell, W.J. & Saidi, A.T. 2014. Factors influencing the adaptation and distribution of *Colophospermum mopane* in southern Africa's mopane savannas – A review. *Bothalia* 44(1), Doi: 10.4102/abc.v44i1.152.

in high temperature areas (Table 2.2), and various authors confirms that minimum temperature of <5^{o}C limits its distribution (Whitecross *et al.* 2012), especially in the southern part (Stevens *et al.* 2014). However, although mopane prefers to occupy frost-free areas, the species is capable of withstanding light frost (Thompson 1960), while tall mopane trees of >4 m in height can survive minimal frost damage (Whitecross *et al.* 2012).

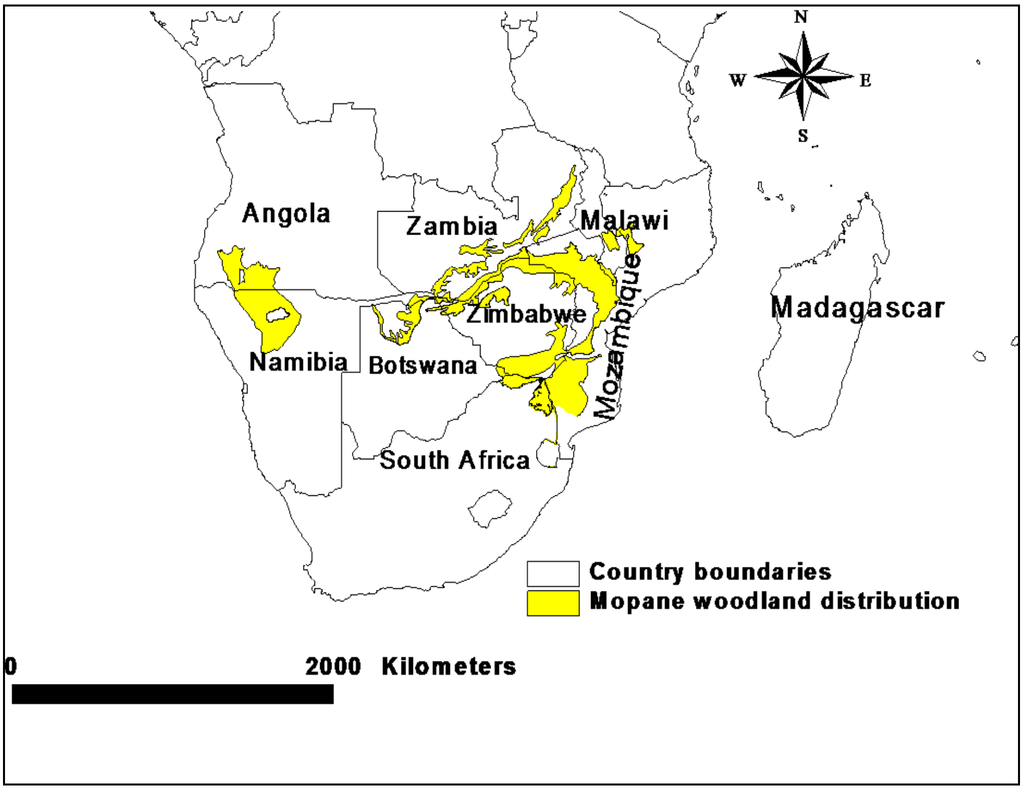

Figure 2.1: Distribution of mopane woodlands in southern Africa. This map is an extract from Mucina and Rutherford (2006) data on the vegetation of South Africa, Lesotho and Swaziland (VegMap), and White (1983) data on vegetation of Africa.

Mopane play an important role in sustaining rural people's livelihoods (Makhado *et al.* 2009). Rural dwellers use it for firewood (Liengme 1983), construction of traditional structures (Makhado *et al.* 2009) and to a lesser extent for medicinal purposes (Mashabane *et al.* 2001). In some parts of southern Africa, there has been increasing use of mopane in urban areas for firewood as the costs of electricity increases. Mopane also hosts mopane worms, larvae of the moth *Imbrasia belina*, which are consumed for their nutritional value (Dreyer & Wehmeyer 1982) and traded to generate income (Styles 1996).

Table 2.1: Area covered by mopane woodland in southern Africa.

Country	**Area (km^2)**	**Proportion of country area (%)**	**Proportion of total mopane area (%)**
Angola	112 500	9	20
Zimbabwe	101 500	26	18
Mozambique	98 000	13	18
Botswana	85 000	15	15
Namibia	77 000	9	14
Zambia	43 500	6	8
South Africa	23 000	2	4
Malawi	10 000	9	2
Total	550 500	89	100

Source: Mapaure (1994).

Table 2.2: Environmental factors associated with the distribution of mopane in southern Africa.

Country	**Mean annual rainfall (mm)**	**Mean daily temperature (°C)**	**Altitudinal range (m)**	**Soil types**	**Reference**
Angola	100-600	16-25	100-1200	g,s,a	1;2;7;9
Zimbabwe	450-700	16-30	300-950	c,so,l,g,ss,fe	1;6;7;9
Mozambique	400-700	20-29	100-500	c,ls,s,bs,a	1;2;6;9
Botswana	400-600	13-30	800-900	s,si,cl,c,b,h	1;2;6;9
Namibia	50-600	12-31	150-1000	l,f	2;6;7;8;9;11
Zambia	600-1000	14-30	400-1000	a,fv,sl,g,l,ss,fe,h	1;2;5;6;7;9
South Africa	250-650	15-31	200-800	a,g,b,c,s,l	1;3;4;6;9;10
Malawi	700-800	19-28	450-500	sc,m	1;2;9
Min	50-550	12-25	100-500	-	-
Max	700-1000	20-31	800-1200	-	-
Average	369-700	16-29	313-856	-	-

References: 1=Mapaure 1994; 2=Werger & Coetzee 1978; 3=Acocks 1988; 4=Mucina & Rutherford 2006; 5=Porter 1968; 6=Henning 1976; 7=Madams 1990; 8=Erkkilä & Siiskonen 1992; 9=Du Plessis 2001; 10=Rutherford *et al.* 2006; 11=Okitsu 2005. **Soil types symbols**: a=alluvial, b=basaltic, bs=brown soils, c=clayey, cl=clay loamy, f=ferruginous, fe=ferrallitic, fv=fluvisol-vertisol, g=granitic, h=halomorphic, l=lithosols, ls=loamy sand, m=mopanosols, s=sandy, sc=sandy clays, sl=sandy loamy, si=silt, so=sodic, ss=sandstone.

Dry mopane leaves, twigs and pods provide a valuable source of browse for wild animals such as elephants (Ben-Shahar & MacDonald 2002) and greater kudu (Hooimeijer *et al*. 2005) in mopane woodland, especially during the dry season

(Makhado *et al*. 2016) and drought periods (Macala *et al*. 1992), when the tannins have leached out. In addition, the secretion of *Arytaina mopane* (Figure 2.2); commonly known as lerp, increases the palatability of mopane leaves (Ross 1977) because the lerps have a high sucrose content (Styles 1993). The lerps are highly sought after by baboons, monkeys, birds, and even humans (Herremans-Tonnoeyr & Herremans 1995), due to its sweetness. They contain about 53% water-soluble sugars (Sekhwela 1989).

Figure 2.2: *Arytaina mopane* lerps on mopane leaf. Photo credit: M.J. Potgieter.

Therefore, considering the extensive distribution of mopane in the low-lying areas of southern Africa and its importance to human livelihoods, domestic and wild animals throughout its distribution range, it becomes a research challenge when factors influencing its distribution are not easily determined (Siebert 2012) and even not well understood (Stevens *et al.* 2014).

Various sources have contributed to the understanding of mopane distribution (Thompson 1960; Henning 1976; Werger & Coetzee 1978; White 1983; Cole 1986; Madams 1990; Mapaure 1994; Timberlake *et al.* 1993; Du Plessis 2001), but there is still a gap in identifying the underlying factors influencing mopane distribution in southern Africa (Siebert 2012; Stevens *et al.* 2014). This is creating a gap in the knowledge to better manage mopane and the wild animals it supports. Current climatic changes further contribute to the complexities of predicting the distribution of mopane.

As a result, there is a need to adequately review and augment the limited information in an integrated manner. In this way, better understanding of the factors influencing the distribution of mopane in southern African can be determined and understood. This review is also important because it gives insight into the potential future distribution scenarios of mopane. This was achieved through conducting an extensive review of a mixture of literature (such as journal articles, books, conference proceedings and reports) specifically dealing with adaptation of mopane and factors influencing its distribution in southern Africa.

The aim of this chapter is therefore to provide a review of the mechanisms that enable mopane to survive disturbances caused by fire, browsing activity by large herbivores, and environmental stresses in the savanna ecosystem. The chapter further depicted the effect of environmental factors on the distribution of mopane in southern Africa’s savanna ecosystem.

2.2 ADAPTATION OF MOPANE TO FIRE AND BROWSING ACTIVITY

Mopane is widely distributed in the southern African savanna (Mapaure 1994); an ecosystem which experiences frequent fires (Kennedy 2000) and supports large herbivores (Sankaran & Anderson 2009). Fire negatively affects the morphology of mopane (Gandiwa & Kativu 2009), destroys the aerial components of mopane shrub (Henning 1976) and causes a reduction in mopane height and stem circumference (Kennedy & Potgieter 2003).

In addition, mopane is highly browsed by large herbivores such as elephants (Ben-Shahar & MacDonald 2002), mainly owing to its high nutritional value (Hooimeijer *et al*. 2005). The preference of elephants for mopane makes it susceptible to elephant-induced damage (Lewis 1991). There is evidence that elephants’ feeding behaviour can modify mopane woodlands to coppice shrubby stands (Seloane 2017). Furthermore, elephants also inhibit height recruitment of mopane by repeatedly breaking the branches, ring-barking, heavy browsing and toppling the tree (Smallie & O'Connor 2000). As a result, fire and browsing activity has a greater effect on mopane structure, which also has implications for the growth and distribution of mopane in southern Africa's savannas.

Despite the disturbances caused by fires and browsing activity by large herbivores on mopane, the species is capable of surviving through its coppicing ability and production of chemical defence. Various authors show that mopane coppice rapidly (Tietema 1989; Mushove 1992; Mushove & Makoni 1993; Luoga *et al.* 2004; Mlambo & Mapaure 2006) after it has been disturbed by fire and browsing animals.

In addition, mopane wood contains crystals of calcium oxalate which contribute to high wood density (Prior & Cutler 1992) and also enhance the wood resistance to fire (CICA 1996). These crystals affect the burning properties of the wood through producing considerable amounts of carbon dioxide that retards the production of flames (CICA 1996). Mopane also produces a high concentration of secondary metabolites, such as tannins and phenols, during the growing season in order to deter herbivores from browsing it (Wessels *et al*. 2007), regardless of its high nutritional value (Hooimeijer *et al*. 2005).

2.3 ADAPTATION OF MOPANE TO ENVIRONMENTAL STRESSES

It is well documented that mopane has the ability to survive low to moderate rainfall (Henning 1976), water stresses (Choinski & Tuohy 1991; Mantlana 2002) and high temperatures (Henning 1976; Dye & Walker 1980), but how the species is able to survive such 'harsh' environmental conditions in southern Africa has not been adequately researched. It is, however, the physical characteristics (Henning 1976; Madams 1990) and physiological mechanisms (Dye & Walker 1980; Choinski & Tuohy 1991; Henning 1976; Johnson *et al.* 1996; Mantlana 2002), which enables mopane to tolerate water stress and high temperature conditions.

The ability of mopane to tolerance those 'harsh' conditions enables it to dominate most low-lying parts of southern Africa's savanna. The physical and physiological abilities of mopane are discussed in this chapter in order to better explain the mechanisms that enable the species to survive in hot-dry low-lying areas of southern Africa. It is the responses of mopane roots and leaves to changes in the surrounding environment that enables it to survive these ‘harsh’ environmental conditions, and dominate most low-lying parts of southern Africa’s savanna.

2.3.1 Roots-related adaptations

Mopane is essentially a shallow-rooted species with a high root biomass (Smit & Rethman 1998). It is considered a shallow-rooted because its roots are mainly found at a depth of 20–120 cm (Thompson 1960), but can also reach 2 m on deep soils (Sebego 1999). Mantlana (2002) indicated that the total root density for short and tall mopane was highest in the first 20 cm of the soil profile, and then declined with increase in soil depth.

The combination of a shallow-rooting system and high root biomass places mopane at a competitive advantage in areas where conditions lead to the development of a zone of maximum water retention and nitrogen near the surface (Mlambo *et al.* 2005). The swallow rooting system of mopane, complemented by its high root biomass, especially at a depth of 20–120 cm (Thompson 1960), are important as they facilitate quick water and nutrient acquisition and transport (Madams 1990; Mantlana 2002), which are near the soil surface. This enable mopane to survive ‘harsh’ environmental conditions of southern Africa’s savanna.

Another advantage is that the B horizon under mopane sodic soils is relatively impermeable (Dye & Walker 1980), which provides more moisture retention to the A and O horizons where the bulk of mopane roots are found. The relatively impermeable B horizon further restricts moisture from filtrating down to the C horizon. As indicated by Dye and Walker (1980), these characteristics enable shallow-rooted species such as mopane to have a competitive advantage for moisture uptake over deep-rooted species.

The roots furthermore play a critical role in the survival of mopane. Mopane coppice easily (Mushove & Makoni 1993), mainly because the roots have the ability to produce root suckers, which in turn enables the shoots to grow faster than the newly established seedlings (Luoga *et al.* 2004). As indicated by Mantlana (2002), the ability of mopane roots to coppice confers a degree of resilience to natural and anthropogenic disturbance, which is critical in ensuring its future survival.

2.3.2 Cell sap-related adaptations

Stressed mopane shows a marked increase in relative nitrogen content, which suggests that the resistance of mopane to severe soil moisture stress is partly caused by the build-up of soluble nitrogenous compounds within the cell sap. In addition, the uptake of magnesium also plays a direct role in the maintenance of water use efficiency of mopane, by catalysing the metabolic production of organic solutes, thereby increasing the osmotic pressure of the cell sap, and thus enhancing the ability of mopane to withstand moisture stresses (Henning 1976).

2.3.3 Leaf-related adaptations

Mopane is physiologically adapted to dry (moisture-stressed) environmental conditions of southern Africa (Choinski & Tuohy 1991). It is adapted through restricting transpiration, a mechanism which enables the species to maintain high water potential (Henning 1976). This is largely done through folding the leaves, stomatal responses and osmotic adjustment, which are considered critical mechanisms in enabling mopane to survive the water-stressed and high temperature conditions of southern Africa.

2.3.3.1 Leaf responses

Mopane leaf has two triangular leaflets shaped like the wings of a butterfly. The leaves are leathery and resinous (Henning 1976). The leathery membrane on the leaf acts as a buffer layer to deflect direct heat from the sun and also reduces the rate of water loss through evapotranspiration. It is further indicated that mopane has a tendency to fold its leaflets together, especially during the heat of the day (Makhado *et al*. 2014). When the leaflets are folded together, especially when the leaf temperature exceeds 30°C, it reduces direct heat from the sun.

This means that the few exposed stomata will close, which also assists in reducing the loss of water through evapotranspiration. When the stomata are closed, the rate of photosynthesis is also reduced, confirming the findings by Prior (1991) who indicated that photosynthesis of mopane leaves is lower during the heat of the day than during the night or cool days when the temperature is relatively low. In addition, mopane is a deciduous species and sheds its leaves during the dry season, mainly from August to October. The ability of mopane to lose its leaves enables it to conserve water that could have been lost during evapotranspiration.

2.3.3.2 Stomatal responses

Stomata are randomly distributed on the adaxial (top) and abaxial (bottom) surface on mopane leaf, occupying mainly the area around the minor veins (Potgieter & Wessels 1998). However, mopane has fewer stomata on the exposed adaxial leaf surface compared with most other species (Prior 1991), which implies that the stomata are mainly distributed on the abaxial surface. The few exposed stomata on the adaxial surface of mopane leaves therefore limit the number of openings on the leaf, hence less moisture is lost through the leaves. It was further shown that mopane stomatal conductance declines almost linearly at light saturation from March to August, at 585 m-^{2}s-^{1} to 172 mmol m-^{2}s-^{1}, respectively (Mantlana 2002).

The decline in mopane stomatal conductance occurs when the soil moisture is low, especially during dry seasons and drought conditions. This mechanism enables mopane to conserve water during hot-dry conditions. Mantlana (2002) indicated that the reduction in stomatal conductance observed, when soil water deficit increased, may be explained by the reduction in pre-dawn leaf water potential.

However, it is explained in this chapter that leaf temperature needs to be taken into account because it also has an influence on mopane stomatal conductance. Nevertheless, the ability of mopane to close the stomata during high temperature and water-stress periods enables it to reduce the loss of moisture and nutrients, which is critical in ensuring its future survival under the hot, dry conditions of southern Africa.

2.3.3.3 Osmotic adjustment

The ability of mopane to grow and tolerate water-stressed conditions is also due to osmotic adjustment (Henning 1976). This processes lower cell osmotic potential, thereby enabling intercellular water to flow towards the inside of cells. It is an important mechanism in maintaining cell turgor pressure under reduced soil water potential, and thus enables the plant to tolerate drought or water-limiting conditions (Hsiao *et al.* 1976; Chen & Jianga 2010).

As a result of the osmotic adjustment, mopane has the ability to germinate and establish root growth at lower water potentials than would otherwise be possible. The seeds of mopane can germinate and withstand water stress from −0.2 MPa to −0.51 MPa without wilting (Henning 1976; Choinski & Tuohy 1991; Johnson *et al.* 1996). Although the pre-dawn xylem pressure potential analysis for mopane suggests high water stress in the dry season (February *et al.* 2007), the species is able to survive water-stress conditions because of its ability to use water efficiently (Mantlana 2002), which is probably the result of its osmotic adjustment.

By using a combination of physical and physiological adaptations, mainly involving roots and leaves, mopane is able to tolerate the hot dry conditions mainly found in low-lying areas of southern Africa. All these adaptation mechanisms enable mopane to use the available limited moisture and nutrients effectively to survive semi-arid to arid conditions in southern Africa. This chapter further reviewed and determined the effect of environmental factors on the distribution of mopane in southern Africa. The variables used include rainfall, temperature, altitude, and soil types.

2.4 ENVIRONMENTAL DRIVERS AND FACTORS INFLUENCING MOPANE DISTRIBUTION

Various authors have shown that the distribution of mopane in southern Africa is associated with climatic and edaphic factors (Werger & Coetzee 1978; Madams 1990; O’Connor 1992). Its distribution is principally influenced by moisture availability expressed through rainfall, temperature, altitude and soil texture (Henning 1976; Werger & Coetzee 1978; Stevens *et al.* 2014). It should be noted that rainfall and temperature co-vary with altitude; however, Stevens *et al*. (2014) indicated that there is little evidence of which factors, or combinations thereof, determine the distribution limit of this species. This chapter therefore reviews and discusses the extent to which rainfall, temperature, altitude and soil types influence the distribution of mopane in southern Africa. The data used were derived from various sources (Tables 2.1 and 2.2). The areas covered by mopane in southern Africa (Table 2.1) was plotted against minimum (Min), average and maximum (Max) rainfall (R), temperature (T) and altitude (Alt) (Figures 2.3–2.5).

2.4.1 Rainfall

Mopane is distributed along variable rainfall gradient, ranging from 50 mm in Namibia to 1000 mm in Zambia per annum (Table 2.2). However, areas receiving low to moderate rainfall, especially between 400 and 800 mm per annum, better correlate with the distribution of mopane in southern Africa (Werger & Coetzee 1978; Madams 1990; Mapaure 1994). The above finding is closer to the average of 369–700 mm per annum as estimated in this chapter (Table 2.2). It includes all countries within its distribution, with the exclusion of Zambia where rainfall can reach 1 000 mm per annum. However, it should be noted that areas receiving 250 mm to 450 mm of rainfall per annum are considered as the most favourable environmental niche for the growth and distribution of mopane (Thompson 1960; Siebert 2012). This confirms that mopane prefers to occupy the low to moderate rainfall areas of most parts of southern Africa (Table 2.2).

The review showed that low rainfall positively correlates with the distribution of mopane in southern Africa, but the association becomes weak when the annual rainfall exceeds 600 mm per annum (Figure 2.3). This corroborates well with the findings by Porter (1968) and Henning (1976), who both indicated that an increase in rainfall to >800 mm per annum becomes the limiting factor for mopane distribution. As also indicated by Thompson (1960), the limitation of mopane from higher rainfall zones is most likely the result of competition with other species, which are more suited to those wetter conditions, low temperatures, acidic soil conditions, and high frequency of disturbances such as fires.

It seems that there is positive correlation between rainfall and mopane distribution, but this study concurs with Stevens *et al*. (2014) that rainfall alone cannot be considered as the major factor determining the distribution of mopane. It is further indicated that the probability of mopane presence drops to <50% when precipitation exceeds 380 mm in the wettest quarter (Stevens *et al*. 2014), which confirms that the species favours low rainfall areas (Figure 2.3). The likelihood of rainfall decline as a result of climate change means that it will further favour the distribution of mopane in areas such as Zambia, which is currently considered a high rainfall area.

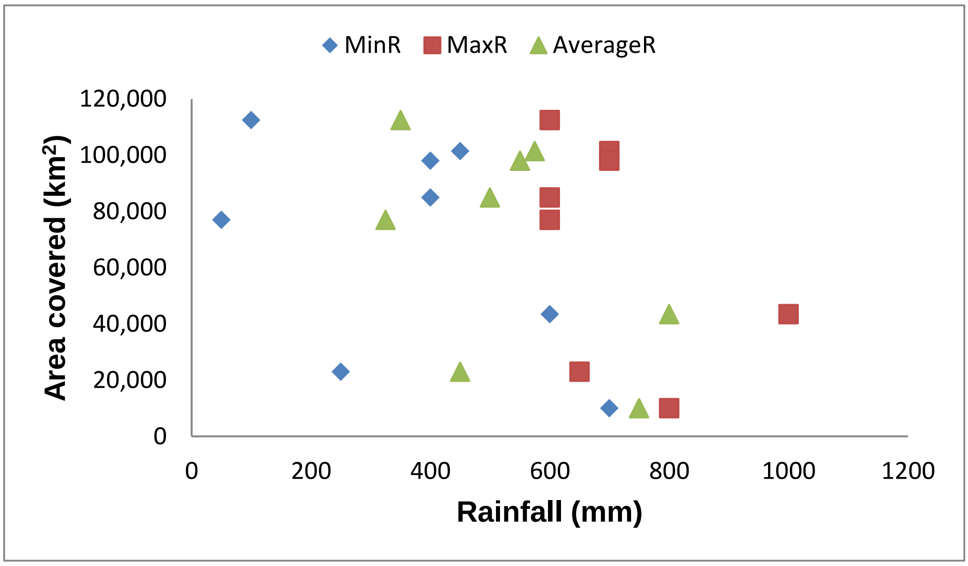

Figure 2.3: Effect of rainfall on the distribution of mopane in southern Africa.

2.4.2 Temperature

Mopane is distributed in hot and dry environments, where temperatures can exceed 35°C (Mucina & Rutherford 2006). Low winter temperature and frost are important limiting factors for mopane distribution, especially along its southernmost boundary (Siebert 2012; Stevens *et al.* 2014). The mean daily temperature regime within its distribution in southern Africa ranges from 12 to 31°C (Table 2.2), averaging between 16°C and 29°C, as also found by Du Plessis (2001). However, its distribution is limited in areas where the minimum winter temperature is below 5°C (Stevens *et al.* 2014), which confirms that the species is adapted to high temperature areas.

The review revealed that the distribution of mopane is best associated with an average daily maximum temperature of 30°C, but that relationship declines when the mean daily maximum temperature drops (Figure 2.4). According to Stevens *et al*. (2014), minimum temperature in the coldest month was the strongest determinant for mopane distribution, accounting for 42.2% of the modelled distribution. However, these results do not give a high degree of confidence of at least more than 50.0% to better explain an important factor associated with the distribution of mopane. It therefore means that temperature alone cannot be considered as the most important factor determining the distribution of mopane in southern Africa. It is, however, important to take into account that the probability of mopane presence drops below 50.0% at minimum temperatures, which is less than 5°C in the coldest month of July. Therefore, minimum temperature is predicted to limit the distribution of mopane from entering the cold interior of the southernmost boundary of southern Africa (Stevens *et al*. 2014). The limitation of mopane at low temperature zones is because of occasional events of frost (Whitecross *et al*. 2012; Stevens *et al*. 2014), which mainly destroys trees and shrubs less than 4 m in height (Whitecross *et al*. 2012). However, an increase in temperature, as a result of climate change, will further facilitate the distribution of mopane in areas currently considered as cold, especially in westwards and slightly southward areas (Stevens *et al*. 2014).

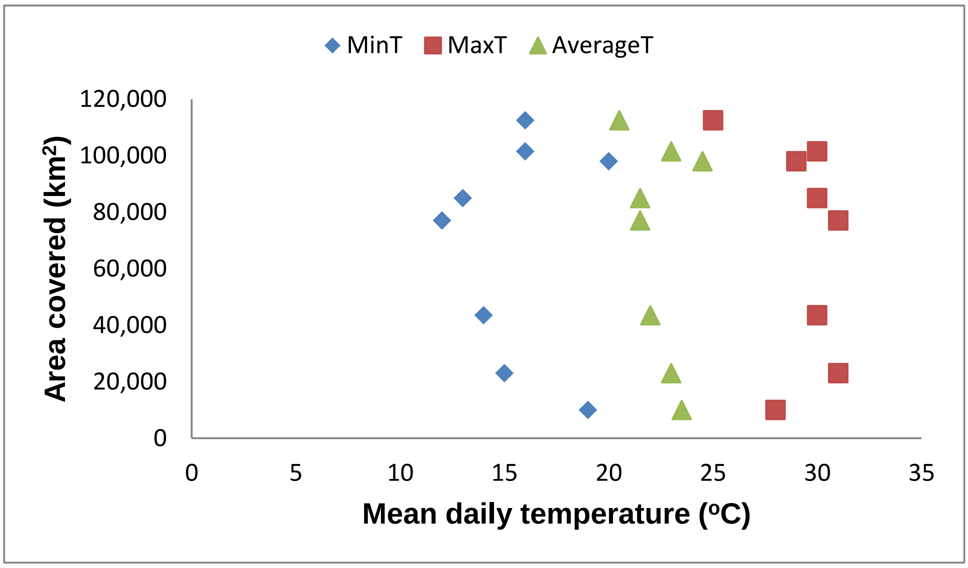

Figure 2.4: Effect of temperature on the distribution of mopane in southern Africa.

2.4.3 Altitude

Sebego (1999) indicated that topographic location may be one of the important factors determining the distribution of mopane. Siebert (2012) found that the occurrence of mopane is associated with low-lying, flat and undulating areas. The distribution of mopane is normally along the flood plains and valley bottoms of large rivers such as the Cunene, Chobe, Limpopo, Luangwa, Okavango, Shire and Zambezi (Werger & Coetzee 1978; Mapaure 1994). However, the information in this chapter indicates that mopane can be found at variable altitudes ranging from 100 m to 1200 m (Table 2.2), attaining optimal distribution and growth at altitudes ranging from 313 m to 856 m on average (Table 2.2), which is closer to the 200–600 m and 400–700 m average as indicated by White (1983) and Mapaure (1994), respectively. Porter (1968) further indicated that mopane rarely occurs at altitudes greater than 900 m, but this chapter suggests that it can occasionally be found at >900 m altitude in countries such as Angola, Namibia and Zambia (Table 2.2). These are normally areas where unfavourable soil conditions prevent the growth of other species (Henning 1976), thus favouring the distribution of mopane.

This review found that altitude alone cannot be considered as the most important factor determining the distribution of mopane in southern Africa (Figure 2.5). However, it is important to consider that while the distribution of mopane correlates well at low altitude, that relationship declines at higher altitudes (Figure 2.5). This finding corroborates the findings from various authors who also indicated that the distribution of mopane is associated with low-lying, flat and undulating areas (Werger & Coetzee 1978; Cole 1986; Mapaure 1994; Siebert 2012). This implies, as also indicated by Henning (1976), that the limited distribution of mopane at higher altitudes might be the result of combined influences of increased precipitation, lower temperatures, acidic soils, and disturbances such as fires.

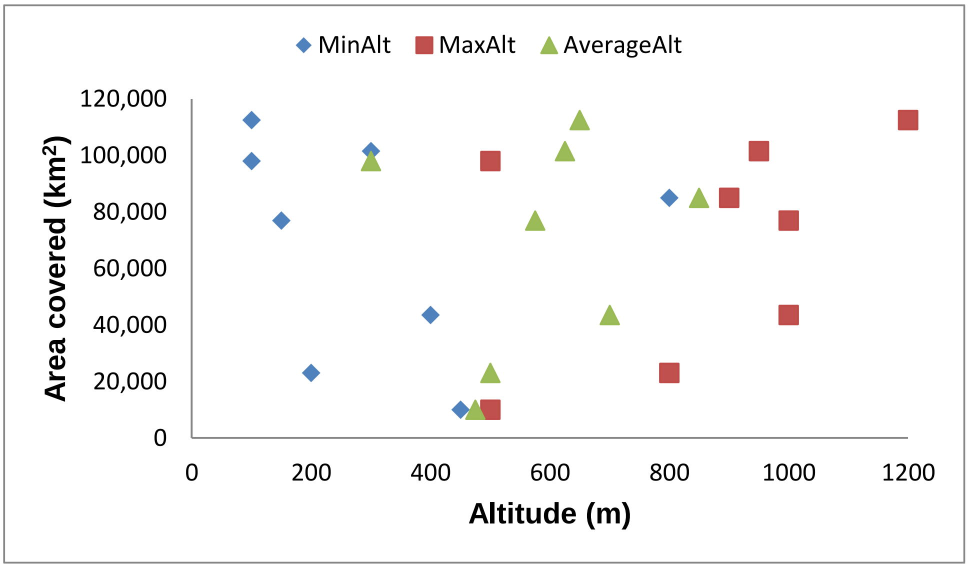

Figure 2.5: Effect of altitude on the distribution of mopane in southern Africa.

2.4.4 Soil type

According to Madams (1990), soil types also correlate well with the distribution of mopane. It is further shown that mopane is capable of surviving on a variety of soil types (Henning 1976; Madams 1990). It grows in arid areas on relatively fertile fine-grained soil, and sandy-loamy soil to clay soil (Table 2.2). Mopane is most frequently associated with shallow soils (Henning 1976), and normally found in alluvium and colluvium soils (Mapaure 1994). It is sometimes found in deep soil (Werger & Coetzee 1978), but it is viewed that the calcrete layer near the surface hinders mopane root penetration into the deep soil (Makhado *et al*. 2014). The soils in mopane areas tend to have high exchangeable sodium content (Werger & Coetzee 1978; Dye & Walker 1980) which inevitably results in reduced permeability and increased susceptibility to soil erosion (Scholes 1997). Mopane mainly survives on alkaline soils (Werger & Coetzee 1978), and is less common in acidic soils (Henning 1976). White (1983) further indicated that mopane does not occur on true saline soils in which water soluble salts exceed 0.2–0.3%. As a result, mopane is thus considered as an indicator species of alkaline soil (Werger & Coetzee 1978).

Soil having low nitrogen (<0.2% at 0–10 cm), phosphorus (<1.5 ppm), low moisture (15.0%) and exchangeable magnesium favours the growth and performance of mopane, but an increase in soil sodium and potassium levels results in a decline in the growth yield, which may be due to increased soil osmotic suction, whilst increasing magnesium seems to improve soil moisture uptake (Henning 1976). Therefore, mopane exhibits a shrub structure on shallow sodium-rich soils or clay soils derived from basalt (Mlambo 2006). These are areas with limited soil depth, normally occupied by ‘bonsai’ shrubby mopane, which grows up to 1.5 m in height. The ‘cathedral’ mopane grows quite tall on deep nutrient-rich alluvial soils (Mapaure 1994). It can grow up to 6 m in height on heavy impervious soils and up to 25 m in areas having sandy-loamy and alkaline soils (Werger & Coetzee 1978). It is also important to indicate that the distribution of mopane is limited in the acrisolic soils, possibly because acrisols are derived from acid igneous and metamorphic rocks that limit the growth of mopane, but support the growth of other species such as *Senegalia*, *Vachellia*, *Boscia*, *Grewia*, *Combretum* and *Terminalia* (Madams 1990).

2.5 ORDINATION OF MOPANE DISTRIBUTION

An ordination diagram was created, and it reinforces the influential environmental factors indicated in Table 2.2 that affected the distribution of mopane in different countries in southern Africa (Figure 2.6). The ordination graph shows that mopane is distributed under variable environmental conditions in different countries, but some countries have similar environmental conditions that influence the distribution of mopane. For instance, mopane in Namibia occurs under similar environmental conditions to those in Angola, but quite different from those in Mozambique, Malawi and Botswana (Figure 2.6). In addition, mopane in South Africa occurs under similar environmental conditions to those in Zimbabwe and Zambia, but quite different from those in Angola, Namibia, Mozambique, Malawi and Botswana (Figure 2.6). However, mopane demonstrates a relatively wide tolerance range for the various environmental factors under which it occurs within its distribution range.

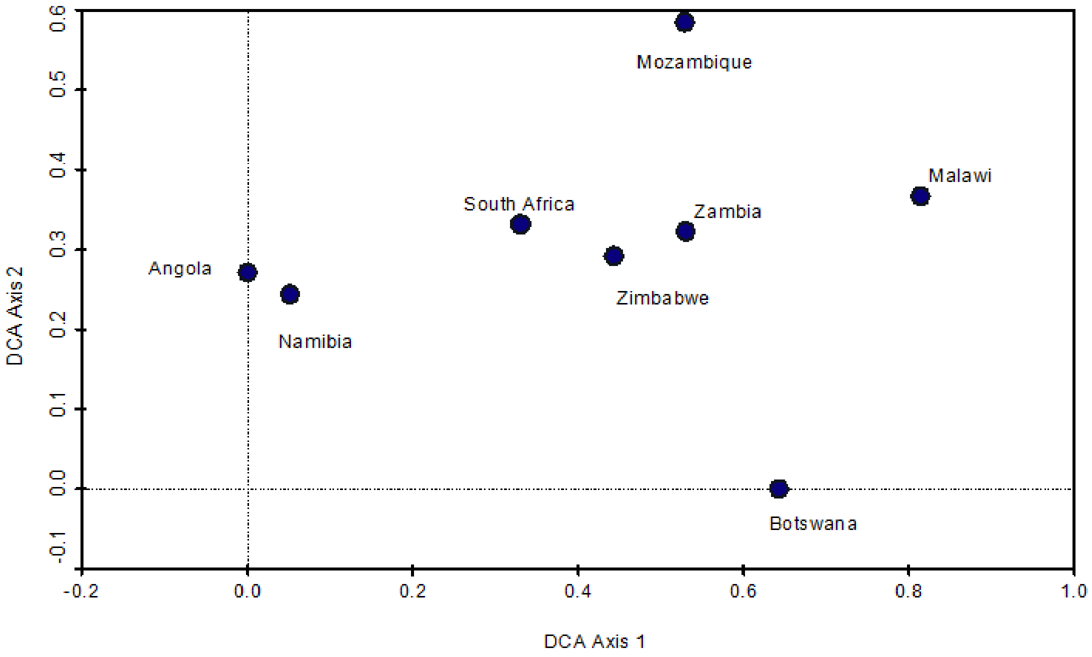

Figure 2.6: Ordination of the drivers of mopane distribution in different countries in southern Africa.

2.6 CONCLUSION

Colophospermum mopane is distributed along variable local climatic, topographical and edaphic factors in the low-lying areas of southern Africa. It mainly occupies areas receiving low to moderate rainfall, low-lying altitudes, high temperature areas and variable soil types. An increase of annual rainfall (>800 mm), altitude (>800 m), acidic soil and a decline of minimum winter temperature (<5^{o}C) limits the distribution of mopane. Limited distribution of mopane in areas receiving high rainfall, low temperatures and in higher altitudes is probably the result of the combined effects of freeze events, competitive interactions with other species and disturbances such as fires. An increase in temperature has the potential to drive mopane from its current distribution in high temperature areas to colder zones at its southernmost boundaries, whilst a reduction in annual rainfall could drive mopane from its current distribution in low to moderate rainfall areas to high rainfall zones. However, this chapter demonstrated that the distribution of mopane in southern Africa is not fundamentally determined by climatic factors, but possibly by edaphic factors (soil type and nutrients), competitive interaction with other species, and disturbances such as fires and browsing activity by large herbivores.

It is further concluded that the physical, chemical and physiological responses of mopane enable it to survive various disturbances and ‘harsh’ environmental conditions in southern Africa’s savanna ecosystem. This means that a better understanding of the adaptation mechanisms and distribution of mopane is critical and can be used to explain the distribution and survival of the species in these ‘harsh’ conditions in southern Africa. This understanding can also be used to further identify the ecology of the many mammalian and invertebrate herbivores that are found within the mopane ecosystem. Such information is essential for a holistic management of mopane woodland and shrublands in southern Africa.

However, because of the complexity associated with identifying factors which associate best with the distribution of mopane in southern Africa, this chapter recommends that such complexity be addressed through the development of an integrated model. Such a model needs to include climatic factors (rainfall and temperature), topographical factors (altitude and slope), edaphic factors (soil types and soil nutrients) and disturbances (fires, herbivory and competition). Once developed, such a model can significantly improve the precision of predicting the distribution of not just mopane, but also other vegetation formations and associated wild animals in the savannas.

CHAPTER 3

COLOPHOSPERMUM MOPANE LEAF PRODUCTION AND PHENOLOGY IN SOUTHERN AFRICA'S SAVANNA ECOSYSTEM[2]

3.1 INTRODUCTION

Colophospermum mopane is distributed in the hot and dry environments of southern Africa's savanna biome (Siebert 2012). It is physiologically adapted to tolerate water stress and high temperature conditions (Choinski & Tuohy 1991). Mopane folds its leaflets together (Madams 1990), closes the stomata (Mantlana 2002), and directs intercellular water to flow towards the inside of cells (Chen & Jianga 2010) during the heat of the day (Madams 1990). These physiological responses enable mopane leaves to restrict water loss through transpiration (Henning 1976), which allows mopane to tolerate drought conditions (Choinski & Tuohy 1991; Johnson *et al*. 1996).

Mopane leaves are alternate, with a single pair of large triangular leaflets (Henning 1976). The leaves are nutritious, containing between 6 and 13% of crude protein (Hooimeijer *et al*. 2005). In addition, mopane maintains its foliage well into the dry season, thus providing important forage for browsers and intermediate feeders (Kos *et al.* 2012). Dry mopane leaves are a valuable source of browse for herbivores (Curlewis 2016) such as elephants (Ben-Shahar & MacDonald 2002), greater kudu (Hooimeijer *et al*. 2005) and other ungulates found in mopane woodland, particularly during the dry season (Makhado *et al.* 2016).

Considering the ability of mopane to survive water stress conditions (Choinski & Tuohy 1991; Johnson *et al*. 1996) and its value in supplying nutritious forage to browsers within its distribution range in southern Africa's savanna biome (Hooimeijer *et al*. 2005), knowledge of mopane leaf production and phenology

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[2] Makhado, R.A., Potgieter, M.J. & Luus-Powell, W.J. 2018. *Colophospermum mopane* leaf production and phenology in southern Africa's savanna ecosystem - A review. *Insights of Forest Research* 2(1): 84–90.

becomes important. It is essential to determine the availability and quality of mopane leaves, which also has a direct influence on habitat selection by browsers and their spatial distribution in mopane woodland. The attainment of knowledge on mopane leaf availability and quality requires a better understanding of leaf production and phenology. Unfortunately, limited research has been undertaken in these areas. Studies on mopane leaf production are limited to those of Hrabar (2005), Ghazoul (2006), Wessels *et al*. (2006), Hrabar *et al*. (2009) and Kohi *et al*. (2010). Limited studies on mopane leaf phenology have also been done by Guy *et al.* (1979), Styles and Skinner (1997) and Kohi *et al.* (2010). Considering that mopane is widely distributed in southern Africa's savanna, this knowledge gap makes it difficult for game ranchers and conservationists to fully understand the availability and quality of forage in mopane-dominated areas. It further hinders effective monitoring of the state of health of mopane and the spatial distribution of browsers in the mopane woodland.

As a result, there is a need to review and integrate the available and accessible information extensively in order to fully understand mopane leaf production and phenology and its implication for browsers in southern Africa's savanna. The availability of information is important in informing game ranchers and conservationists about how mopane woodland can best be managed in order to supply browsers with sustainable, adequate and quality browse. It is also critical for guiding future research, management of mopane and the herbivores it supports through forage in the mopane woodland.

3.2 MOPANE LEAF PRODUCTION

It is important to assess mopane leaf production because it has a significant effect on leaf availability to browsers (Smit 2001). However, the optimum productivity of mopane leaves is affected by factors such as defoliation by mopane worms (Adelabu 2013), fires (Seydack *et al*. 2014), browsing pressure (Ben-Shahar 1993) and climatic variability (Seydack *et al*. 2014) including frost (Whitecross *et al*. 2012).

Wessels *et al*. (2006) simulated the browsing effect on mopane leaf production through coppicing and pruning in the Musina area, Limpopo Province. In addition, Kohi *et al*. (2010) simulated the browsing effect on mopane leaf production through defoliation at 50%, 75%, 90% and 100% in the Kruger National Park. The results indicated that the number of leaves between different defoliation levels were not different (Kohi *et al*. 2010). The mean number of leaves remained highest almost continuously for the control plants. During early summer, the plants from the 100% defoliation treatment produced a larger number of leaves than those subjected to the 50% treatment. At the end of the experiment, the 100% defoliated plants had the lowest number of leaves (Kohi *et al*. 2010), which suggests that heavy browsing could have a negative effect on mopane leaf production.

Hrabar (2005) also indicated that defoliation of mopane leaves by mopane worms significantly reduces the density of mopane leaves as compared with non-defoliated trees. In addition, the number of mopane leaves on trees browsed by elephants was significantly lower than the number of leaves on non-pruned trees (Hrabar *et al*. 2009). The causes of the reduction in the number and density of leaves in recovered defoliated and pruned mopane trees are uncertain, but could be due to resources being stored for reproduction instead of flushing new leaves. Hrabar (2005) and Hrabar *et al.* (2009) explained that pruning by elephant's results in the production of longer shoots with larger leaves, while defoliation by mopane worms results in flushing of shorter shoots and smaller leaves.

Other studies put forth that rainfall (Wessels *et al*. 2006) and stem basal area (Scholes 1990) also have an influence on leaf production. This suggests that above average rainfall and trees with large basal stem areas can increase leaf production. Wessels *et al*. (2006) adds that mopane leaf production does not follow any consistent pattern during the growing season but is greatly triggered by rainfall (Mlambo & Nyathi 2008). The production of mopane leaves starts after the first rain (Sebego 1999), normally during late October to early November (Dekker & Smit 1996; Figure 3.1). According to Curlewis (2014), the production of new leaves did not cease during the wet season, but continued to a lesser degree during the late wet season into the early dry season. Mopane trees and shrubs reach optimum leaf production between February and March (Figure 3.1). Growth season cumulative leaf production reaches its maximum in June and starts to decrease in August (Figure 3.1), possibly because of reduction in soil moisture following decline in rainfall.

Smit (2001) indicated that plant thinning increases mopane leaf biomass, but that varies annually following rainfall patterns (Mlambo & Nyathi 2008). Estimates show that mopane leaf biomass in the northern Limpopo Province, South Africa is 1.1 tonnes/ha (Smit 1994), which is lower than the 1.6 tonnes/ha estimated in south-eastern Zimbabwe (Kelly & Walker 1976 cited in Mutakela 2009). Dekker and Smit (1996) also indicated that the total leaf dry matter of mopane in the Limpopo mopane woodland was 1.4 tonnes/ha, which is within the 0.6–1.7 tonnes/ha estimated in the same locality by Smit and Rethman (1998). An important point is that mopane contributes significantly to the total leaf dry matter in all communities in the Limpopo mopane woodland (Dekker & Smit 1996). Therefore, it is the high leaf production of mopane (Dekker & Smit 1996) and its nutritional content (Hooimeijer *et al*. 2005) that make it an essential species in providing forage for browsers, especially during the dry season (Makhado *et al*. 2016).

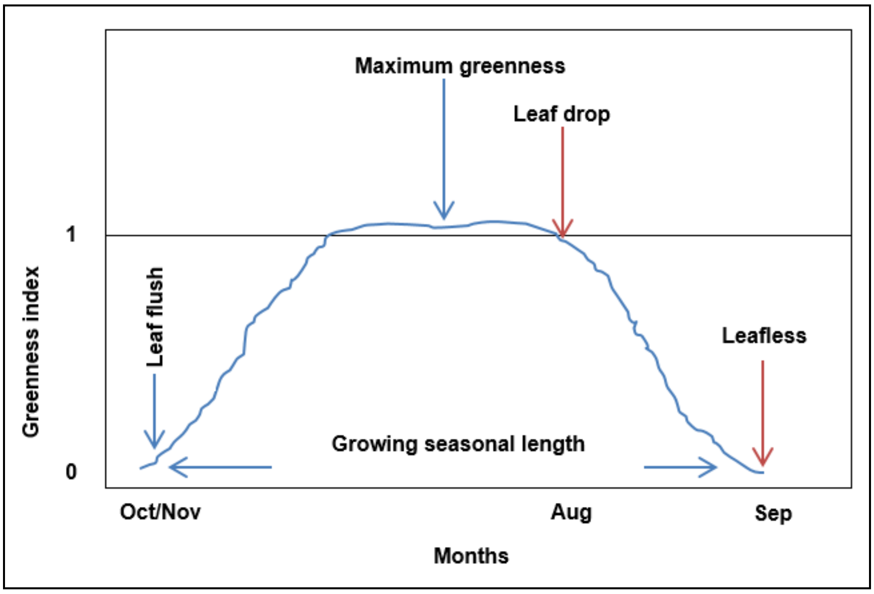

Figure 3.1: Theoretic analysis of mopane leaf production and phenology.

3.3 MOPANE LEAF PHENOLOGY

Leaf phenology is defined in this study as the timing of leaf flush, growth and fall (Figure 3.1). Leaf flush and fall are attributed to changes in environmental conditions, and also the effect of fire and browsers on the plant. According to Fuller (1999), leaf phenology is an essential indicator of plant health and environmental stresses such as soil moisture, soil nutrients and solar radiation. Phenological studies assists in monitoring and predicting vegetation responses to interannual climatic variability (White *et al.* 1997). Changes in leaf phenology also indicate modifications in the environment. For instance, leaf flush shows the availability of moisture in the soil, while leaf fall directs specifies a deficiency of soil moisture. Phenology is therefore recognised as one of the simplest and most effective indicators to study the impact of climate change (Menzel 2002; IPCC 2007), fires and herbivores on plants (Scholes & Archer 1997; Sankaran *et al.* 2005).

According to Guy *et al*. (1979), there are five main phenological stages in southern Africa's savannas, which are the pre-rain (September–October), early rainy (November–December), mid-rainy (January–February), late rainy (March–April) and dry seasons (May–August). The dry (May–September) and wet (October–April) seasons are critical periods for determining leaf phenology and production. Mopane leaf flush occurs after the first summer rain (Wessels 2002), usually during October and November (Madams 1990). Styles and Skinner (1997) observed that in Namibia and Botswana mopane leaf flush may be independent of rain. This implies that the ability of mopane to flush its leaves before the first summer rain is mainly due to its ability to store energy, nutrients and water, which are used to flush new leaves even before the first rain.

Newly emerged mopane leaves are soft (Potgieter & Wessels 1998), appear at the beginning of November (Dekker & Smit 1996) and become leathery when they mature (Potgieter & Wessels 1998). The mature green mopane leaves remain on the tree until they turn yellowish or reddish-brown with the onset of the dry season, particularly around May. However, most of the dry or dead leaves remain on the tree until they are blown off by wind (Guy *et al.* 1979), especially from August to early September (Dekker & Smit 1996). Mopane leaves are shed in an irregular fashion at the onset of the dry season (Wessels 2002), and the trees are generally leafless from August to early October (Dekker & Smit 1996), although some of the leaves may remain on the tree until the beginning of summer.

According to Chidumayo and Frost (1996), the leaves may be shed early in the dry season when rainfall is below average, but during above average rainfall, the leaves may remain on the plant until late into the dry season. According to Fuller (1999), the mopane leaf's phenological pattern enable it to have a prolonged growing season. The growing season may last for 10 months (Figure 3.1), giving mopane longer leaf carriage than most other species in the mopane woodland.

The phenology of species in mopane woodland seems to be related to rainfall and temperature, but rainfall seems to be the main factor influencing variation in leaf phenology (Chidumayo 2001). Studies by Archibald and Scholes (2007) as well as Wessels *et al*. (2011) in the savanna, confirm that soil moisture, as a function of rainfall, is the major influence on the phenology of savanna species. In addition to environmental influences on mopane leaf phenology, browsers such as mopane worms, greater kudu and elephants also have an influence on mopane leaf phenology.

For instance, mopane worm browse 90% of mopane leaves (Toms & Thagwana 2005), which disturbs leaf growth and phenology (Adelabu 2013). The tree flushes new leaves after defoliation (Guy *et al*. 1979), but leaf development and phenological stages are disturbed. The flushed leaves after trees have been defoliated could explain why mopane has a prolonged growing season, as depicted in Figure 3.1.

Defoliation of mopane leaves by mopane worms seems to be a more significant disturbance of leaf phenology than browsing by mammalian herbivores. This is due to the high number of mopane worms on a tree, against the one or two browsing mammals which feed on a few leaves and then move to the next tree. In addition, browsing of mopane leaves by mammalian herbivores during the growing season is limited by high production of secondary metabolites such as tannins and phenols (Wessels *et al*. 2007). This suggests that the impact on mopane phenological stages by browsing mammals could be minimal, but is significant for defoliation caused by mopane worms.

3.4 IMPLICATION OF LEAF PRODUCTION AND PHENOLOGY FOR BROWSERS

Mopane leaf production and phenology have great implications for browsers because they determine the availability and quality of forage. Janecke and Smit (2011) indicated that plant phenology has a profound effect on browsers. Browsers such as the greater kudu are negatively affected by a shortage in forage supply (Owen-Smith 1979) as well as the quality of the forage. The distribution and habitat selection of many browsers is therefore determined, among others, by forage availability (Janecke & Smit 2011) and quality in a particular season.

Seasonal differences in the relative contribution of woody plants to browsers' diet are also related to phenological changes during certain seasons and between seasons. However, seasonal variations in diet composition are not entirely attributable to variations in forage availability but also to the accessibility of preferred species for browse (Curlewis 2014). Shortage of forage supply and quality can result in mortality of browsers such as the greater kudu, especially in fenced protected areas (Smit 2001).

Leaf production therefore influences the time that browsers can stay in a particular habitat, while phenology influences the diet selection of browsers, as determined by forage quality, during different phenological stages. As indicated by Curlewis (2014), the selection of diet by browsers such as the greater kudu may vary between seasons, with species being favoured in one season but rejected in another. For instance, mopane leaves are highly browsed during the dry season (Makhado *et al*. 2016) but not preferred during the wet season, even though the quality is higher (Hooimeijer *et al*. 2005), mainly because of a high concentration of secondary metabolites such as tannins and phenols (Wessels *et al*. 2007).

During dry season (May to September), fallen dry mopane leaves constitute a significant amount of leaves on the ground in the mopane woodland (Dekker & Smit 1996). These leaves add to a sustainable supply of forage to browsers in mopane-dominated areas and contribute significantly to the diet of browsers (Macala *et al*. 1992) such as the greater kudu (Hooimeijer *et al*. 2005), elephant (Kos *et al.* 2012) and other ungulates. The ability of the mopane tree to carry its leaves longer into the dry season (Dekker & Smit 1996; Figure 3.1), when most savanna species are leafless (Kos *et al.* 2012), makes it the most influential fodder resource for many browsers in the mopane woodland (Mlambo & Nyathi 2008).

3.5 CONCLUSION

Leaf production and phenology are important parameters to measure the temporal and spatial changes in the leaves, which is critical in determining the availability and quality of forage for browsers in a particular season. It is also important in determining leaf physiology and stress. The availability and quality of leaves seems to be mainly associated with leaf growth, which is a factor of soil moisture. The variation in soil moisture is triggered by rainfall.

Leaf production and phenology therefore play a significant role in determining the season in which mopane will be highly preferred by browsers. Mopane leaves are preferred by mammalian browsers during the dry season, when the leaves are dry and secondary metabolites are relatively low. In addition, the high leaf production and the ability of mopane to carry its leaves longer into the dry season than most savanna species makes it one of the more important species in providing essential browse in the mopane woodland, and it is thus highly browsed during that period.

CHAPTER 4

NUTRITIONAL VALUE OF *COLOPHOSPERMUM MOPANE* AS SOURCE OF BROWSE AND ITS CHEMICAL DEFENCES AGAINST BROWSERS: A REVIEW[3]

4.1 INTRODUCTION

Colophospermum mopane is a deciduous species (Henning 1976) and flushes its leaves after the first summer rains (Wessels 2002), usually during October/November (Madams 1990; Dekker & Smit 1996). Young mopane leaves are reddish brown and glossy (Palgrave 1981 cited in Timberlake 1995), and become green as they mature (Werger & Coetzee 1978). The leaves turn yellowish with the onset of the dry season (Styles & Skinner 1997), and reddish-brown before being shed (Werger & Coetzee 1978). The dry or dead mopane leaves remain on the plant until blown off by wind, mainly from August to October (Dekker & Smit 1996). The pods are yellowish brown and contain numerous scattered resin glands on the surface. They can be readily dispersed by wind. Seeds are reniform and corrugated, with numerous small sticky reddish glands (Jordaan & Wessels 1999), which enable the seeds to be easily dispersed by browsers.

Mopane is highly browsed by the greater kudu (Hooimeijer *et al*. 2005; Curlewis 2014), elephant (Kos *et al*. 2012), and domestic animals such as cattle (Bonsma 1942 cited in Timberlake 1995) and goats (Lundu 2012). The nutritional value in mopane makes it to be an important dry-season browse for herbivores (Hooimeijer *et al*. 2005). Mopane maintains its foliage well into the dry season, and thus provide important forage for browsers and intermediate feeders when most other trees and shrubs in the mopane savanna are leafless (Kos *et al.* 2012). In addition, mopane twigs, seeds and pods are also highly nutritious and provide essential dry

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[3] Makhado, R.A., Potgieter, M.J. & Luus-Powell, W.J. 2016. Nutritional value of *Colophospermum mopane* as source of browse and its chemical defences against browsers: A review. *Journal of Animal & Plant Sciences* 26: 569–576.

season browse (Macala *et al.* 1992). The minimum value of crude protein in mopane leaves, twigs and pods during September is 8.4%, 4.2% and 8.6%, respectively (Table 4.1); while grasses contain less than 6% in that month (Bonsma 1942 cited in Timberlake 1995). This implies that the nutritional value of mopane is generally higher than grasses (Codron *et al*. 2007), which makes mopane leaves, twigs, seeds and pods to be highly accepted by browsers, especially during the dry season (Hooimeijer *et al*. 2005).

Browse nutritional value of mopane therefore explain why many rangelands, game reserves, and national parks in the southern Africa's savanna are found in the mopane woodland. Most browsers utilise mopane forage during the dry season (Hooimeijer *et al*. 2005), but it is less favoured during the wet season, due to the high levels of secondary metabolites such as phenols and tannins (Wessels *et al*. 2007).

Despite the value of mopane in providing nutritional browse to animals in mopane woodland, especially during the dry season (Makhado *et al*. 2016) and drought years (Macala *et al*. 1992), there is lack of consolidated datasets on mopane leaf quality. Previous studies on mopane nutritional values are limited (e.g. Bonsma 1942; Van Voorthuizen 1976; DHV 1979; Mosimanyana & Kiflewahid 1988; Macala *et al*. 1992; Hooimeijer *et al*. 2005). In addition, there are limited studies documenting the type and quantity of secondary metabolites in mopane forage (e.g. Styles & Skinner 1997; Hooimeijer *et al*. 2005; Wessels *et al*. 2007; Kohi *et al*. 2010) throughout the year, and its effects on browsers. Considering that mopane is widely distributed in the mopane woodland, this knowledge gap is making it difficult for ranchers and conservationists to better understand the browsing behaviour of wild animals, and their spatial distribution in relation to forage quality in the mopane woodland. It further hinders on effective implementation of plans and strategies for the management of mopane woodland and the browsers it supports. As a result, there is a need to extensively review and integrate the available scanty information on mopane quality. Such information is necessary in order to better understand the browser-plant relationship in the mopane woodland.

4.2 ATTRACTANCE TO BROWSERS – NUTRITIONAL VALUE

Mopane is rich in vital nutrients such as crude protein, calcium, phosphorus (Bonsma 1942; Table 4.1) and essential fatty acids (Lawton 1968 cited in Timberlake 1995). The leaves also contain a high concentration of energy which is essential to the diet of browsers (Styles & Skinner 1997). These nutrients are required for healthy growth and development of browsers.

This review shows that the percentage of these nutrients in mopane leaves varies little throughout the year (Table 4.1; Figure 4.1), which suggests that the nutrients are relatively constant regardless of the season. However, these nutrients, excluding phosphorus, increased slightly from September and reached a maximum in December–January, during the leaf growing season. The concentration of nutrients starts to decline from February and reached its lowest levels in July, following a decline in rain (Table 4.1; Figure 4.1). The increase and decline of nutrients levels in mopane leaf is related to the age and growth of the leaves (Wessels *et al.* 2006; Kasale 2013), which seems to be triggered by rainfall (Table 4.2).

Table 4.1: Seasonal nutritional values of *Colophospermum mopane*.

Parts	**Jan**	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**	**Reference**
Leaves													
CP (%)	13.7	13.7	12	12.4	11.2	11.5	*	13.8	8.4	11.6	16.6	12	a
	14.7	*	*	8.1	*	*	12.3	*	10.2	*	*	12.6	b
	11.1	10.1	10.0	10.6	12.6	11.0	10.5	10.6	9.5	6.2	9.4	11.3	c
	*	*	*	*	10.53	9.01	9.23	8.97	*	*	*	*	d
	15.92	*	*	12.9	*	*	9.31	*	*	9.94	*	*	e
Min	11.1	10.1	10.0	8.1	10.5	9.0	9.2	9.0	8.4	6.2	9.4	11.3	
Max	15.9	13.7	12.0	12.9	12.6	11.5	12.3	13.8	10.2	11.6	16.6	12.6	
Average	13.9	11.9	11.0	11.0	11.4	10.5	10.3	11.1	9.4	9.2	13.0	12.0	
s.d.	2.0	2.5	1.4	2.2	1.1	1.3	1.4	2.5	0.9	2.8	5.1	0.7	
P (%)	0.19	0.18	0.14	0.13	0.20	0.12	*	0.19	0.12	0.12	0.23	0.19	a
	*	*	*	*	0.19	0.15	0.14	0.14	*	*	*	*	d
Average	0.19	0.18	0.14	0.13	0.20	0.14	0.14	0.17	0.12	0.12	0.23	0.19	
Ca (%)	0.51	1.80	2.04	1.41	2.28	1.33	*	1.35	3.23	2.98	1.15	1.37	a
	*	*	*	*	1.74	1.42	1.45	1.40	*	*	*	*	d
Average	0.51	1.80	2.04	1.41	2.01	1.38	1.45	1.38	3.23	2.98	1.15	1.37	
EN (%)	18.55	*	*	19.45	*	*	20.43	*	*	19.12	*	*	f
MO (%)	43.05	*	*	41.13	*	*	32.73	*	*	45.81	*	*	f
CF (%)	28.1	27.6	26.8	26.7	25.1	24.8	*	21.9	24.9	25.3	22.1	27.6	g
Seeds													
CP (%)	*	*	*	19.5		*	*	*	*	*	*	*	b
P (%)	*	*	*	0.43		*	*	*	*	*	*	*	b
Ca (%)	*	*	*	0.35		*	*	*	*	*	*	*	b
Pods													
CP (%)	*	*	*	8.6-15.9		*	*	*	*	*	*	*	b, i
P (%)	*	*	*	0.16		*	*	*	*	*	*	*	b
Ca (%)	*	*	*	0.82		*	*	*	*	*	*	*	b
Twigs													
CP (%)	*	*	*	4.2-5.0		*	*	*	*	*	*	*	b, j
P (%)	*	*	*	0.07		*	*	*	*	*	*	*	b
CA (%)	*	*	*	1.40		*	*	*	*	*	*	*	b
AverR (mm)	76.95	70.15	54.9	31.9	11.05	8.45	7	9.25	12.15	28.65	48.7	58.6	h
AverT (ºC)	24.7	24.05	22.8	19.7	16.1	12.95	12.85	15.3	18.85	21.4	23	24.05	h

References: a=Bonsma 1942, b=DVH 1979, c=Hooimeijer *et al*. 2005, d=Macala *et al*. 1992, e=Mantlana 2002, f=Styles & Skinner 1997, g=Van Voorthuizen 1976, h= World Bank Climate Data for South Africa and Botswana 1960-1990, i=Myre & Coutinho 1962, j=Walker 1980. **Symbols**: CP=Crude Protein, P=Phosphorus, Ca=Calcium, EN=Energy, MO=Moisture, CF=Crude fibre; AverR=Average Monthly Rainfall, Max=Maximum, Min=Minimum, AverT=Average Monthly Temperature, s.d=standard deviation, *=no data.

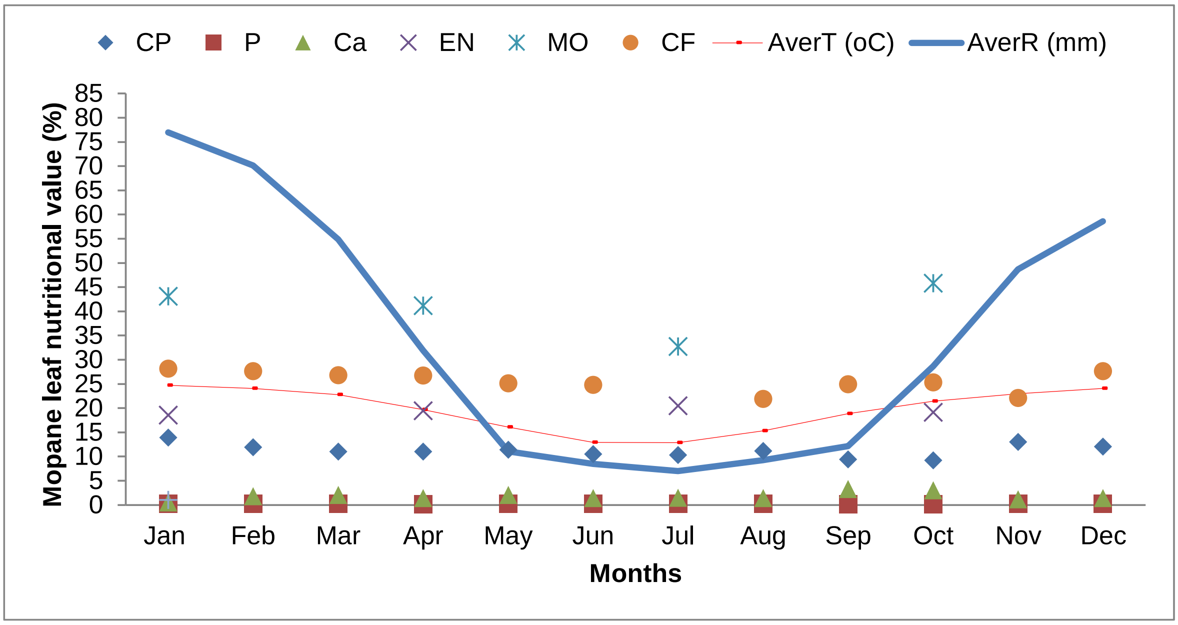

Figure 4.1: *Colophospermum mopane* leaf nutritional value. The CP, P, Ca, CF levels shows no significant variation over the year. Data used to plot the graph derived from Table 4.1. Symbols: CP= Crude Protein, P=Phosphorus, Ca=Calcium, EN=Energy, MO=Moisture, CF=Crude fibre, AverT=Average Monthly Temperature, AverR=Average Monthly Rainfall.

4.2.1 Crude protein

Protein synthesises amino acids, which are critical in enhancing the immune response, cellular repairs and formation of blood cells and tissues (FAO 2004). Mopane leaves, twigs, seeds and pods contain crude protein (Table 4.1) which is an essential nutrient in the diet of browsers. The average crude protein values in mopane leaves ranged from a minimum of 9.2%±2.8% in October to a maximum of 13.9%±2.0% in January (Table 4.1). In addition, the level of crude protein in mopane twigs and pods ranged from 4.2–5.0% and 8.6–15.9%, respectively (Table 4.1). Owen-Smith and Cooper (1989) indicated that the protein requirement for browsers such as the greater kudu is 9% at the end of dry season and 12–14% in the late wet season. This suggests that the levels of crude protein in mopane are within the required levels to meet the greater kudu diet requirement. The concentration of crude protein in mopane leaves is high during the summer season, but declines during the winter season. Crude protein values start to decline from its highest level in February until it reaches its lowest level in October. High values of crude protein in mopane leaves were observed in November, December and January at 13.0%±5.1%, 12.0%±0.7% and 13.9%±2.0% on average, respectively (Table 4.1; Figure 4.1). However, the slight seasonal variation in the amount of crude protein is due to the age of the leaf (Wessels *et al*. 2006; Kasale 2013), which is also triggered by rainfall and temperature patterns (Figure 4.1; Table 4.2). As a result, the average monthly rainfall and temperature datasets for South Africa and Botswana (World Bank 1960–1990), where these studies were carried out, were used to test the correlation between mopane leaf quality and climatic variables (Table 4.2). The statistics shows a positive correlation between leaf quality and climatic variables, especially rainfall, which suggests that rainfall is the main variable that triggers the variation in the quantity of nutrients and secondary metabolites in mopane leaves (Table 4.2).

Table 4.2: Pearson Correlation Coefficient Analysis between mopane leaf quality and climatic variability. Data used to test the correlation is presented in Tables 4.1 and 4.3.

	Correlation (*r*)			
	Average crude protein	Total phenols	Condensed tannins	Protein-precipitating tannins
Rainfall	0.860	0.681	0.824	0.648
Temperature	0.540	0.865	0.928	0.789

4.2.2 Phosphorus and calcium

Phosphorus and calcium play a vital function in maintaining healthy bones and teeth (Harty 2014). The concentration of phosphorus in mopane leaves seems to be constant and does not appear to vary significantly throughout the year (Figure 4.1) which suggests no pattern, except perhaps in the age of leaf after flushing. The concentration of phosphorus in mopane leaves ranges from a minimum of 0.12% from September to a maximum of 0.23% in November (Table 4.1; Figure 4.1).

In contrast, the concentration of calcium in mopane leaves ranges from a minimum of 0.51% in January to a maximum of 3.23% in September. The level of calcium in mopane leaves is generally less than 2.1% for the months of January to August and November to December. However, the highest amount of calcium in mopane leaves is 3.23% in September (Table 4.1; Figure 4.1), which does not correlate with either the growth of the leaf or climatic patterns, but the lack of data might be the main cause of the indistinct pattern. The level of phosphorus in mopane seeds, pods and twigs is 0.43%, 0.16% and 0.07% during April, respectively. In addition, calcium concentration in mopane seeds, pods and twigs is 0.35%, 0.82% and 1.40%, respectively, within the same month (Table 4.1).

4.2.3 Energy, moisture and crude fibre

Energy plays a critical role in animal physical health, while moisture facilitates the digestibility of the forage. Moist forage with low crude fibre and secondary metabolites and high energy concentration are essential for the good health of animals. The concentration of energy in mopane leaves is lowest in January (18.55%) and reaches its maximum in July (20.43%) (Table 4.1; Figure 4.1). The amount of energy in mopane leaves shows insignificant variation throughout the seasons, which suggests that seasonal changes have a limited effect on the amount of energy in mopane leaves.

However, although mopane leaves contain energy needed by browsers, the digestibility of the leaves can also be influenced by fibre. According to Cooper and Owen-Smith (1985), fibre influences the digestibility as well as acceptability of the leaves by browsers. The amount of fibre shows little variation throughout the year, but seems to be at its greatest during the summer season, while declining during the winter season (Table 4.1; Figure 4.1). Though there is limited data from this review, Wessels *et al*. (2006) and Kasale (2013) both indicated that the level of fibre in mopane leaf is primarily associated with the growth of the leaf. Based on the view of Cooper and Owen-Smith (1985) that fibre influences digestibility as well as acceptability of the leaves by browsers, it is therefore suggested in this chapter that mopane leaves can be easily digested during winter season, when the leaves are dry, as opposed to summer season when the leaves are still growing.

4.2.4 Essential fatty acids and oil

Mopane leaves also contain essential fatty acids (Lawton 1968 cited in Timberlake 1995), which promotes good health for browsers. However, there is no data available on the amount of fatty acids in mopane leaves. This suggests that there is a need to quantify the amount of essential fatty acids found in mopane leaves.

However, various compounds were identified in mopane leaf oil. These compounds mainly comprise α-pinene (Brophy *et al*. 1992; Chagonda *et al.* 2011), which plays a significant role as an antibiotic and thus prevents animals from being affected by various diseases. Brophy *et al*. (1992) indicated that the concentration of α-pinene compound in mopane leaf oil is high at 67% during the summer season and declines slightly to 55% during the winter season. Similarly, Chagonda *et al*. (2011) observes that α-pinene compound in mopane leaf oil is 71.6% in green mopane leaves during summer and then declines to 58.2% during winter.

4.3 DETERRENCE TO BROWSERS – SECONDARY METABOLITES

Plants and herbivores of African savanna have co-existed for millions of years. As a result, they have developed different approaches that enable them to co-exist in the same ecosystem (Scholes & Walker 1993). Mopane, for instance, produces secondary metabolites such as tannins and phenols to reduce browsing pressure during the growing season (Wessels *et al*. 2007). However, the level of secondary metabolites in mopane leaves varies per season (Table 4.3; Figure 4.2). The concentration of total phenols, condensed tannins and protein-precipitating tannins in mopane foliage ranged from a minimum of 48.4 mg g^{-1}, 53.1 mg g^{-1} and 58.8 mg g^{-1} in August to a maximum of 96.7 mg g^{-1}, 112.4 mg g^{-1} and 142.0 mg g^{-1} in December, respectively (Table 4.3).

The concentration of tannins and phenols starts to increase from September with the onset of the rains, and reached maximum levels in December to January. As indicated by Wessels *et al*. (2007), green young mopane leaves contain high amounts of tannins and phenols, as opposed to reddish-brown older leaves. This confirms a pattern observed and presented in Table 4.3 and Figure 4.3, which shows that phenols and tannins start to decline from February and reached the lowest level in July and August, when the leaves are at senescene stage. This further confirms that the variation in the concentration of secondary metabolites is associated with the age and growth of the leaf (Coley 1988; Wessels *et al*. 2006;

Kasale 2013), as well as a natural adaptation mechanism to inhibit herbivores from browsing the leaves, during the growing season (Wessels *et al*. 2007). In addition, the variation in the amount of secondary metabolites appears to be triggered by rainfall (Table 4.2; Figure 4.2).

The increased levels of secondary metabolites during the summer season therefore support the ‘induced defence’ theory that mopane increase herbivore deterring substances (Wessels *et al*. 2007) as a mechanism to reduce browsing pressure. This implies that browsing on mopane is mainly experienced during winter rather than in summer.

Table 4.3: Concentration of secondary metabolites in mopane leaves. There is significant variation on the amount of TP, CT and PPT throughout the year, which follows leaf flush.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Reference
TP (mg g-1)	*	74.7	*	69.6	*	51.2	*	48.4	*	91.5	*	96.7	a
P (%)	8.0	3.5	4.2	5.2	6.0	5.6	6.8	6.3	5.8	3.6	13.0	7.5	b
CT (mg g-1)	*	98.0	*	83.9	*	62.4	*	53.1	*	101.0	*	112.4	a
CT (mg g-1)	*	63.19	*	70.87	*	*	74.29	*	*	80.05	*	*	c
PPT (mg g-1)	*	90.0	*	87.5	*	68.7	*	58.8	*	111.6	*	142.0	a
AverR (mm)	76.95	70.15	54.9	31.9	11.05	8.45	7	9.25	12.15	28.65	48.7	58.6	d
AverT (oC)	24.7	24.05	22.8	19.7	16.1	12.95	12.85	15.3	18.85	21.4	23	24.05	d

References: a=Wessels *et al*. 2007; b=Hooimeijer *et al*. 2005; c=Styles and Skinner 1997; d= World Bank Climate Data for South Africa and Botswana, 1960-1990. Symbols: TP = total phenols, P=phenol, CT = condensed tannins, PPT = protein-precipitating tannins, AverR=Average Monthly Rainfall, AverT=Average Monthly Temperature; *=no data.

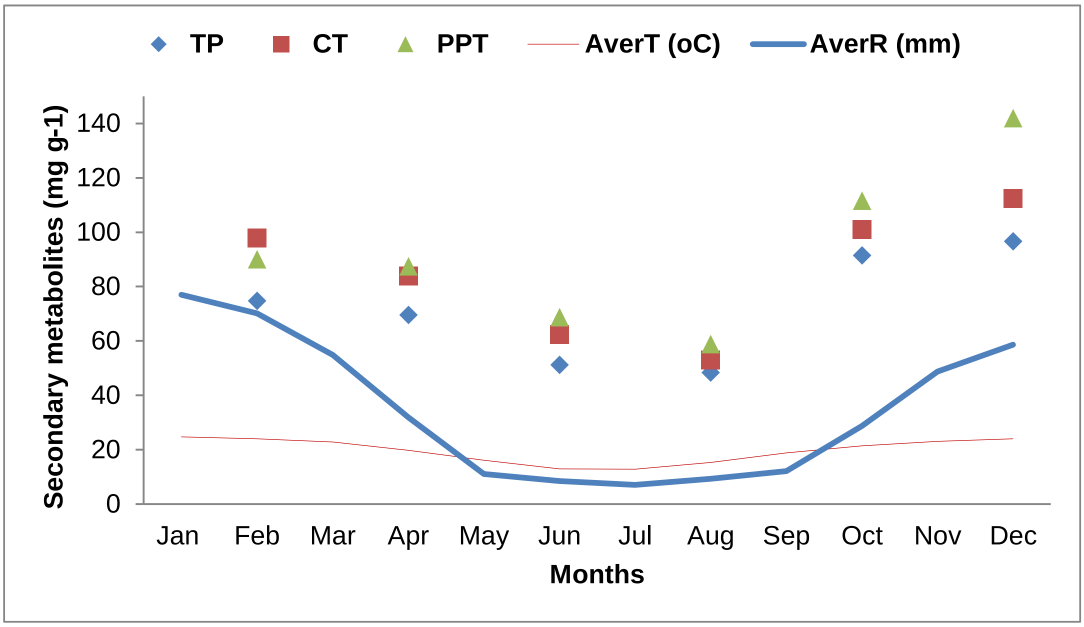

Figure 4.2: Concentration of secondary metabolites in mopane leaves. Data used to plot the graph derived from Table 4.3. Symbols: TP = total phenols, CT = condensed tannins, PPT = protein-precipitating tannins, AverT=Average Monthly Temperature, AverR=Average Monthly Rainfall.

4.4 MOPANE LEAF QUALITY AND ITS IMPLICATIONS FOR BROWSERS

Despite the nutritional value of mopane leaves, twigs, seeds and pods (Table 4.1; Figure 4.1), mopane is browsed mainly during the dry season (Makhado *et al*. 2016) when the chemical deterrents such as tannins and phenols are at lower concentrations (Wessels *et al*. 2007; Table 4.2; Figure 4.2). According to Cooper and Owen-Smith (1985), plants containing more than 5% of condensed tannins are rejected as food during the wet season period. This implies that forage containing more than 5% of condensed tannins reduces the crude protein digestibility of browse (Cooper & Owen-Smith 1985). In addition, green mopane leaves have a bitter taste (Macala *et al*. 1992), which might contribute to their low acceptability by browsers, especially during summer.

Savanna plants such as mopane invest most of its resources, which are used for growth and development, during the growing season (Scholes & Walker 1993). However, part of its resources is used to produce secondary metabolites in order to defend itself against browsers, especially during the growing season (Wessels *et al*. 2007). The consumption of browse with high concentrations of secondary metabolites such as phenols and tannins can cause the loss of appetite and digestion challenges to browsers (Van Hoven 1991). In addition, phenolic compounds render the leaves less palatable to herbivores (Cooper & Owen-Smith 1985).

Tannins, for instance, bind with dietary, enzymatic and microbial protein to form insoluble complexes that are not degraded in the rumen, resulting in a reduced digestibility and intake (Tanner 1988). High amounts of tannin can also cause direct toxic effects on the gut (Kreber & Einhellig 1977). According to Woodward and Reed (1989), diet containing high tannin concentration can reduce the growth rate of animals, which happens as a result of the reduction in forage intake and lack of nutrients, especially nitrogen. The role of condensed tannins is therefore to protect the living leaf against microbial attack and deter mammalian browsers (Scholes & Walker 1993).

Regardless of high secondary metabolites during summer and the risk associated with browsing such chemical compounds, Hooimeijer *et al*. (2005) found that mopane was browsed by the greater kudu, though at a low quantity, even during the summer season when secondary metabolites are at a high level. This implies that browsers such as the greater kudu can slightly tolerate secondary metabolites during the summer season, possibly by diversifying its diet (Hooimeijer *et al*. 2005) which assists in neutralising the build-up of secondary metabolites.

In addition, herbivores that can produce proline-rich glycoproteins in their saliva are capable of binding tannins, and can prohibit them from causing a negative effect on the herbivores (Havenga 2014). The proline-rich glycoprotein therefore plays a critical role in the deactivation of tannins (Cooper *et al*. 1988), and thus increases nitrogen production and digestibility of forage (Havenga 2014). Although it requires further study, it is suggested in this review that browsers such as the greater kudu and elephant, which utilise mopane during the summer season, although at low quantity compared to winter season, might have proline-rich glycoprotein in their saliva, which is used to deactivate chemical compounds. In addition, the ability of browsers such as the greater kudu to diversify its diet

(Hooimeijer *et al*. 2005) enables it to marginally tolerate secondary metabolites in the mopane leaf, especially during the summer season.

4.5 CONCLUSION

Mopane leaves, twigs, seeds and pods are nutritious and provide essential browse for herbivores, especially during the dry season. The concentration of nutrients in mopane does not vary significantly over the year; however, the concentration of secondary metabolites varies between summer and dry seasons. The digestibility of mopane by browsers is high during the dry season, but declined during the summer season, which is influenced by high levels of secondary metabolites.

Mopane develop secondary metabolites during the growing period in order to limit browsing pressure, which thus enables it to grow and produce with minimal browsing disturbances. It is further concluded that the variation in mopane leaf quality is mainly related to the growth and age of the leaf, as triggered by rainfall, which thus defines the growing seasons.

CHAPTER 5

DESCRIPTION OF THE STUDY AREA

5.1 INTRODUCTION

This chapter provides a detailed description of the study area. The chapter presents the climatic conditions, geology, soil, fauna and flora of the study area.

5.2 STUDY AREA

The study area is around Musina town, which is located in the Vhembe District of Limpopo Province, South Africa. Musina is in the far northern part of Limpopo Province. The international border gate between South Africa and Zimbabwe and Botswana is in Musina town. This study was conducted at the Musina Nature Reserve, which is found along the N1 road from Makhado to Zimbabwe. The reserve covers 4 976 hectares and is situated 5 km south-east of Musina town at 22°24’36”S, 30°03’00”E (Figure 5.1).

The altitude at Musina Nature Reserve ranges from 400–750 m above sea level. The reserve is a state-owned nature reserve, formerly known as the Baobab Forest Reserve (BFR). The reserve was proclaimed in 1926 for the protection of the *Adansonia digitata* L., commonly known as the baobab.

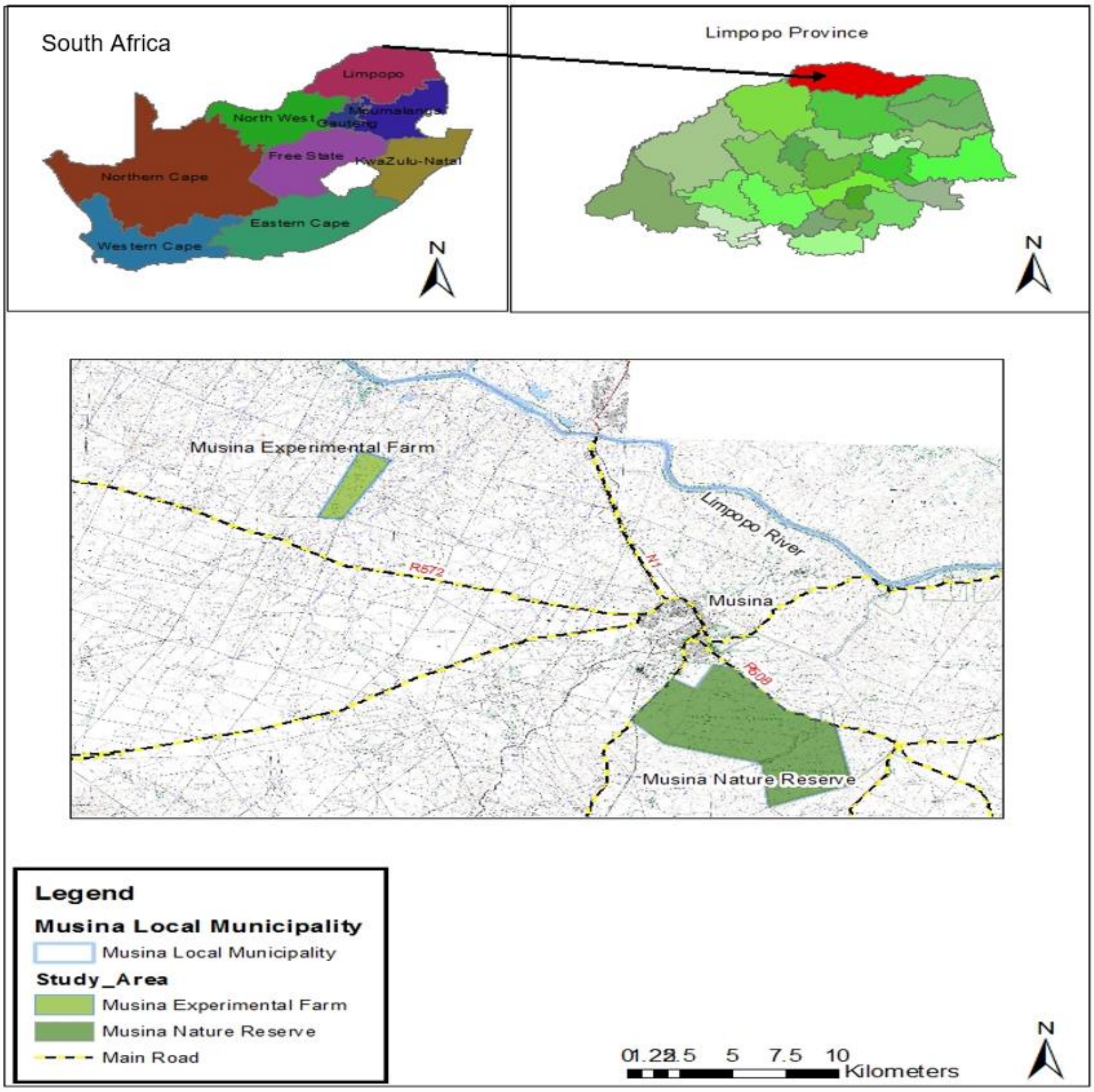

Figure 5.1: Topographical map of the Musina Nature Reserve.

5.3 CLIMATE

Climatic data was obtained from 0809706X and 08085672 weather stations for the period 1981–2014 (SA Weather Services 1981–2014). The study area is characterised by low summer rainfall and high summer temperatures. Rainfall, temperature, thunderstorms, hail, fog, humidity and wind in the study area are discussed in the sections that follow.

5.3.1 Rainfall

Musina falls within a typical savanna climate and experiences erratic summer rainfall in the form of thundershowers. More than 80% of rainfall occurs from

November to March. Rainfall typically occurs during the summer months and declines drastically during dry seasons. The average rainfall is 331 mm per annum, but typically the long-term mean ranges from 300 to 400 mm per annum (Figure 5.2). The finding of this study is corroborated by other studies, which indicate that the mean annual rainfall for the area is 357 mm (Dekker 1996; Hooimeijer *et al.* 2005), which is within 300–400 mm per annum (Figure 5.2).

Rainfall typically starts in late September until early October and reaches a maximum in November, December, January and February. Rainfall may reach an average of 55 mm and 53 mm in November and December, respectively. Rainfall increases in January and February to about 63 mm on average, and starts to decline from an average of 41 mm in March to 0 mm in August. Less than 5 mm rainfall on average is normally recorded during the winter months of June, July and August. This implies that August is normally a month where there is no rainfall (Figure 5.2).

5.3.2 Temperature

Musina is characterised by high summer temperatures. The average annual minimum temperature calculated for the period 1981−2014 ranged from 16^{o}C to the average annual maximum temperature of 30^{o}C (Figure 5.3). The temperature declines slightly during the dry season (June and July) and increases to a maximum during the wet season (November, December, January and February). The average monthly minimum temperature is 8^{o}C in June and July, increasing to an average of 21^{o}C in November, December, January and February. The average monthly maximum temperature is 25^{o}C in June and July, increasing to an average of 33^{o}C in November, December, January and February. The highest monthly maximum temperatures recorded range from 33^{o}C in June to the highest maximum of 45^{o}C in February and September (Figure 5.3). The lowest minimum temperatures were recorded in May (2007), June (1980), July (1985), August (1981) and September (1990) at -1.5^{o}C, -1.7^{o}C, -1.5^{o}C, 1.5^{o}C and 4.4^{o}C, respectively (Figure 5.3).

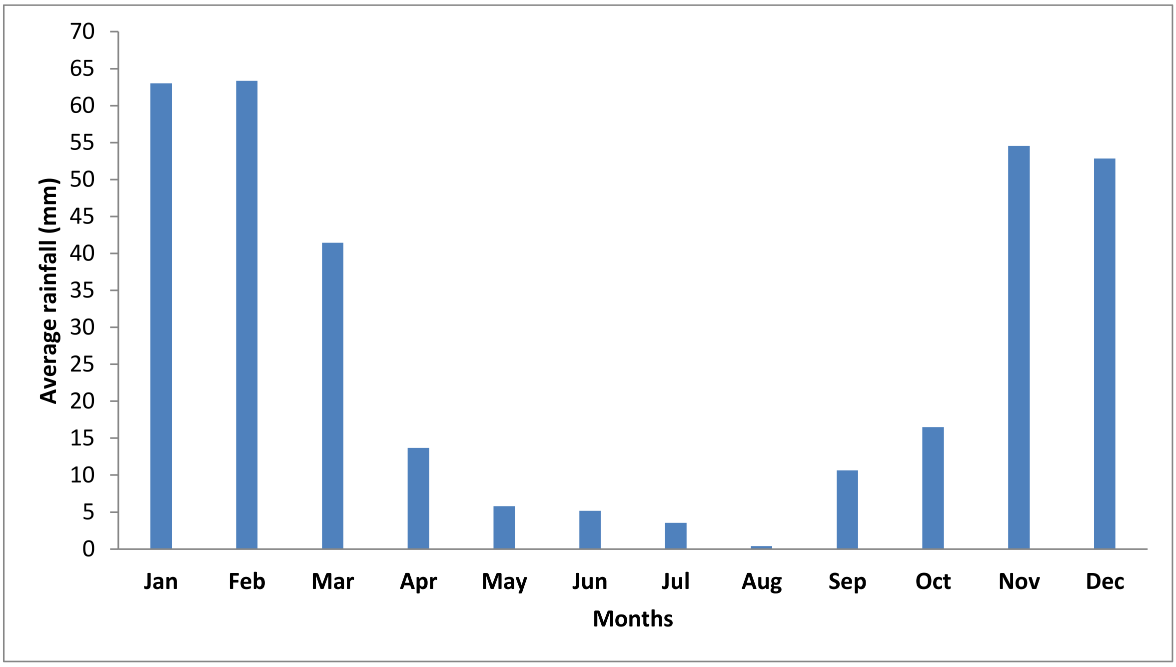

Figure 5.2: Average monthly rainfall at Musina, Limpopo Province. Data source: SA Weather Services (1981–2014).

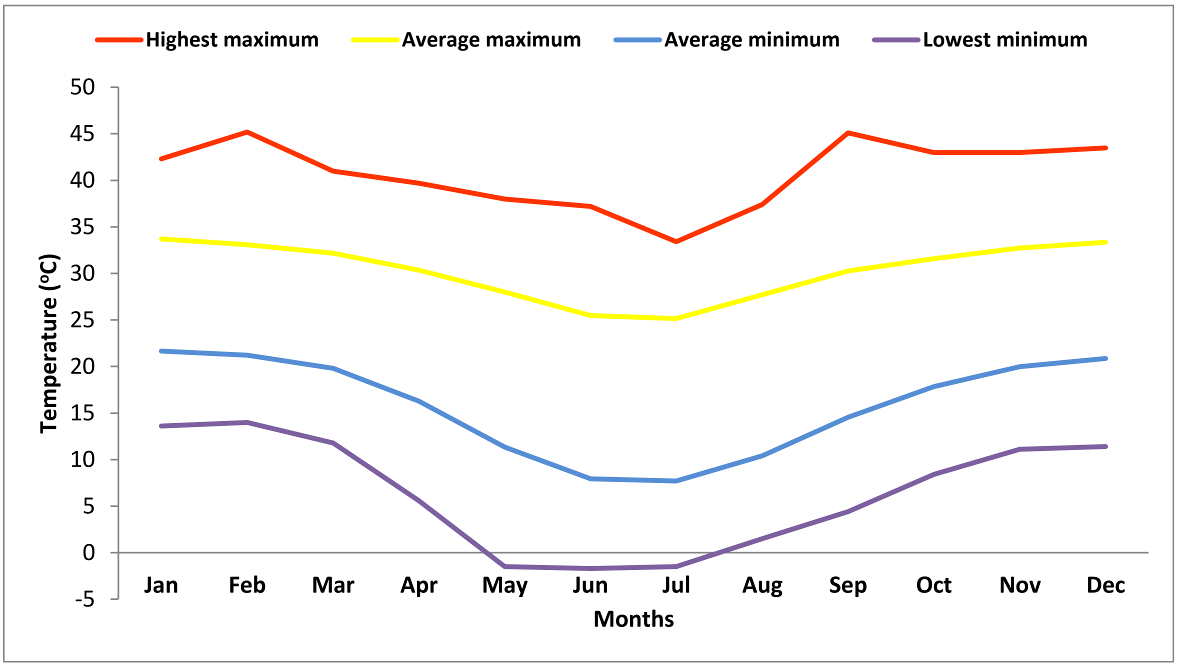

Figure 5.3: Temperature at Musina, Limpopo Province. Data source: SA Weather Services (1981–2014).

5.3.3 Thunderstorms, hail and snow

The average number of days with thunderstorms is zero in June and July, but starts to increase from three days on average in August and reaches the highest peak of four days on average in November. This shows that the month with the highest number of days on average with thunderstorms is November. From August to February, the number of days with thunderstorms is three on average, but this declines to a day on average in March to May (Figure 5.4).

The number of days with hail is zero on average in June and July, but starts to increase to one day on average in August to January. However, the number of days with hail declines to less than one day on average in February to May (Figure 5.4). On the other hand, the average number of days with snow was zero from January to December in the period 1981–2014. This suggests that the area is prone to thunderstorms and hail, especially during the summer months, but has low probability for snow occurrence (Figure 5.4).

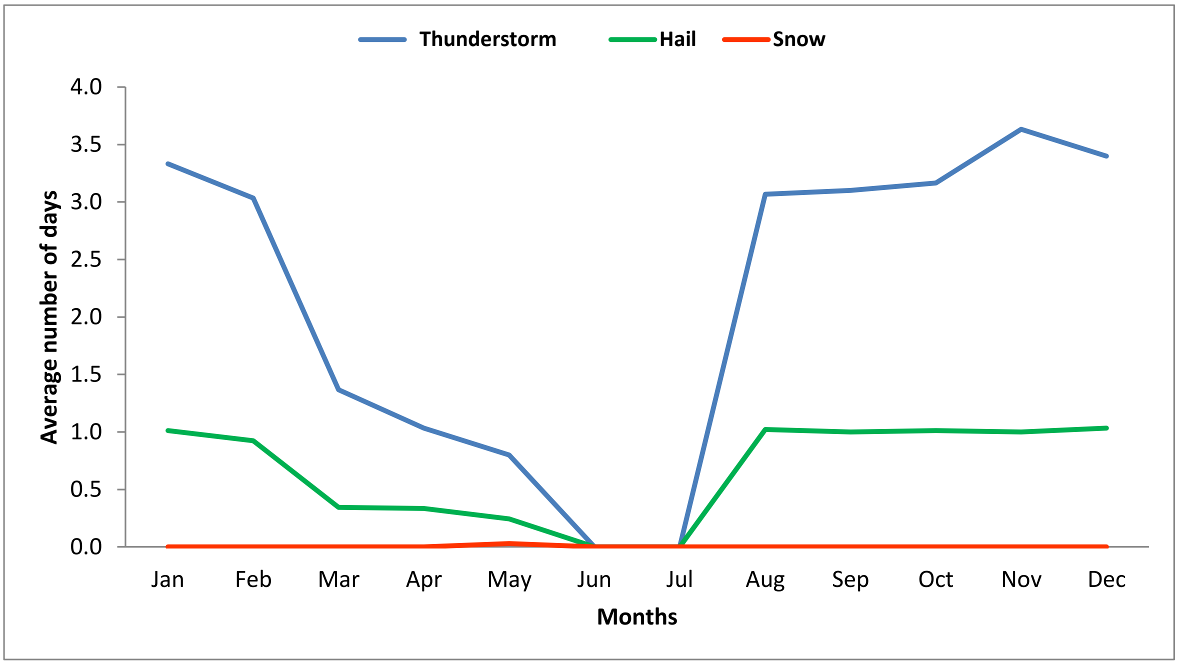

Figure 5.4: Days with thunderstorms, hail and snow at Musina, Limpopo Province. Data source: SA Weather Services (1981–2014).

5.3.4 Relative humidity

The average minimum relative humidity ranges from 12% in September to 28% in February. Relative humidity declines from February to September, but starts to increase again from October, reaching its maximum in February. However, the area has low relative humidity of less than 30% from January to December (Figure

5.5). Relative humidity of less than 30% means that the area is dry because of high temperatures and low rainfall.

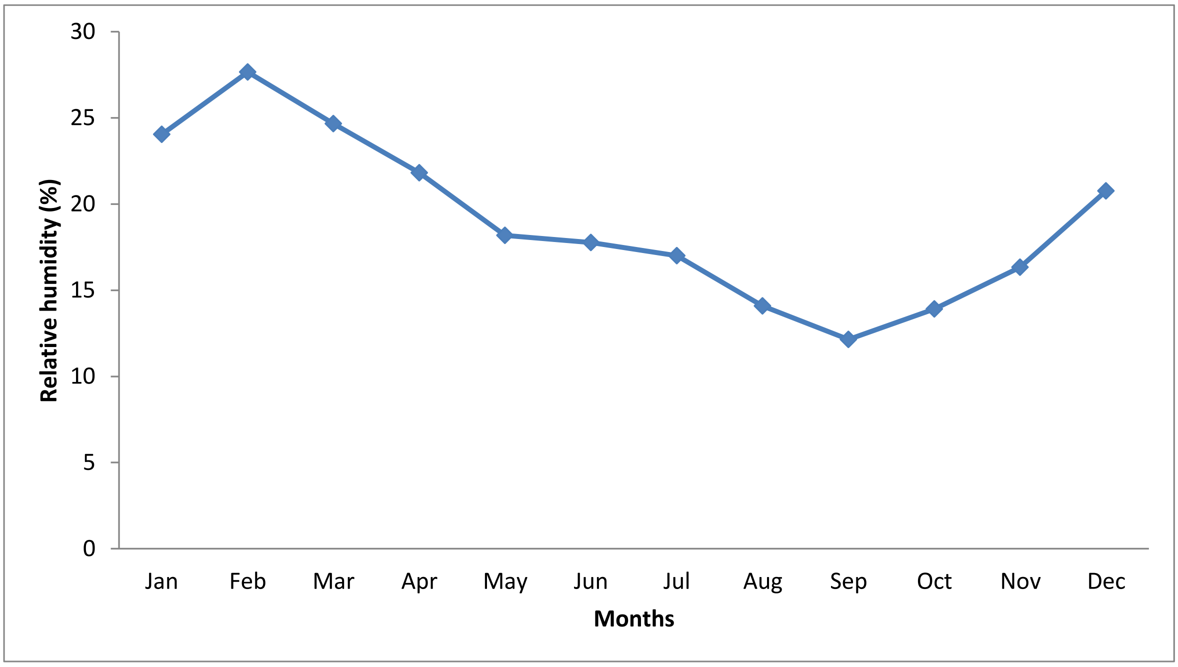

Figure 5.5: Average minimum relative humidity at Musina, Limpopo Province. Data source: SA Weather Services (1981–2014).

5.3.5 Wind

The annual average wind direction for Musina is mainly from the eastern side, at a wind speed of 8–11 m/s. However, wind can also come from the northeastern and southeastern directions. The average monthly high wind speed is 8–11 m/s, occurring in August, September, October, November, December, January and February. The wind speed from March to July is relatively low, averaging 5–8 m/s (Figure 5.6).

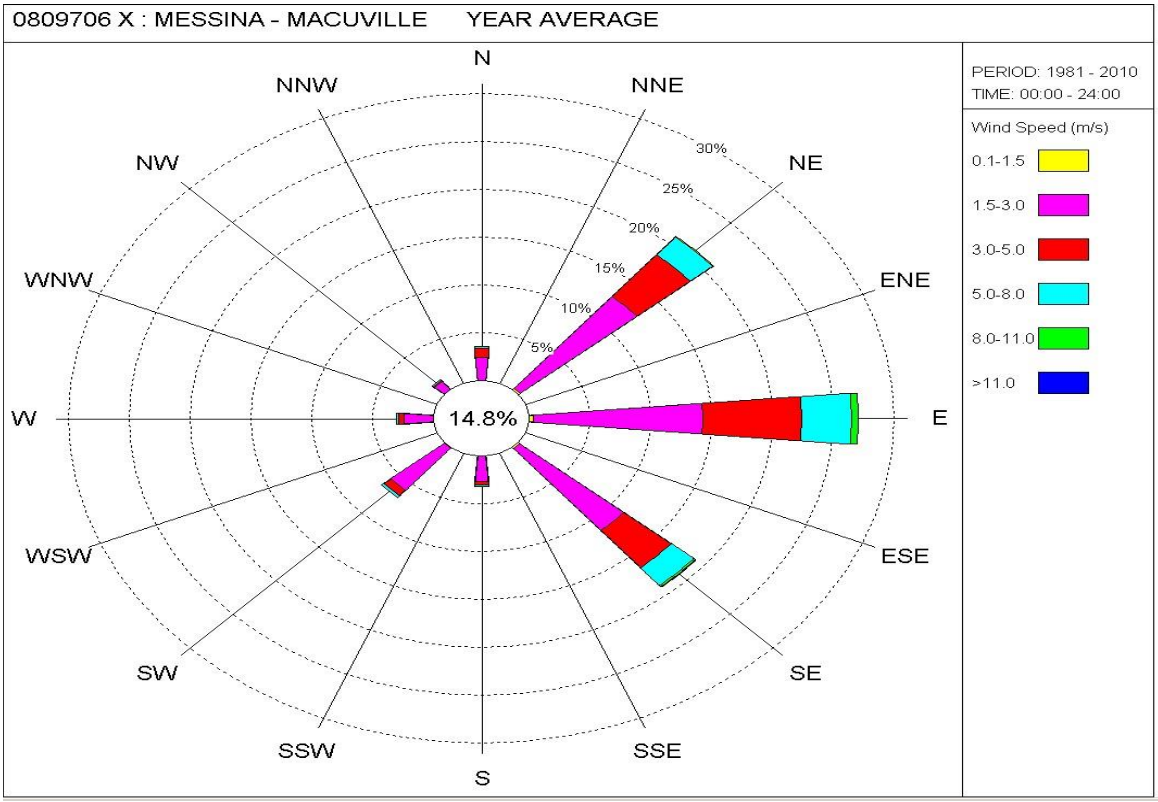

Figure 5.6: Average wind direction and speed at Musina, Limpopo Province. Data source: SA Weather Services (1981–2010).

5.4 GEOLOGY AND SOIL

The study area is situated within the central zone of the Limpopo Belt, which is a classic late Archaean high-grade gneiss terrain (Van Reenen *et al.* 1992). The rock formation is classified as the Beit Bridge Complex and is the oldest rock formation in South Africa (SACS 1980). The geology is classified under Limpopo Ridge Bushveld, and consists mostly of rocks of the Beit Bridge Complex (Swazian Erathem), as well as sediments (including sandstones of the Clarens Formation) and basalt (particularly in the east) of the Karoo Supergroup (Mucina & Rutherford 2006).

The geology is underpinned by the Archaean Beit Bridge Complex which consists of gneisses and meta-sediments. The geology is structurally very complex, except where it is covered by much younger Karoo sandstones and basalts (Mucina & Rutherford 2006).

Soils at Musina Nature Reserve are variable, as also determined by vegetation types. The shallow gravel and sand (Glenrosa and Mispah forms) comprise calcareous clayey soils. The soils range from deep red/brown clays to freely drained sandy soils under the Musina Mopane Bushveld, while the Limpopo Ridge Bushveld is occupied by shallow gravel and sand with calcareous clayey soils (Mucina & Rutherford 2006).

5.5 TERRAIN

The terrain of Musina Nature Reserve ranges from plains, flat areas, wet and dry drainage lines and gentle slopes to steep slopes (Curlewis 2014). The terrain has an influence on the distribution of plants and animals in the reserve. The clayey bottomland is dominated by *C. mopane* and the uphill area is dominated by *C. apiculatum*.

5.6 FLORA

The flora of Musina is classified under mopani veld (Acocks 1988), also known as mopane woodland (Low & Rebelo 1996), and recently the mopane bioregion (Rutherford *et al.* 2006) of the semi-arid savanna biome. The savanna is the most widespread biome in South Africa, covering about 38.8% of the total area (Rutherford *et al.* 2006; Figure 5.7). Within the mopane bioregion there are eight vegetation units, namely Musina Mopane Bushveld, Limpopo Ridge Bushveld, Cathedral Mopane Bushveld, Mopane Basalt Shrubland, Tsende Mopaneveld, Lowveld Rugged Mopaneveld, Phalaborwa-Timbavati Mopaneveld, and Mopane Gabbro Shrubland (Figure 5.7). The section that follows discusses the vegetation units and plant communities that occur in the Musina Nature Reserve.

5.6.1 Vegetation units at Musina Nature Reserve

The Musina Nature Reserve is located within the Musina Mopane Bushveld and Limpopo Ridge Bushveld of the mopane bioregion (Figures 5.7 and 5.8). The Musina Mopane Bushveld vegetation unit is the most widespread in South Africa (Figure 5.7). It is characterised by open woodland, mid-dense to closed shrubland dominated by *C. mopane* on clayey lowlands and *C. apiculatum* on the hills. Other tree and shrub species found include *Commiphora edulis*, *Grewia* species, *Terminalia* species, *Vachellia* species, *Senegalia* species, *Boscia albitrunca*, *Sclerocarya birrea* and *Dichrostachys cinerea*.

The Limpopo Ridge Bushveld on the other hand is characterised by moderately open savanna with a poorly developed herbaceous/grass layer. Plant species such as *Kirkia acuminata* are prominent on some ridges and often occur together with large individuals of *Adansonia digitata*, which occur on shallow calcareous gravel. Shrubs such as *Catophractes alexandri* are dominant on the calci-silicate soils. However, the tree and shrub component in this vegetation unit is dominated by *C. mopane*, *Commiphora mollis*, *Commiphora glandulosa*, *Commiphora tenuipetiolata*, *Maerua parvifolia* and *Terminalia prunioides* (Rutherford *et al.* 2006; LEDET 2012–2017).

The grass layer in these vegetation units is poorly developed but it is dominated by *Schmidtia pappophoroides* (LEDET 2012–2017). Other grass species found include *Cenchrus ciliaris* and *Stipagrostis uniplumis*.

Grasses such as *Enneapogon cenchroides* and *Aristida congesta* are found on overgrazed areas. The forbs are characterised by *Indogofera*, *Abutilon*, *Monechma*, *Barleria*, *Monsonia*, *Barleria*, *Hibiscus*, *Ocimum*, *Tephrosia* and *Melhania* species (Curlewis 2014).

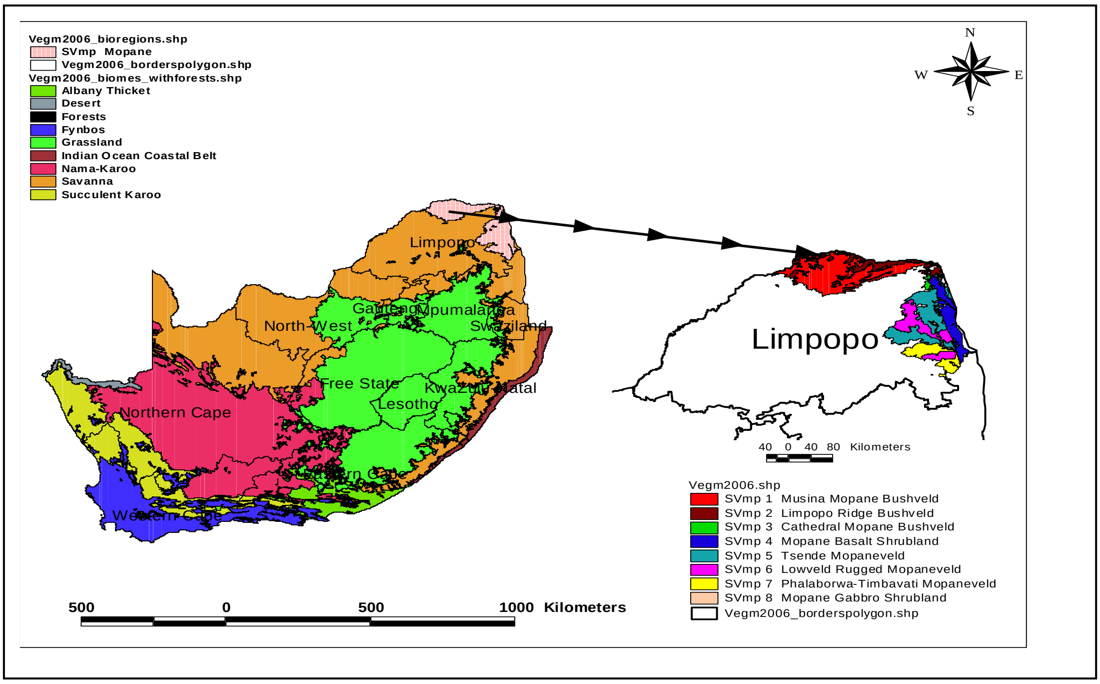

Figure 5.7: The distribution of mopane vegetation in South Africa's savanna biome. South Africa's mopane bioregion is characterised by eight vegetation units, but Musina Nature Reserve is characterised by the Musina Mopane Bushveld and Limpopo Ridge Bushveld. Data source: Mucina and Rutherford (2006).

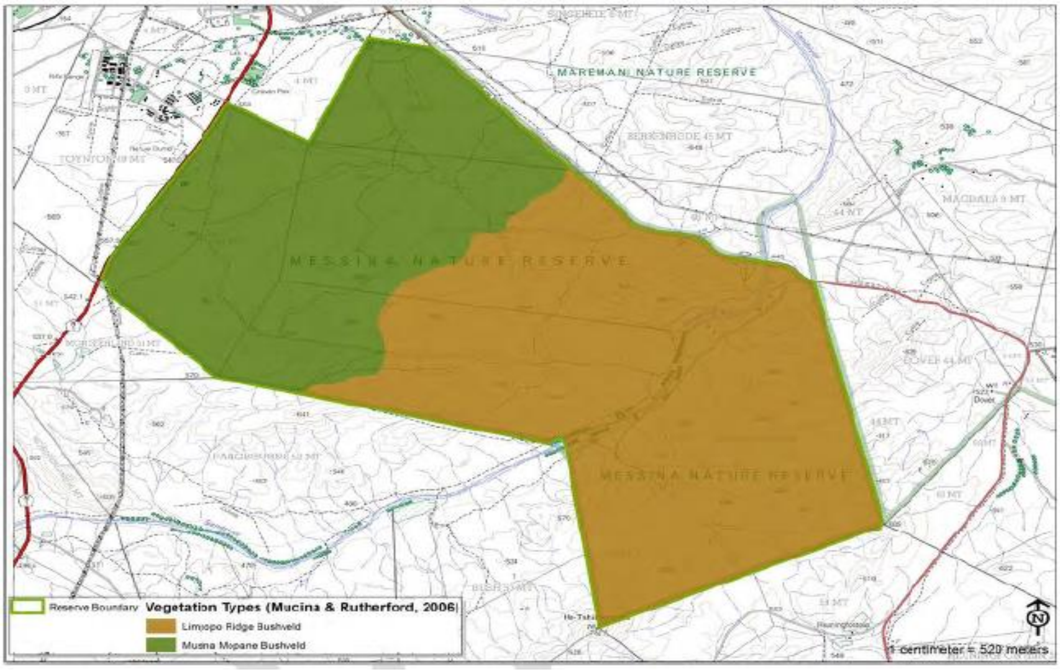

Figure 5.8: The vegetation map of Musina Nature Reserve. Source: LEDET (2012–2017).

5.6.2 Plant communities of Musina Nature Reserve

Plant species in Musina Nature Reserve were classified into five plant communities. According to Marais (1995), those plant communities are mixed veld, mixed hilly veld, riparian bush, sand veld and disturbed veld (Figure 5.9). The species found in those five plant communities are indicated as follows:

A – Mixed veld	*Adansonia digitata, Colophospermum mopane, Dichrostachys cinerea, Grewia* sp. and *Terminalia prunioides*
B – Mixed hilly veld	*Adansonia digitata, Colophospermum mopane, Dichrostachys cinerea, Terminalia prunioides* and *Sesamothamus lugardii*
C – Riparian bush	*Senegalia* sp. and *Xanthocercis zambesiaca*
D – Sand veld	*Colophospermum mopane*
E – Disturbed veld	*Vachelia* sp. and *Dichrostachys cinerea*

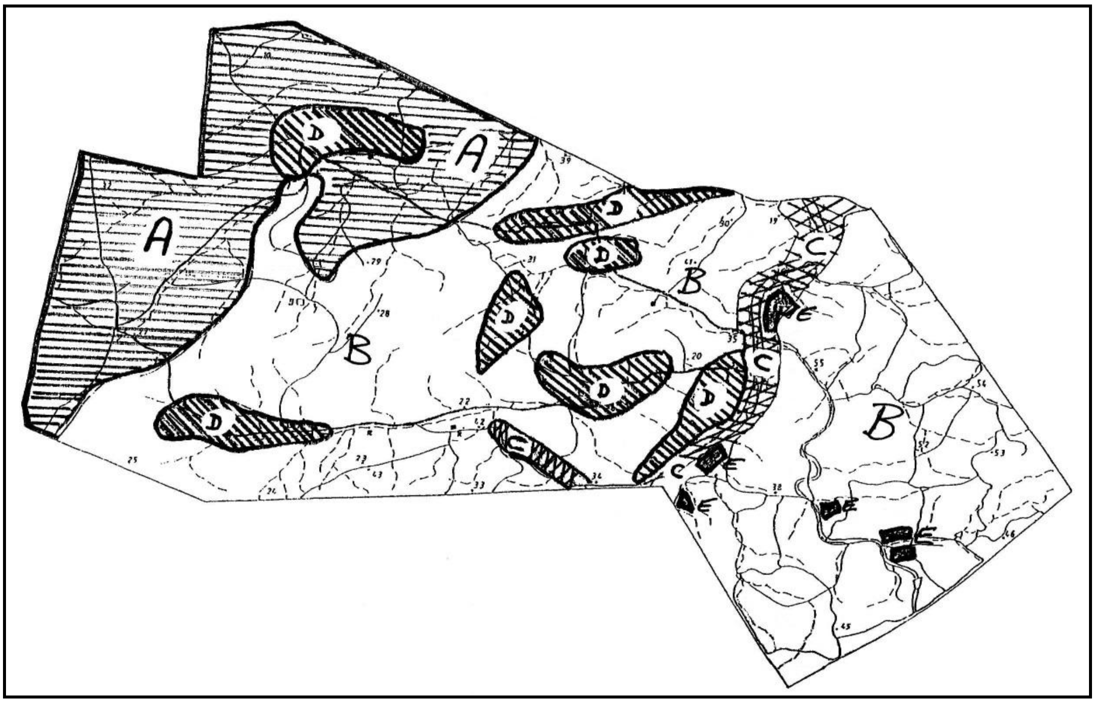

Figure 5.9: Plant communities of the Musina Nature Reserve. Source: Marais (1995).

5.7 FAUNA

Table 5.1 presents a list of mammals recorded at Musina Nature Reserve during the 2003-2006 census. Mammals marked * have not been sighted or no signs of the species have been recorded during the study period. Mammals smaller than the mongoose were not counted in Table 5.1.

An aerial census conducted in 2012 recorded a total of 1 311 head of game. These included eland (87), gemsbok (16), giraffe (114), kudu (95), nyala (45) and sable antelope (22), among others. It has further been indicated that Musina Nature Reserve currently supports populations of mammal species such as blue wildebeest, Burchell's zebra, common duiker, gemsbok, impala, klipspringer, sable antelope, steenbok and warthog (grazers); eland, giraffe, kudu and nyala (browsers); black-backed jackal and brown hyaena (predators); and chacma baboon (other feeders). Predators such as the African wild dog, spotted hyaena, brown hyaena and leopard were also recorded within the Musina Nature Reserve (LEDET 2012–2017). A total of 41 individuals of sable antelope were documented in the reserve during an aerial survey conducted in 2010; however, in 2012 only 22 were seen. Reasons for the population decline were suggested to be competition, overgrazing and/or poaching. However, the mammal species of conservation concern at Musina Nature Reserve include the brown hyaena, sable antelope and leopard (LEDET 2012–2017).

Table 5.1: Mammals that occur at Musina Nature Reserve

Common name	**Scientific name**
Aardvark	*Orycteropus afer*
Aardwolf	*Proteles cristatus*
African civet	*Civattictis civetta*
Banded mongoose	*Mungos mongo*
Brown hyena *	*Hyaena brunnea*
Bush pig	*Potamochoerus porcus*
Caracal	*Felis caraca*
Chacma baboon	*Papio ursinus*
Dwarf mongoose *	*Helogale parvula*
Giraffe	*Giraffa camelopardalis*
Honey badger	*Mellivora capensis*
Lesser bushbaby	*Galago moholi*
Leopard	*Panthera pardus*
Pangolin *	*Manis temminckii*

Porcupine	*Hystrix africaeaustralis*
Rock hyrax	*Procavia capensis*
Russet spotted genet *	*Genetta tigrina*
Scrub hare	*Lepus saxatillis*
Slender mongoose	*Gelerella sanuinea*
Small spotted genet	*Genetta genetta*
Spotted hyaena	*Crocota crocota*
Tree squirrel	*Paraxerus cepapi*
Vervet monkey	*Cercopithecus aethiops*
Warthog	*Phacochoerus aethiopicus*
White-tailed mongoose *	*Ichneumia albrcauda*
	Antelope
Blue wildebeest	*Connochaetes taurinus*
Bushbuck	*Tragelaphus scriptus*
Common grey duiker	*Sylvicapra grimmia*
Eland	*Taurotragus oryx*
Gemsbok	*Oryx gazelle*
Impala	*Aepyceros melampus*
Klipspringer	*Oreotragus oreotragus*
Greater kudu	*Tragelaphus strepsiceros*
Nyala	*Tragelaphus angasii*
Sable antelope	*Hippotragus niger*
Sharpe’s grysbok	*Raphicerus sharpei*
Steenbok	*Raphicerus campestris*

Source: Curlewis (2014)

5.8 MANAGEMENT OF MUSINA NATURE RESERVE

The Musina Nature Reserve forms part of the former Baobab Forest Reserve, which was proclaimed by the then Messina Town Council in 1926. The reserve was initially established with the aim of protecting the individuals of baobab found in the area from economic exploitation. The reserve was later extended to include a portion of the Sand River as well as a number of interesting geological formations. It was one of the first reserves in the former Transvaal Province to house sable antelope and nyala. Currently, Musina Nature Reserve is home to a variety of plant, mammal and bird species. The reserve is completely fenced in, which means that animals have limited movement. Animal numbers are therefore managed by culling from vehicles during winter to control their population. The reserve is a state-owned nature reserve and forms part of the Vhembe Biosphere Reserve. The Limpopo Department of Economic Development, Environment and Tourism (LEDET) is directly responsible for the conservation management of the reserve, while the departmental entity, the Limpopo Tourism Agency, is directly responsible for the management of tourism in the reserve (LEDET 2012–2017).

5.9 CONCLUSION

Musina Nature Reserve is located within mopane woodland. The area experience high temperature and low rainfall. These type of conditions favours the growth of diverse plant species though the grass layer is poorly developed. The dominant species within the study area is *C. mopane*. The mopane woodland also support wide range of wildlife. The detailed methodology followed when conducting this study is explained in Chapters 6 to11.

CHAPTER 6

EFFECTS OF PRUNING ON *COLOPHOSPERMUM MOPANE* LEAF PHENOLOGY AND PRODUCTION[4]

6.1 INTRODUCTION

Plant phenology is the timing of the development of vegetative and reproductive plant organs, most notably leafing, flowering and fruiting (Haugaasen & Peres 2005). Knowing the timing of phenology is important for monitoring and predicting vegetation responses to various stressors (Fuller 1999), as triggered by prevailing weather conditions (IPCC 2007), fires and browsers (Sankaran *et al.* 2005). These stressors can alter the timing of phenological events (Cleland *et al*. 2007), but the extent of change may vary among species depending on their phenological plasticity (Stevens *et al*. 2016).

Phenology of plants in an ecosystem that experiences large seasonal extremes, such as the mopane woodland savanna, will have a profound effect on herbivores (Janecke & Smit 2011). The timing of phenophases has major implications for plant community structure, function and regeneration, as well as the quantity and quality of forage available to browsers (Williams *et al*. 1999). Any delay in leaf production can affect their survival and reproductive success (Owen-Smith & Cooper 1989).

The savanna biome is characterised by extreme weather conditions (Scholes & Walker 1993) resulting in high seasonal variation in leaf cover (Childes 1989), which has the potential to alter plant growth (Cleland *et al*. 2007). Thus the identification of factors controlling leaf phenology and production, particularly in this ecosystem, is essential for understanding the response of plants to seasonal

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[4] Makhado, R.A., Potgieter, M.J. & Luus-Powell W.J. 2020. Effects of pruning on the concentration of *Colophospermum mopane* leaf phenology and production. *African Journal of Ecology* 58(1): 145–148.

changes (Stevens *et al*. 2016). This would have an impact on the quantity and quality of forage available to herbivores in the savanna.

Species such as *Colophospermum mopane* is adapted to harsh conditions in southern Africa's savanna (Makhado *et al*. 2014). Mopane is a dominant tree or shrub in the mopane woodland (Werger & Coetzee 1978). Mopane is a deciduous plant (Werger & Coetzee 1978) and its dry leaves are a valuable source of browse for herbivores (Curlewis 2014) particularly during the dry season (Makhado *et al.* 2016). The leaves are nutritious, containing between 6% and 13% crude protein (Hooimeijer *et al*. 2005).

Considering the ability of mopane to survive in water-stressed environments (Johnson *et al*. 1996), and its role in supplying nutritious forage to browsers (Hooimeijer *et al*. 2005), it is surprising that there is limited research available to determine the phenology and production of mopane leaves. There are also limited studies determining the effect of browsers on mopane leaves' quality and availability. The available and accessible literature on mopane leaf phenology is restricted to studies conducted by Guy *et al.* (1979), Chidumayo and Frost (1996), Dekker and Smit (1996), Styles and Skinner (1997), Chidumayo (2001) and Kohi *et al.* (2010). Limited studies on mopane leaf production were conducted by Dekker and Smit (1996), Styles and Skinner (1997), Smit and Rethman (1998), Smit (2001), Hrabar (2005), Wessels *et al*. (2006), Mlambo and Nyathi (2008), Hrabar *et al*. (2009) and Kohi *et al*. (2010). However, the methodology applied makes it difficult to consolidate and compare the existing data. In some instances, the available data is based on just one or two sampling points, which does not properly reflect seasonal leaf quantity and quality variations.

Various researchers are currently advancing the understanding of phenophases and the factors influencing such changes in the savanna system, through the use of remote sensing data (Chidumayo 2001; Fox *et al*. 2005; Archibald & Scholes 2007; Wessels *et al*. 2011; Jin *et al*. 2013; Adelabu 2013). However, some of these studies are based on large-scale analysis without separating the response of individual species to seasonal variability. Field data and information on mopane leaf phenology and production are scanty. The lack of field data and information makes it difficult to understand the seasonal changes in mopane leaf phenology and production, and their influence on animals' browsing behaviour during different seasons. This study was therefore undertaken in an attempt to close this knowledge gap by determining the effect of pruning on mopane leaf phenology and production.

Mopane was selected for this study because of its widespread distribution in the mopane woodland (Mapaure 1994), and its competitive success in the hot-dry environment of southern Africa (Stevens *et al*. 2016). The pruning experiment was intended to simulate the effect of browsing by large herbivores (Wessels *et al*. 2007), such as the greater kudu, on mopane leaf quality. This study therefore contributes to a better understanding of mopane leaf phenology and production, which is important for the sound management of browsers in the mopane woodland.

6.2 METHODOLOGY

6.2.1 Study area

This study was conducted in the Musina Nature Reserve in the northern Limpopo Province, South Africa. The reserve is situated 5 km south-east of the town of Musina at 22°24'36"S, 30°03'00"E, and covers 4 976 hectares. The altitude of the reserve ranges from 400 m to 750 m above sea level. The slope of the experimental site is relatively flat. Rainfall in Musina typically starts in late September until early October and reaches its maximum in November, December, January and February. The average rainfall is 331 mm per annum and typically ranges from 300 to 400 mm per annum. The mean annual temperature is 16^{o}C in winter and can reach a maximum of 45^{o}C in summer. The annual average maximum temperature is 30^{o}C. The relative humidity of the area is very low, ranging from 12% in September to 28% in February (SA Weather Services 1981–2014).

The geology is underpinned by the Archaean Beit Bridge Complex, which consists of gneisses and meta-sediments. Soils range from deep red/brown clays at the bottom of slopes to freely drained sandy soils at the top of slopes. The soil has high sodium content and is alkaline (Mucina & Rutherford 2006).

Musina Nature Reserve is located within the Musina Mopane Bushveld and Limpopo Ridge Bushveld of the Mopane bioregion (Mucina & Rutherford 2006). The experimental site (1 hectare) is located in the Musina Mopane Bushveld vegetation zone, and dominated by mopane (Rutherford *et al.* 2006), with an estimated density of 1 344 trees per hectare (Wessels *et al*. 2007). The grass layer is poorly developed, but dominated by *Schmidtia pappophoroides* (LEDET 2012–2017). The reserve has a diverse range of antelope including greater kudu, eland, gemsbok, nyala, sable antelope, blue wildebeest, common duiker, gemsbok, impala, klipspringer and steenbok (LEDET 2012–2017).

6.2.2 Sampling procedures

6.2.2.1 Pruning experiment

Pruning and control experiments were initiated during the wet season of February 2014 in a homogenous stand of similar-sized (3 m high) mopane trees. The wet (October–April) and dry (May–September) seasons in South Africa are critical periods for determining leaf quality. During the sampling period in 2014, the average rainfall in Musina Nature Reserve was 316 mm. Rainfall started in September (5 mm) and reached its maximum in January (85 mm), thereafter declining to 0 mm in August (Table 6.1). The leaves started to flush in October, possibly in response to temperature.

Seven healthy tertiary side branches, near the main stem, of relatively equal circumference (20 mm), from each of 20 mopane trees, were randomly selected from different sides of the tree (north, south, east and west). The twigs were pruned back 50 mm by hand shears. The selected branches were marked to assist with future identification in this longitudinal study. Pruning was conducted to simulate the effects of browsing by large herbivores (Wessels *et al*. 2007), such as the greater kudu, on mopane leaf quality. The total amount of leaf and shoot biomass removed was less than 10% from the selected branch, which is a reasonable approximation of what is taken by herbivores (Scholes & Walker

1993), such as the greater kudu, in a single visit. Twenty trees were not treated and used as controls. These control trees were interspersed with experimental trees growing in the same red/brown oakleaf soil form. The experimental area was excluded from further browsing through fencing.

6.2.2.2 Recording of leaf phenology

Treatment and control mopane trees were used to record different leaf phenological stages on a 55-day basis. Leaf phenology was measured during February, May, June, August, October and December of the same year. The first measurement was done after the treatment was administered. Different phenological stages were quantified following procedures described by Archibald and Scholes (2007). Leaf greenness was classified as: 0 (no green leaves), 1 (a few green leaves), 2 (some green leaves), 3 (half of the tree is green), 4 (more than half of the tree is green), and 5 (in full green leaf). The leaf green-up month was defined as the month when the greenness value was at 1, the leaf fall month as the month when the greenness was below 5, the growing season as the leaf fall month minus the green-up month, and the maximum greenness period as the maximum phenological value, which was 5 (Table 6.1). The obtained ordinal scale data was then normalised to a range of 0–1, through dividing the obtained greenness value (x) by a maximum classification value (*5*) (Figure 6.1).

6.2.2.3 Recording of leaf production

Treatment and control mopane trees were used to record the number of leaves on a 55-day basis. The number of leaves per tree on all the marked branches was counted during February, May, June, August, October and December of the same year. The first count was done after the treatment was administered.

6.2.3 Statistical analysis

Collected datasets were analysed using descriptive and inferential statistical analysis. Descriptive statistical analysis was used to determine the mean and standard deviation. Collected data, particularly in February and December, did not follow a normal distribution. Consequently, the effect of pruning on the monthly and annual leaf phenology and production was tested using a two-tailed Mann-

Whitney U-test (IBM SPSS Statistics 24, USA). A significant difference was accepted when $P < 0.05$.

6.3 RESULTS

6.3.1 Mopane leaf phenology

Pruning increased leaf greenness after commencement of the experiment (May), but it levelled off at the end of the experiment in December. Leaf green-up started in October in the control and pruned trees. Maximum greenness was attained during December and February, and thereafter started to drop in May, reaching its lowest levels in August. This shows that the number of months in which the leaves are at maximum greenness and photosynthetic active is about three to four. The leaf growing season started in October and ended in August, equating to about 10 months of leaf carriage (Figure 6.1; Table 6.1). There was no difference between the experimental and control group during the initiation of the experiement in February (P=0.992) and at the conclusion of the experiment in December (P=0.992). However, during May, June, August and October, the level of leaf phenology between control and pruned mopane trees statistically differed significantly (P=0.0001) (Table 6.2). Table 6.2 further showed that the annual effect of pruning on mopane trees leaf phenology was statistically significant (P=0.002).

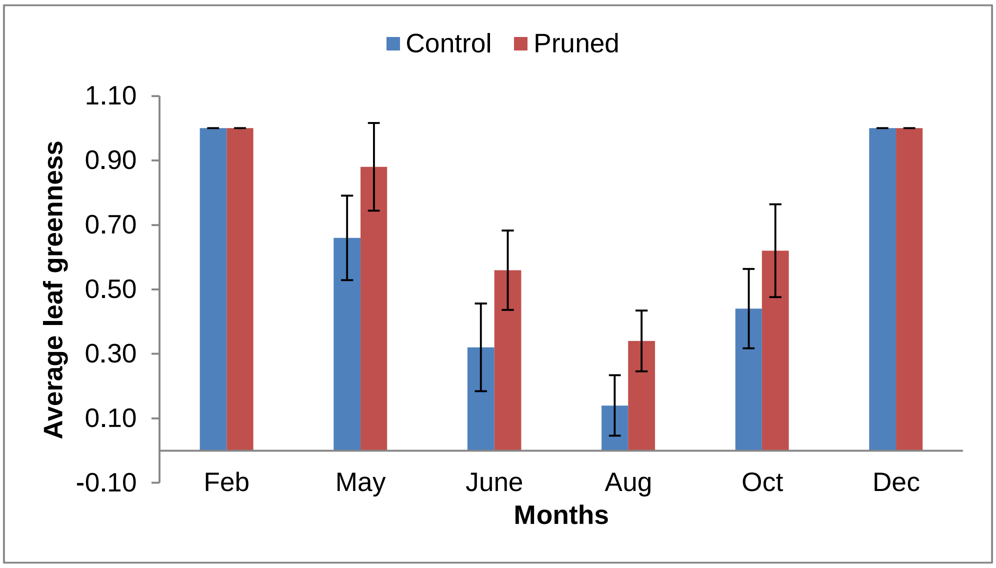

Figure 6.1: Average leaf greenness in the control and pruned mopane trees. Bars indicate standard deviation.

Table 6.1: Mean (±S.D.) leaf phenology in the control and pruned mopane trees (*n*=20).

Month	Experiment	Leaf greenness mean	Leaf greenness S.D.	Monthly Rainfall (mm)*	
Feb	Control	5.00	0.00	Jan	85.1
	Pruned	5.00	0.00	Feb	51.7
May	Control	3.30	0.67	Mar	46.5
	Pruned	4.40	0.70	Apr	9.4
June	Control	1.60	0.70	May	5.5
	Pruned	2.80	0.63	Jun	0.5
Aug	Control	0.70	0.48	Jul	1.5
	Pruned	1.70	0.48	Aug	0
Oct	Control	2.20	0.63	Sep	4.5
	Pruned	3.10	0.74	Oct	25.5
Dec	Control	5.00	0.00	Nov	45.8
	Pruned	5.00	0.00	Dec	39.5

Symbols: SD=standard deviation, mm=millimetre. **Note:** *=Monthly Rainfall Data for Musina Nature Reserve (2014).

Table 6.2: Monthly and annual effect of pruning on mopane leaf phenology.

	Pruned versus control	
	Z-Score	*P-value*
Feb	0.014	0.992^a
May	-3.828	0.0001^b
June	-4.098	0.0001^b
Aug	-4.260	0.0001^b
Oct	-3.287	0.001^b
Dec	0.014	0.992^a
Annual	-3.112	0.002^b

Note: ^{a}=Not significant at $P < 0.05$, ^{b}=Significant at $P < 0.05$. Statistical superscripts refer to rows in the table.

6.3.2 Mopane leaf production

There was a difference in the number of leaves produced between the pruned and control trees, throughout the study period. The number of leaves per marked branches during February was 79.25±8.35 and 74.20±12.74 on average in control and pruned trees, respectively. Pruning resulted in a decline in the number of leaves during the initiation of the experiment in February as compared to control trees. However, during October, pruned trees flushed slightly more leaves than control trees. The number of leaves increased during December to 39.85±8.93 and 51.00±12.68 on average in the control and pruned trees, respectively (Figure 6.2; Table 6.3).

The monthly number of leaves produced in the pruned and control mopane trees did not differed significantly during the initial stage of the experiment in February (P=0.332). As the experiment progressed during May, June, August, October and December, the effect of pruning in the number of leaves was statistically significant at P<0.05 (Table 6.4). However, the annual number of leaves produced in the pruned and control mopane trees did not differed significantly (P=0.134) (Table 6.4).

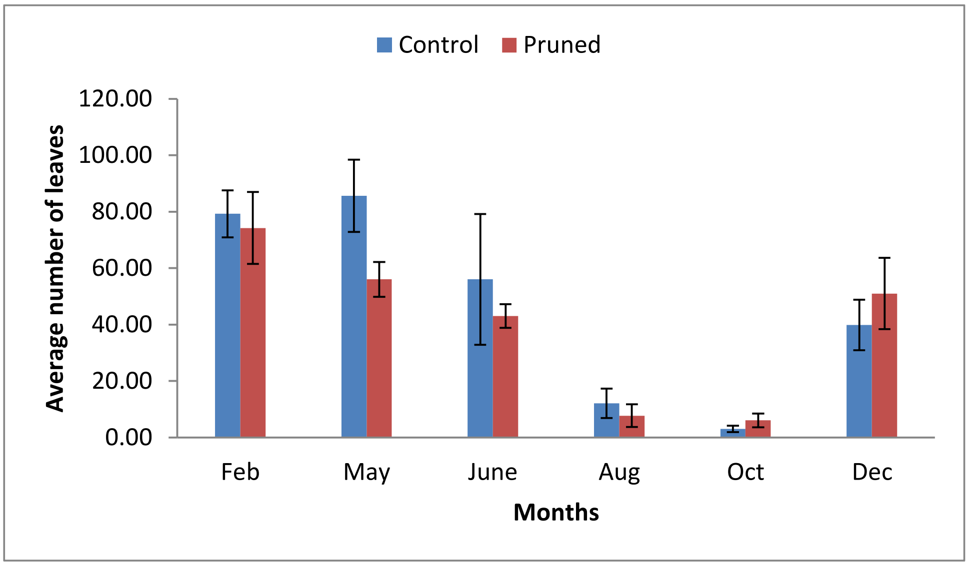

Figure 6.2: Average number of leaves in the control and pruned mopane trees. Bars indicate standard deviation.

Table 6.3: Mean (±S.D) number of leaves in the control and pruned mopane trees (*n*=20).

		No. of leaves	
Month	Experiment	mean	S.D.
Feb	Control	79.25	8.35
	Pruned	74.20	12.74
May	Control	85.60	12.81
	Pruned	56.00	6.21
June	Control	56.00	23.14
	Pruned	43.00	4.17
Aug	Control	12.10	5.19
	Pruned	7.70	4.04
Oct	Control	3.00	1.12
	Pruned	6.05	2.44
Dec	Control	39.85	8.93
	Pruned	51.00	12.68

Symbols: SD=standard deviation.

Table 6.4: Monthly and annual effect of pruning on the number of leaves.

	Pruned versus control	
	Z-Score	*P-value*
Feb	-0.974	0.332[a]
May	-5.153	0.0001[b]
June	-3.774	0.001[b]
Aug	-2.921	0.004[b]
Oct	3.652	0.0003[b]
Dec	2.353	0.019[b]
Annual	-1.503	0.134[a]

Note: [a]=Not significant at $P < 0.05$, [b]=Significant at $P < 0.05$.

6.4 DISCUSSION

6.4.1 Mopane leaf phenology and production

Mopane flushes its leaves in October, and they start to fall in May, reaching their lowest presence level in August (Figures 6.1-6.2). Trees tend to be without leaves in September. Leaf flush and fall seem to be mainly associated with the available soil moisture (Stevens *et al*. 2016), a factor that is triggered by rainfall (Mlambo & Nyathi 2008). Though soil moisture seems to be an important variable in determining leaf flush and fall, mopane leaf flush can be triggered independently of rain. The ability of mopane to flush its leaves before the first summer rains (Styles & Skinner 1997) appears to be mainly driven by its high fine root densities (Smit & Rethman 1998), which facilitate water and nutrient acquisition and transport (Mantlana 2002), even during periods of drought (Mosimanyana & Kiflewahid 1988).

Early leaf flush is not unique to mopane, but also common to other tropical dry forest trees (Do *et al*. 2004), such as *Hardwickia binata* (Chaturvedi & Raghubanshi 2016). It appears that the stored energy, nutrients and water are used to flush new leaves even before the first rain of the season. Although early flush of leaves appears to be a high risk and costly exercise to the tree, especially if there are delays in rainfall (Archibald & Scholes 2007), it is equally an effective competitive strategy for mopane. Early flush ensures that the plant makes the most of the pulse of nutrients that is released with the onset of the first rains

(Scholes & Walker 1993). In addition, early leaf flush plants are a major source of forage to browsers, such as greater kudu, in the southern African savanna (Owen-Smith & Cooper 1989) at the end of the dry season, a time when all herbivores are struggling to satisfy their metabolic requirements (Archibald & Scholes 2007).

As the leaves reach maximum greenness during the wet season (Figure 6.1), the rate of leaf phenology and production is high (Hrabar *et al*. 2009), but they are rejected by browsers (Hooimeijer *et al*. 2005). This is due to high concentrations of tannins and phenols (Wessels *et al*. 2007). As a result, browsers such as the greater kudu predominantly include mopane leaves in their diet during the dry season (Makhado *et al*. 2016) when those chemicals are at lower concentrations (Hooimeijer *et al*. 2005). During the dry winter season, fallen dry mopane leaves constitute a significant amount of forage on the ground in the mopane woodland (Dekker & Smit 1996). The dry leaves contribute immensely to the diet of browsers (Styles & Skinner 1997) such as the greater kudu (Curlewis 2014), elephant (Styles & Skinner 2000) and other ungulates, when forage is scarce and most savanna species are leafless (Kos *et al.* 2012). It seems in this study that leaf phenology has an influence on the diet selection of browsers, while leaf production influences the amount of forage that can be produced to support browsers in the following season.

6.4.2 Effect of pruning on mopane leaf phenology and production

Plants’ response after being browsed depends on the timing, type and extent of damage (Hrabar 2005). Messina *et al*. (2002) indicated that pruning tends to increase leaf production of resprouting shoots. However, this study found that <10% pruning initially reduces the number of leaves, which increases later, particularly during October and December (Figure 6.2). This suggests that when browsers prune the twigs, it increases leaf flush during the growing season (Fuller 1999). This enables mopane to have longer leaf carriage than most other species in the mopane woodland (Dekker & Smit 1996). The ability of mopane to have long leaf carriage periods (Figure 6.2), therefore underpins its potential value as a fodder resource in the mopane woodland (Dekker & Smit 1996).

Pruning eventually increases the greenness of the leaves (Du Toit *et al*. 1990). It also increases the production of longer shoots (Hrabar 2005) with larger leaves (Bergström *et al*. 2000), particularly during the growing season. Pruning further enhances leaf flush (Hrabar *et al*. 2009) during the growing season (Figure 6.2), which is essential in sustaining forage for browsers in the mopane woodland. However, heavy browsing, such as 100% pruning of mopane, has the potential to reduce the number of leaves (Kohi *et al*. 2010). This suggests that heavy browsing by megavores, such as elephants, might initially reduce the production of mopane leaves, but would increase in the following season.

In addition, the ability of mopane to coppice after disturbance (Mushove & Makoni 1993), and vigorous resprout enables it to cope with the browsing pressure inflicted by mega-herbivores and other disturbances. As a result, mopane is an important forage species in the mopane woodland (Hooimeijer *et al*. 2005), contributing most to the total leaf biomass in all plant communities found in the mopane woodland (Dekker & Smit 1996). This is an indication of the value and viability of mopane in supplying forage to browsers in that ecosystem.

6.5 CONCLUSION

Leaf phenology and production are essential indicators which can be used to monitor the greenness and availability of forage. Pruning results in variations in mopane leaf phenology and production. This suggests that low browsing (<10% pruning) has an effect on mopane leaf phenology and production. Pruning initially reduce leaf production, which increases during the growing season. This suggest that browsing increases forage in the following growing season, whilst reducing it during the current season. Vigorous flush of mopane leaves during the growing season resulted in a prolonged growing season. The prolonged leaf carriage could enables mopane to supply browsers in the mopane woodland with forage when most species are dormant and during the period of forage scarcity. Through not tested, the leaf phenological response and production in mopane trees appears to be mainly influenced by the available soil moisture, as triggered by the first summer rainfall. The availability of moisture in the soil thus influences mopane leaf flush and fall.

CHAPTER 7

EFFECTS OF PRUNING ON THE CONCENTRATION OF MACRONUTRIENTS IN *COLOPHOSPERMUM MOPANE* LEAVES[5]

7.1 INTRODUCTION

The spatial and temporal variation in nutritional quality of plants consumed by herbivores is regarded as one of the main factors governing animal performance, evolutionary adaptation (Codron 2006), feeding patterns and productivity (Holá 2012). Herbivores also have an influence on plant performance, survival, growth, resource allocation and reproduction (Hendrix 1988). When mammals browse woody plants they frequently prune shoot tips, thus reversing the plant growth stage (Bryant *et al*. 1991). The result of pruning by herbivores is the increased concentration of nutrients such as nitrogen in the remaining shoots, decreased toughness and concentration of secondary metabolites (Bryant *et al*. 1991). Pruning further stimulates leaf productivity (Wessels *et al*. 2006) and improves the quality of the fodder (Du Toit *et al*. 1990; Agrawal & Spiller 2004).

In African savanna ecosystems, plant nutritional quality varies seasonally (Barber & Marquis 2011), as influenced by changes in temperature, light, moisture, soil characteristics (Van Soest 1994) and chemical composition (Cornelissen *et al*. 2003). In addition to environmental and edaphic factors (Du Toit 2003), fire and herbivores also play a role in determining plant quality (Scholes & Walker 1993). In response to this variation, herbivores make trade-offs between acquisition of digestible nutrients and reduction of forage with a high concentration of plant defence compounds (Holá 2012). The variability in responses suggests that plants have adopted different strategies to deal with each type of browsing (Hrabar *et al*. 2009). Understanding how individual plant species respond to herbivores in semi-

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[5] Makhado, R.A., Potgieter, M.J., Luus-Powell, W.J. & Mapaure, I. 2019. Effects of pruning on the concentration of macronutrients in *Colophospermum mopane* leaves*. African Journal of Ecology* 57(2): 260–267.

arid savannas is critical for understanding how plant assemblages respond to changing environments (Hester *et al*. 2006).

Savanna tree species such as *Colophospermum mopane* play an important role in supplying browsers and other ungulates with nutritious fodder (Kos *et al.* 2012). It provides essential browse to wild animals such as greater kudu (Curlewis 2014), elephants (Kos *et al*. 2012), and domestic animals such as cattle (Bonsma 1942 cited in Timberlake 1995) and goats (Macala *et al*. 1992). This makes mopane leaves highly acceptable to browsers (Hooimeijer *et al*. 2005) especially during the dry season (Makhado *et al*. 2016). Mopane is widely distributed in the low-lying areas of the southern African mopane woodland (Mapaure 1994), and various authors have indicated that its leaves contain valuable nutrients (Bonsma 1942; Van Voorthuizen 1976; DHV 1979; Mosimanyana & Kiflewahid 1988; Macala *et al*. 1992; Styles & Skinner 1997; Hooimeijer *et al*. 2005).

However, the quality of mopane leaves differs seasonally. Studies conducted by Bonsma (1942) and Hooimeijer *et al*. (2005) indicated that the level of nutrients in mopane leaves is high during summer and then declines in winter, a common occurrence in most deciduous savanna trees (Tolsma *et al*. 1987). For instance, during the wet season, the crude protein value of mopane leaves was found to be 16.6% (Bonsma 1942), declining to 6.2% during the dry season (Hooimeijer *et al*. 2005). Even though the leaves are highly nutritious during the wet season (Hooimeijer *et al*. 2005), the intake of mopane leaves by browsers occurs mainly during the dry season (Mosimanyana & Kiflewahid 1988; Macala *et al*. 1992; Hooimeijer *et al*. 2005; Curlewis 2014; Makhado *et al*. 2016). The high consumption of mopane leaves by browsers during the dry season as a result of the availability of leaves on the ground (Makhado *et al*. 2016), and the relatively low concentration of secondary metabolites, such as tannins and phenols (Wessels *et al*. 2007).

Considering the nutritional value of mopane leaves to browsers’ diet, their high consumption rate, especially during the dry season, and the large area covered by this tree species, it is surprising that there is a dearth of studies on determining the concentration of macronutrients in mopane leaves and the effect of browsers on mopane leaf quality. The available and accessible literature on mopane leaf macronutrients are limited to calcium (Ca), phosphorus (P) (Bonsma 1942; Macala *et al*. 1992), nitrogen (N) (Mantlana 2002), crude protein (CP) (Bonsma 1942; DVH 1979; Hooimeijer *et al*. 2005; Macala *et al*. 1992; Styles & Skinner 1997; Mantlana 2002), crude fibre (CF) (Van Voorthuizen 1976; Wessels *et al*. 2007), and essential oils such as α-pinene (Brophy *et al*. 1992; Chagonda *et al*. 2011). Lukhele and Van Ryssen (2000) contributed to the generation of knowledge on the nutritional value of mopane as well, but the methodology applied makes it difficult to consolidate and compare their findings with the existing data. As a result, data and information on the nutritional value of mopane are limited, and do not cover other essential macronutrients such as potassium (K), sulphur (S), chlorine (Cl), magnesium (Mg), nitrate (NO_3) and sodium (Na). In some instances the available data is based on one or two sampling points, which does not properly reflect seasonal leaf quality variations. Lack of data and information therefore makes it difficult to understand the seasonal variation in the amount of macronutrients in mopane leaves, and their nutritional contribution to the diet of browsers in the mopane woodland ecosystem. It further limits understanding of the factors influencing the distribution of browsers in the mopane woodland during various seasons.

This study has been conducted with the aim of addressing the knowledge gap that currently exists, by determining the concentration of macronutrients such as Ca, K, N, P, S, Cl, Mg, NO_3, Na, protein and fibre in mopane leaves. The study further determined the effect of management control measures such as pruning on the concentration of macronutrients from mopane leaves. The pruning experiment was intended to simulate the effect of browsing by large herbivores (Wessels *et al*. 2007), such as the greater kudu, on mopane leaf quality. This study therefore contributes to better understanding of the effect of pruning on the concentration of macronutrients in mopane leaves, which is necessary for understanding the distribution of browsers in relation to leaf quality, and effective management of mopane as an important dry season browsing species.

7.2 METHODOLOGY

7.2.1 Study area

This study was conducted in the Musina Nature Reserve, northern Limpopo Province, South Africa. The reserve is situated 5 km south-east of the town of Musina at 22°24’36”S, 30°03’00”E, and covers 4976 hectares. The altitude of the reserve ranges from 400 to 750 m above sea level. Rainfall in Musina typically starts in late September to early October and reaches its maximum in November, December, January and February. The average rainfall is 331 mm per annum and typically ranges from 300 to 400 mm per annum. The mean annual temperature is 16^{o}C in winter and can reach a maximum of 45^{o}C in summer. The annual average maximum temperature is 30^{o}C. The relative humidity of the area is very low, ranging from 12% in September to 28% in February (SA Weather Services 1981–2014).

The geological foundation is the Archaean Beit Bridge Complex, comprising of gneisses and meta-sediments. Soils range from deep red/brown clays at the bottom of slopes to freely drained sandy soils at the top of slopes. The soil has high sodium content and is alkaline (Mucina & Rutherford 2006). Musina Nature Reserve is located within the Musina Mopane Bushveld and Limpopo Ridge Bushveld of the Mopane bioregion (Mucina & Rutherford 2006). The experimental site (1 hectare) is located in the Musina Mopane Bushveld. The dominant species is mopane (Rutherford *et al.* 2006) with an estimated density of 1 344 trees per hectare (Wessels *et al*. 2007). The grass layer is poorly developed, but dominated by *Schmidtia pappophoroides* (LEDET 2012–2017). The reserve has a diverse range of antelope including *Tragelaphus strepsiceros*, *Taurotragus oryx*, *Oryx gazelle*, *Tragelaphus angasii*, *Hippotragus niger*, *Connochaetes taurinus*, *Sylvicapra grimmia*, *Aepyceros melampus*, *Oreotragus oreotragus* and *Raphicerus campestris* (LEDET 2012–2017).

7.2.2 Sampling procedures

7.2.2.1 Pruning experiment

Pruning and control experiments were conducted following the procedures of Wessels *et al*. (2007). These were initiated during the wet season of February 2014 in a homogenous stand of similar-sized (3 m high) mopane trees. The wet (October–April) and dry (May–September) seasons in South Africa are critical periods for determining leaf quality. During the sampling period in 2014, the average rainfall in Musina Nature Reserve was 316 mm. Rainfall started in September (5 mm), reached its maximum in January (85 mm) and thereafter declined to 0 mm in August (Table 7.1). The leaves started to flush in October, possibly in response to temperature.

Seven healthy tertiary side branches, near the main stem, of relatively equal circumference (20 mm), from each of 40 mopane trees, were randomly selected from different sides of the tree (north, south, east and west). The twigs were pruned back 50 mm by hand shears. The selected branches were marked to assist with future identification in this longitudinal study. Pruning was conducted in order to simulate the effects of browsing by large herbivores (Wessels *et al*. 2007), such as the greater kudu, on mopane leaf quality. The total amount of leaf and shoot biomass removed was less than 10% from the selected branch, which is a reasonable approximation of what is taken by herbivores (Scholes & Walker 1993), such as the greater kudu, in a single visit. Forty trees were not treated and used as controls. These control trees were interspersed with experimental trees within the same red/brown oakleaf soil form. The experimental area was excluded from further browsing through fencing.

7.2.2.2 Leaf sampling and analysis

Mature mopane leaves, including petioles, were randomly collected at intervals of 55 days from the experimental and control mopane trees. Mopane leaf samples were collected from treated and control branches during February, May, June, August, October and December of the same year. The first samples were collected after the treatment was administered. Three independent samples composed of seven mopane leaves per 40 mopane trees were randomly collected from the canopies of experimental and control per sampling event, and transported to the laboratory in sealed transparent plastic bags in a cooler box. The samples were dried in plant presses at room temperature. The dried leaves from each three independent samples were mixed separately and a pooled sample of 10 g per treatment per sample cycle (55 days) was sent to the Agricultural Research Council (ARC), Institute for Soil, Climate and Water for the determination of Ca, K, N, P, S, Cl, Mg, NO_3, Na, protein and fibre content. Each macronutrient was analysed three times, per sample cycle, which totalled to 18 samples per treatment per macronutrient. Macronutrients were determined using the inductively coupled plasma atomic emission spectrometry technique (ICP-AES, iCAP 600 Series, Thermo Scientific, Cambridge, UK).

7.2.3 Statistical analysis

Collected datasets were analysed using descriptive and inferential statistical analysis. Descriptive statistical analysis was used to determine the mean and standard deviation for the sampled macronutrients. The effect of pruning on the monthly concentration of macronutrients in mopane leaves was tested using a two-tailed t-Test: Two-Sample Assuming Equal Variance. The seasonal and annual effect of pruning on the concentration of macronutrients in mopane leaves was tested using One-Way Anova (IBM SPSS Statistics 24, USA). A significant difference was accepted when $P < 0.05$.

7.3 RESULTS

7.3.1 Calcium

The mean concentration of Ca in the leaves ranged between 1% and 3% for both pruned and control mopane trees during the sampling period. The amount of Ca in the pruned and control trees increased during the dry season, but declined slightly during the wet season (Figure 7.1). The average maximum concentration of Ca in the control trees was 2.27%±0.27% during August, while Ca in the pruned trees reached its average maximum level during October at 2.46%±0.10% (Table 7.1). The decline in the concentration of Ca in the pruned trees showed a delay compared to the control trees (Figure 7.1), which indicated that the concentration of Ca had reduced slightly after pruning, but increased after that period. This indicates that pruning elevates Ca in the following season (Figure 7.1). Despite the treatment exerted, the concentration of Ca in the pruned and control mopane trees was not significant at *P*<0.05 in all the sampling months (Table 7.2). In addition, the seasonal amount of Ca between pruned and control mopane trees during the wet (*P*=0.203) and dry (*P*=0.369) seasons was statistically insignificant (Table 7.3). The results further showed that the annual concentration of Ca between pruned and control mopane trees did not differed significantly (*P*=0.456) (Table 7.4).

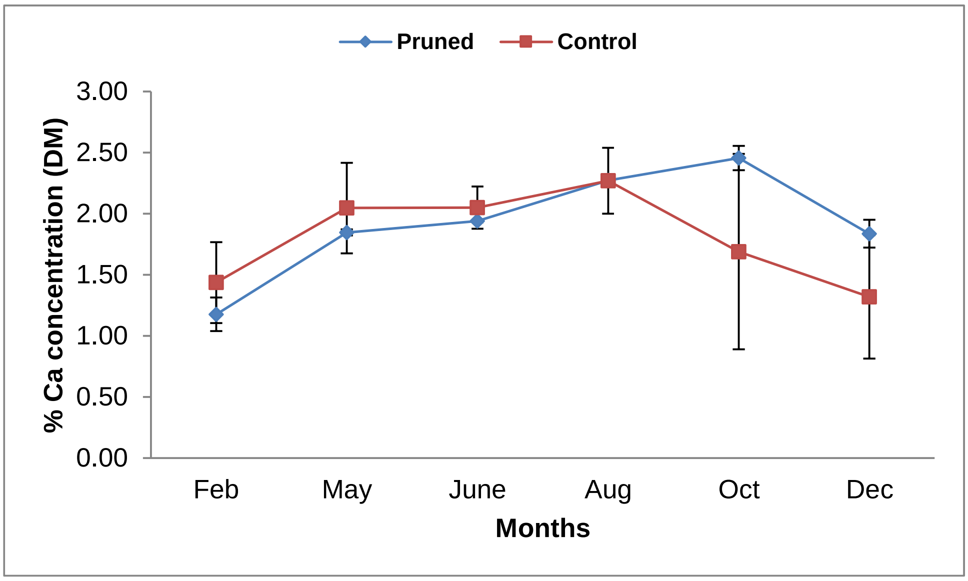

Figure 7.1: Average Ca concentration in the pruned and control mopane trees. Bars indicate standard deviation.

7.3.2 Potassium

Pruning lowered K during the following dry season and early growing season, but this influence was apparently nullified as the second growing proceeded (Figure 7.2). The concentration of K in mopane leaves was relatively constant between May and August, which is the period when the leaves were at the mature stage. The amount of K started to increase in the young mopane leaves from 0.46%±0.09% and 0.82%±0.66% on average in pruned and control trees, respectively during leaf flush in October. The average maximum level was 1.15%±0.16 and 1.14%±0.19% in pruned and control trees, respectively, during December (Figure 7.2; Table 7.1). However, pruning of mopane trees reduced the amount of K in the young leaves as compared to the control trees. Nevertheless, both the control and pruned trees reached the maximum level at the same time during December (Figure 7.2; Table 7.1). The concentration of K in the pruned and control mopane trees was statistically insignificant at *P*<0.05 in all the sampling months (Table 7.2). The amount of K between pruned and control mopane trees was statistically insignificant during the wet season (*P*=0.680), but differed significantly during the dry season (*P*=0.039) (Table 7.3). The results further showed that the annual amount of K between pruned and control mopane trees did not differed significantly (*P*=0.312) (Table 7.4).

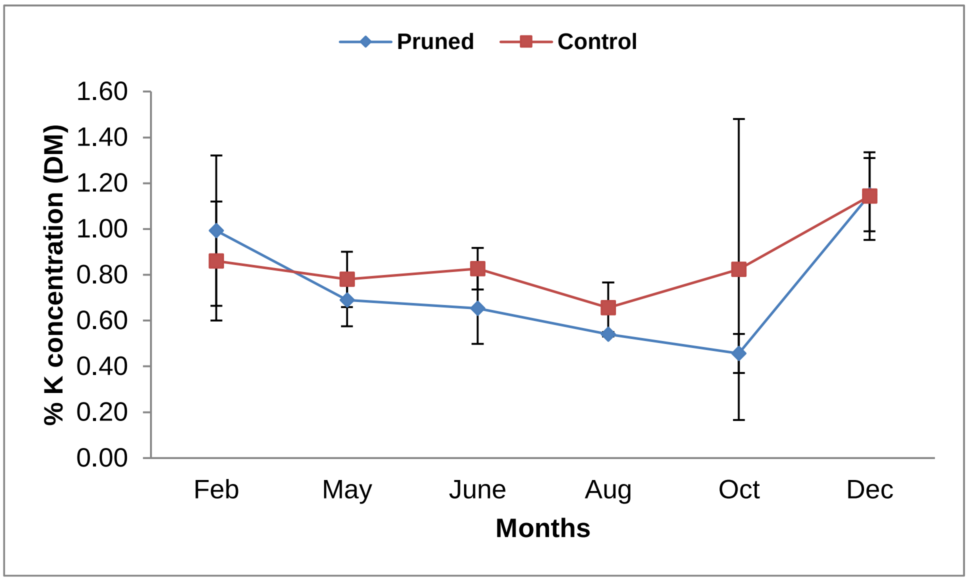

Figure 7.2: Average K concentration in the pruned and control mopane trees. Bars indicate standard deviation.

7.3.3 Nitrogen

The level of N dropped as the leaf matured and aged during the dry season. The lowest concentration of N was 1.51%±0.18% and 1.33%±0.19% during August in the control and pruned trees, respectively. However, the N level started to increase during leaf flush in October, reaching its maximum in December. The average concentration of N in December was 2.76%±0.83% and 2.56%±0.87% in the control and pruned trees, respectively (Figure 7.3, Table 7.1). The overall concentration of N in the leaves ranged from 1% to 3% for both the pruned and control trees, respectively (Figure 7.3; Table 7.1). The amount of N between pruned and control mopane trees was statistically insignificant at *P*<0.05 in all the sampling months (Table 7.2). The concentration of N between pruned and control mopane trees was statistically insignificant during the wet (*P*=0.676) and dry (*P*=0.142) seasons (Table 7.3). In addition, the annual amount of N between pruned and control mopane trees did not differed significantly (*P*=0.315) (Table 7.4).

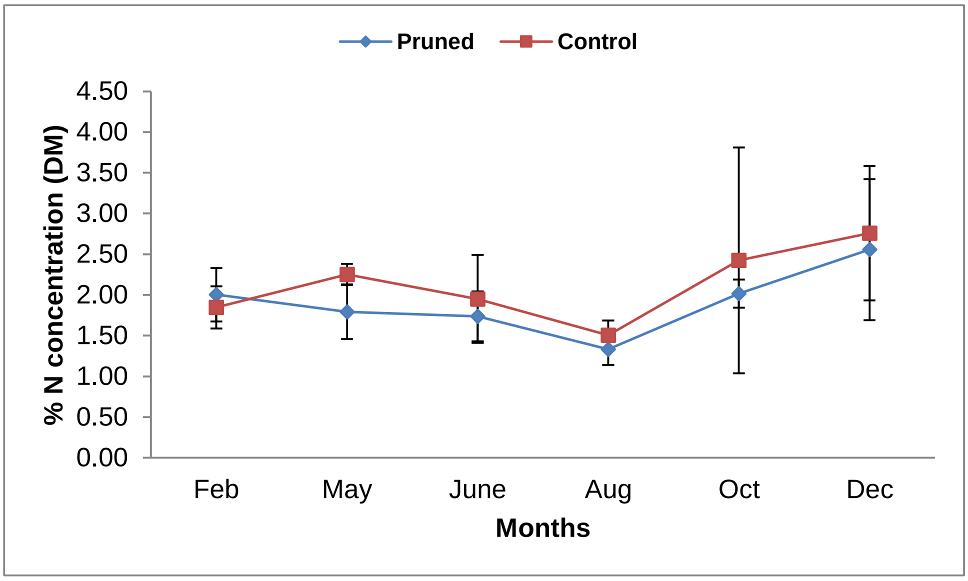

Figure 7.3: Average N concentration in the pruned and control mopane trees. Bars indicate standard deviation.

7.3.4 Phosphorus

The concentration of P was less than 0.5% on average for both pruned and control mopane trees (Figure 7.4; Table 7.1). This study found that pruning resulted in a slight decrease in the concentration of P in the mopane leaves (Figure 7.4; Table 7.1). The amount of P was lowest during August at 0.13%±0.01% and 0.15%±0.01% on average in the pruned and control trees, respectively. The P concentration in the leaves reached a maximum level during October at 0.23%±0.17 and 0.27%±0.14% on average in the pruned and control trees, respectively (Figure 7.4; Table 7.1). The amount of P between pruned and control mopane trees was not significant at *P*<0.05 in all the sampling months (Table 7.2). In addition, the concentration of P between pruned and control mopane trees did not differed significantly during the wet (*P*=0.394) and dry (*P*=0.273) seasons (Table 7.3). Similarly, the annual quantity of P between pruned and control mopane trees was not significant (*P*=0.196) (Table 7.4).

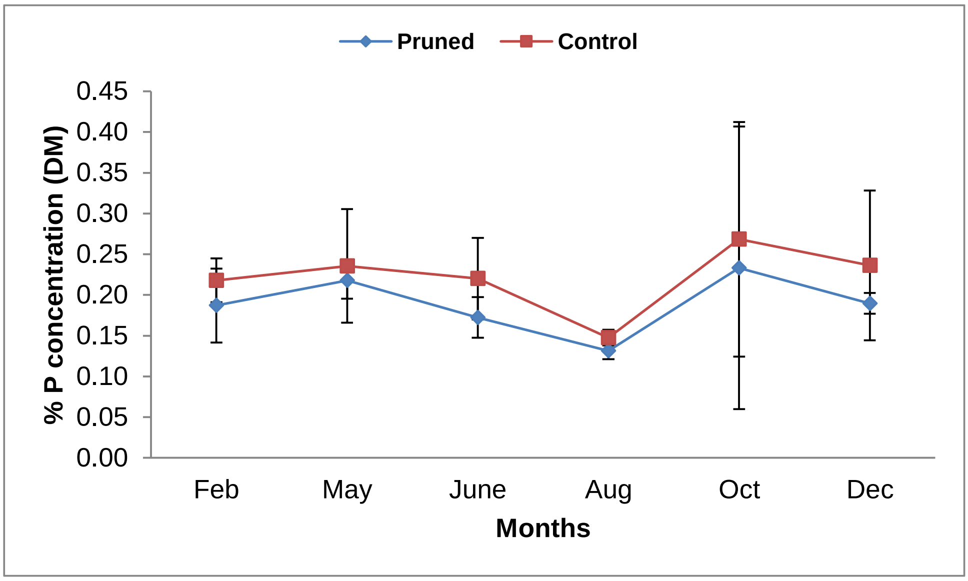

Figure 7.4: Average P concentration in the pruned and control mopane trees. Bars indicate standard deviation.

7.3.5 Sulphur

The concentration of S in the pruned and control trees did not show a clear pattern, but seemed to be high in the control trees than in the pruned trees as time passed (Figure 7.5; Table 7.1). The level of S in the leaves ranged from 0.09% to 0.14% and 0.10% to 0.13% on average in the pruned and control trees, respectively. It seems that pruning resulted in a slight decline in the concentration of S (Figure 7.5). However, concentration of S in the pruned and control mopane trees was not significant at $P<0.05$ in all the sampling months (Table 7.2). The amount of S in the pruned and control mopane trees did not differed significantly during the wet ($P=0.489$) and dry ($P=0.535$) seasons (Table 7.3). In addition, the annual amount of S between the pruned and control mopane trees was statistically insignificant ($P=0.335$) (Table 7.4).

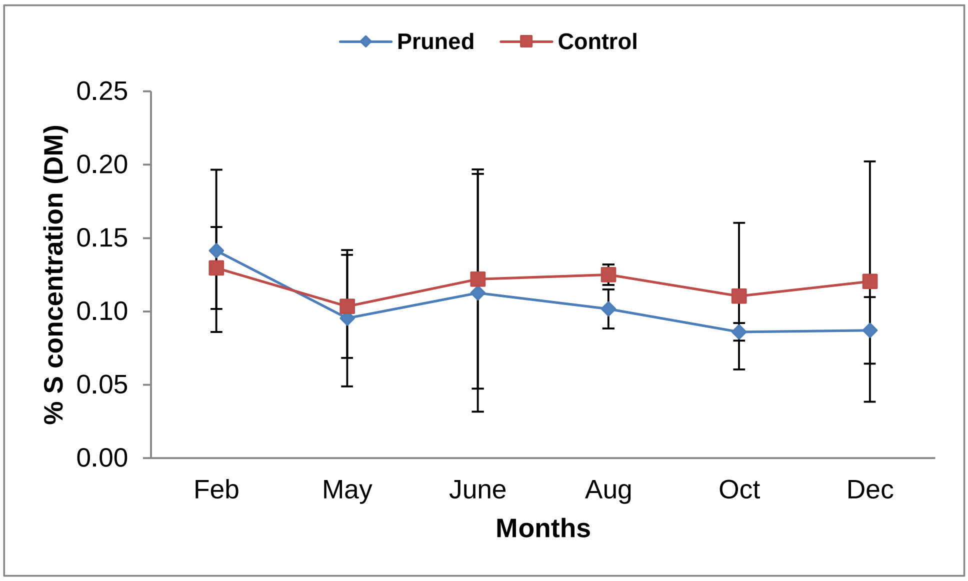

Figure 7.5: Average S concentration in the pruned and control mopane trees. Bars indicate standard deviation.

7.3.6 Chlorine

The concentration of Cl was lower in the pruned trees compared to the control trees. This study showed that leaves contained low Cl concentrations, <0.35% on average for both pruned and control trees (Figure 7.6; Table 7.1). The concentration of Cl in the pruned and control trees was relatively constant, but increased marginally during December. The concentration of Cl between pruned and control mopane trees was not significant at *P*<0.05 in all the sampling months (Table 7.2). The amount of Cl between pruned and control mopane trees did not differed significantly during the wet (*P*=0.615) and dry (*P*=0.636) seasons (Table 7.3). In addition, the annual concentration of Cl between pruned and control mopane trees did not differed (*P*=0.476) (Table 7.4).

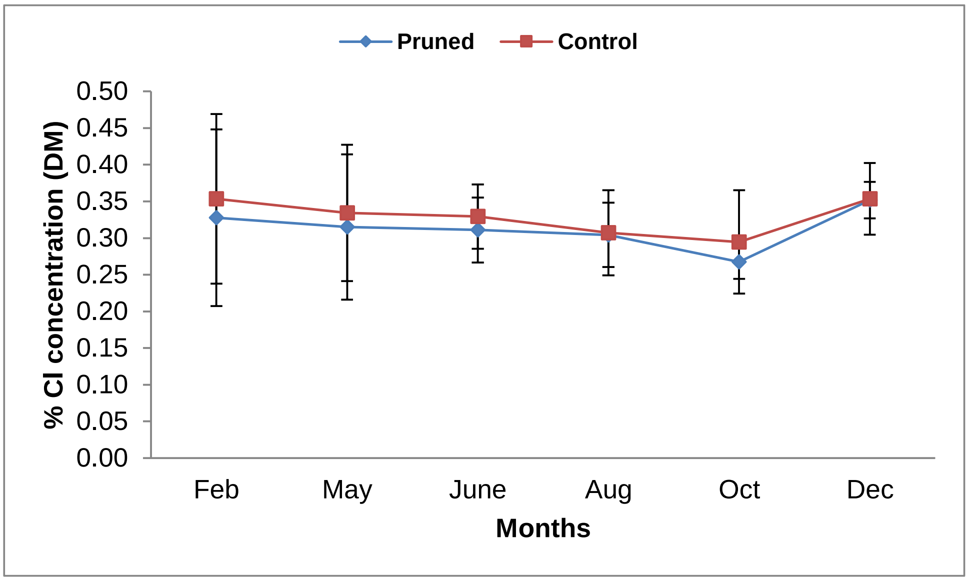

Figure 7.6: Average Cl concentration in the pruned and control mopane trees. Bars indicate standard deviation.

7.3.7 Magnesium

The amount of Mg in mopane leaves reached its maximum level at 0.46%±0.16% and 0.42%±0.20% on average during June in the pruned and control trees, respectively. However, on average, the level of Mg ranged between 0.23%±0.01% and 0.25%±0.03% in December to a maximum of 0.46%±0.16% and 0.42%±0.20% in June in the pruned and control trees, respectively (Figure 7.7; Table 7.1). Contrary to other macronutrients analysed in this study, which built up in the young leaves in October, the concentration of Mg built up in mature and old leaves in June and thereafter declined (Figure 7.7; Table 7.1). However, the concentration of Mg in the pruned and control mopane trees was not significant at $P<0.05$ in all the sampling months (Table 7.2). The seasonal amount of Mg between pruned and control mopane trees did not differed significantly during the wet ($P=0.959$) and dry ($P=0.404$) seasons (Table 7.3). In addition, the annual amount of Mg between pruned and control mopane trees was insignificant ($P=0.483$) (Table 7.4).

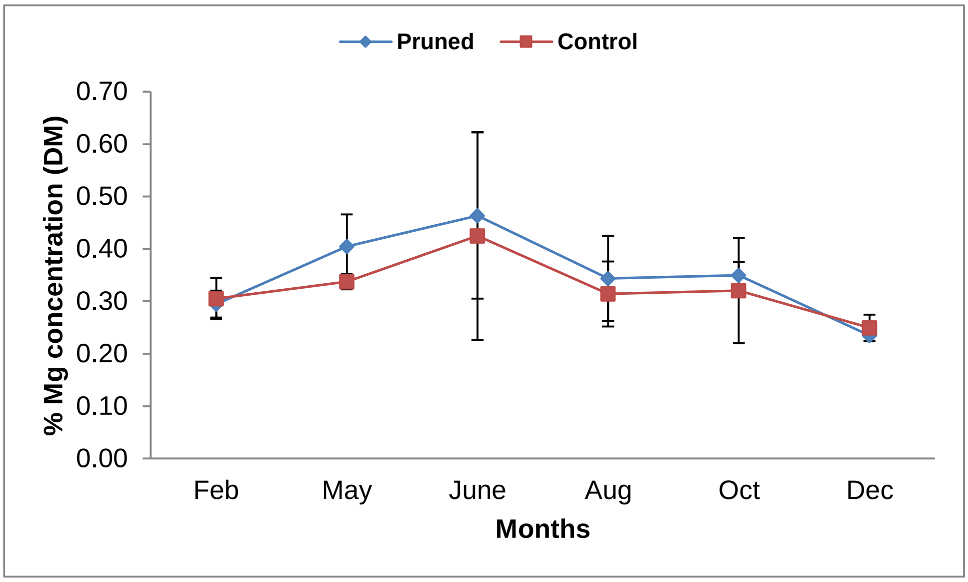

Figure 7.7: Average Mg concentration in the pruned and control mopane trees. Bars indicate standard deviation.

7.3.8 Nitrate

The average maximum level of NO_3 was reached during May at 304.33 mg/kg±117.75 mg/kg and 23.67 mg/kg±48.13 mg/kg in the pruned and control trees, respectively (Figure 7.8; Table 7.1). The concentration of NO_3 started to decline in June-August, thereafter slightly increase in October from an average minimum of 97.33 mg/kg±34.59 mg/kg and 81.33 mg/kg±12.50 mg/kg in the pruned and control trees, respectively. The results indicate that the level of NO_3 was higher in the mature and old leaves than in the young leaves. The concentration of NO_3 in the pruned and control mopane trees was not statistically significant at $P<0.05$ in all the sampling months (Table 7.2). The amount of NO_3 in the pruned and control mopane trees did not statistically differed significantly during the wet ($P=0.312$) and dry ($P=0.398$) seasons (Table 7.3). In addition, the annual amount of NO_3 in the pruned and control mopane trees was insignificant ($P=0.269$) (Table 7.4).

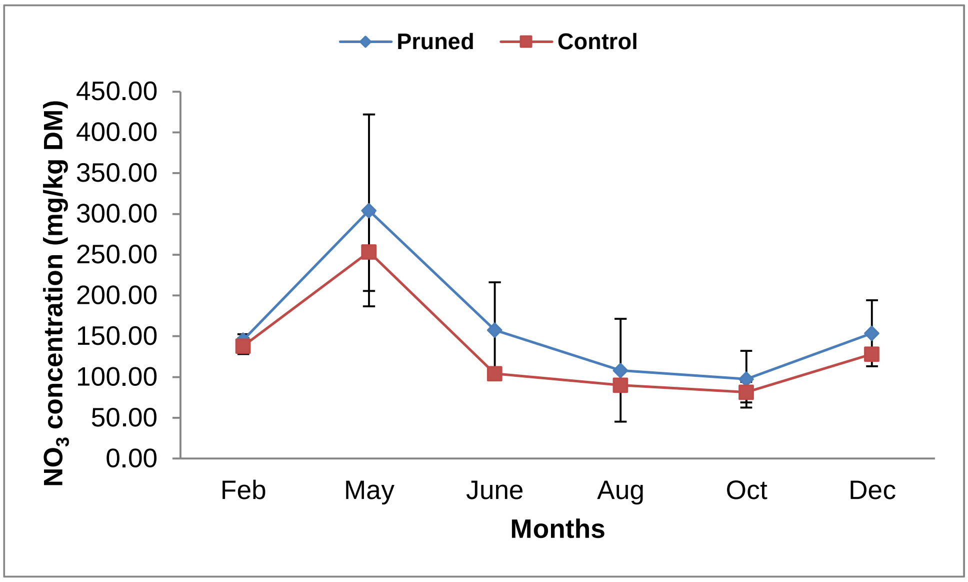

Figure 7.8: Average NO_3 concentration in the pruned and control mopane trees. Bars indicate standard deviation.

7.3.9 Sodium

The average concentration of Na ranged from 450 mg/kg to 594 mg/kg and 450 mg/kg to 554 mg/kg in the pruned and control trees, respectively (Figure 7.9; Table 7.1). The concentration of Na in the pruned and control trees did not show a clear pattern, but appeared to be constant throughout the study period (Figure 7.9). The concentration of Na in the pruned and control mopane trees was not statistically significant at $P<0.05$ in all the sampling months (Table 7.2). The amount of Na in the pruned and control mopane trees did not statistically differed during the wet ($P=0.445$) and dry ($P=0.345$) seasons (Table 7.3). In addition, the annual concentration of Na in the pruned and control mopane trees was insignificant ($P=0.216$) (Table 7.4).

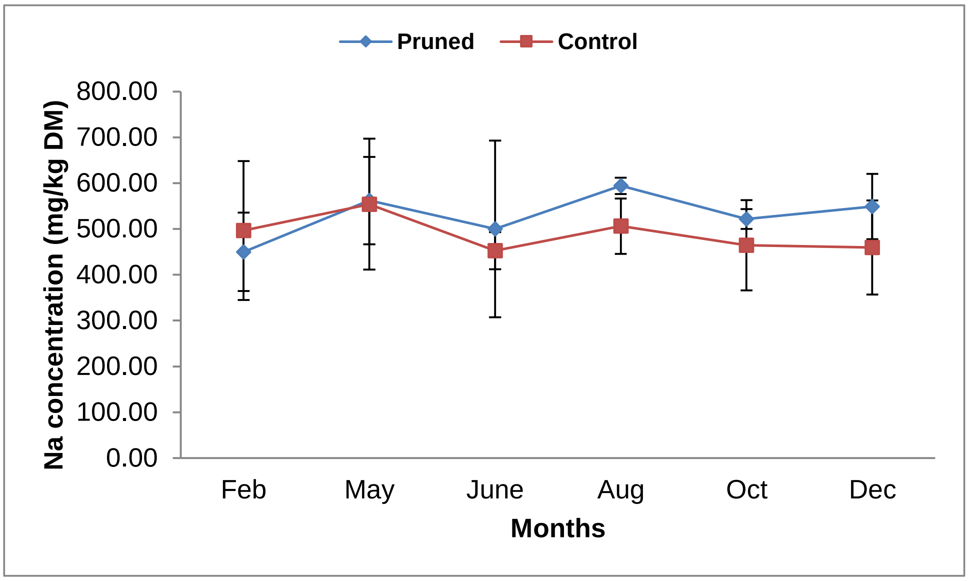

Figure 7.9: Average Na concentration in the pruned and control mopane trees. Bars indicate standard deviation.

7.3.10 Protein

The concentration of protein in the leaves was low during the dry season, particularly in August, but increased with leaf flush in October, and reached its maximum during the wet season (Figure 7.10; Table 7.1). During August, the average protein concentration in the leaves was low at 6.94%±0.93% and 8.49%±0.71% in the pruned and control trees, respectively. The highest average concentration of protein in the control trees was reached during December at 13.62%±0.27, while the maximum level in the pruned trees was reached in February at 12.18%±1.46% on average (Figure 7.10; Table 7.1). As time progressed, pruning slightly reduces the amount of protein in the leaves compared to the control trees (Figure 7.10). However, the concentration of protein in the pruned and control mopane trees was not statistically significant at $P<0.05$ in all sampling months (Table 7.2). The amount of protein in the pruned and control mopane trees was statistically near significant during the wet season ($P=0.097$), but insignificant during the dry season ($P=0.119$) (Table 7.3). In addition, the annual concentration of protein statistically differed between pruned and control mopane trees ($P=0.032$) (Table 7.4).

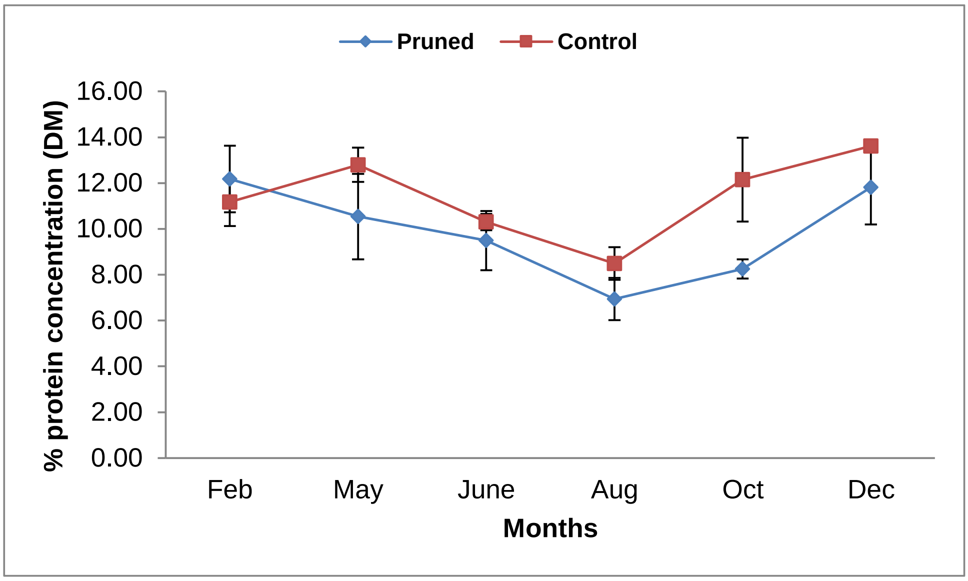

Figure 7.10: Average protein concentration in the pruned and control mopane trees. Bars indicate standard deviation.

7.3.11 Fibre

The average concentration of fibre remained relatively constant throughout the year, but increased from 25.59%±1.08% and 26.81%±1.35% in August to a maximum of 36.99%±10.28% and 33.91%±0.46 in October in the control and pruned leaves, respectively (Figure 7.11; Table 7.1). This study showed that fibre concentration increased to its maximum during the leaf flush period in October (Figure 7.11), but declined as the leaves matured and aged. The concentration of fibre in the pruned and control mopane trees statistically differed during June (P=0.005), but was insignificant at P<0.05 in most sampling months (Table 7.2). The amount of fibre in the pruned and control mopane trees did not differed significantly during the wet (P=0.693) and dry (P=0.136) seasons (Table 7.3). In addition, the annual quantity of fibre in the pruned and control mopane trees did not differed (P=0.976) (Table 7.4).

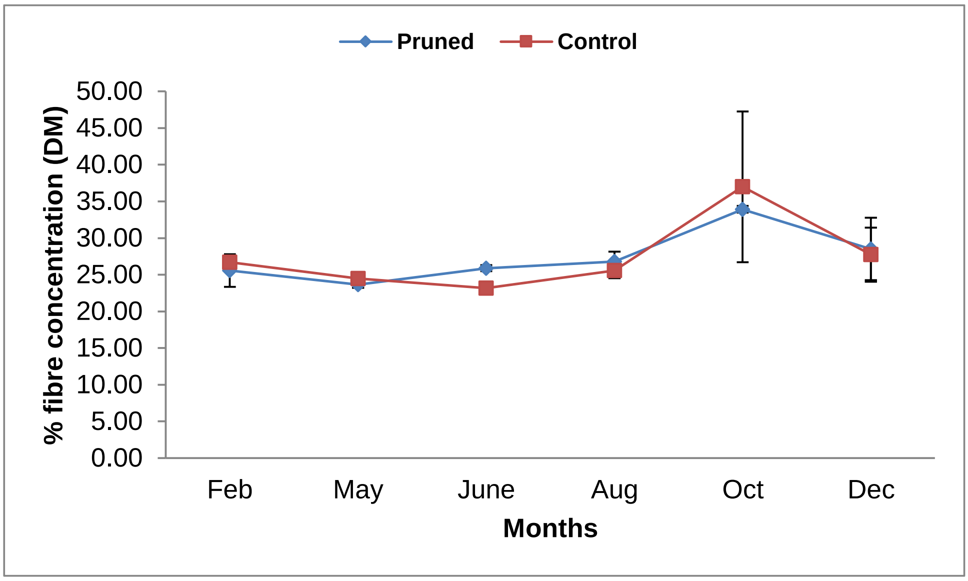

Figure 7.11: Average fibre concentration in the pruned and control mopane trees. Bars indicate standard deviation.

Table 7.1: Mean (±S.D) macronutrients concentration in mopane leaves in the control (*n*=18) and pruned (*n*=18) trees.

	February				May				June				August				October				December			
	Control		Pruned		Control		Pruned		Control		Pruned		Control		Pruned		Control		Pruned		Control		Pruned	
Macronutrients	mean	S.D.	mean	S.D	mean	S.D	mean	S.D	mean	S.D	mean	S.D	mean	S.D	mean	S.D	mean	S.D	mean	S.D	mean	S.D	mean	S.D
Ca (% DM)	1.44	0.33	1.18	0.14	2.05	0.37	1.85	0.03	2.05	0.17	1.94	0.01	2.27	0.27	2.27	0.02	1.69	0.80	2.46	0.10	1.32	0.51	1.84	0.12
K (% DM)	0.86	0.26	0.99	0.33	0.78	0.12	0.69	0.12	0.83	0.09	0.65	0.16	0.66	0.11	0.54	0.01	0.82	0.66	0.46	0.09	1.14	0.19	1.15	0.16
N (% DM)	1.85	0.25	2.00	0.33	2.25	0.13	1.79	0.34	1.95	0.54	1.74	0.31	1.51	0.18	1.33	0.19	2.42	1.39	2.02	0.17	2.76	0.83	2.56	0.87
P (% DM)	0.22	0.03	0.19	0.05	0.24	0.07	0.22	0.02	0.22	0.05	0.17	0.02	0.15	0.01	0.13	0.01	0.27	0.14	0.23	0.17	0.24	0.09	0.19	0.01
S (% DM)	0.13	0.03	0.14	0.06	0.10	0.04	0.10	0.05	0.12	0.07	0.11	0.08	0.13	0.01	0.10	0.01	0.11	0.05	0.09	0.01	0.12	0.08	0.09	0.02
Cl (% DM)	0.35	0.12	0.33	0.12	0.33	0.09	0.32	0.10	0.33	0.04	0.31	0.04	0.31	0.06	0.30	0.04	0.29	0.07	0.27	0.02	0.35	0.05	0.35	0.02
Mg (% DM)	0.31	0.04	0.29	0.03	0.34	0.01	0.40	0.06	0.42	0.20	0.46	0.16	0.31	0.06	0.34	0.08	0.32	0.10	0.35	0.03	0.25	0.03	0.23	0.01
NO_3 (mg/kg DM)	138.0	9.85	145.33	7.23	253.7	48.13	304.3	117.8	104.3	3.79	157.7	58.62	90.00	5.00	108.3	62.92	81.33	12.50	97.33	34.59	128.3	5.77	153.7	40.50
Na (mg/kg DM)	496.7	151.44	450.0	85.44	554.0	143.0	562.0	95.14	452.5	40.50	511.0	192.9	506.0	60.51	594.0	18.0	464.3	98.46	521.5	21.50	459.7	102.6	549.0	71.0
Protein (% DM)	11.17	1.05	12.18	1.40	12.80	0.75	10.54	1.86	10.30	0.36	9.49	1.29	8.49	0.71	6.94	0.93	12.15	1.83	8.26	0.42	13.62	0.27	11.82	1.62
Fibre (% DM)	26.69	0.17	25.56	2.24	24.49	0.45	23.66	0.44	23.17	0.17	25.89	0.42	25.59	1.08	26.81	1.35	36.99	10.28	33.91	0.46	27.73	3.70	28.50	4.25
Mean Rainfall	January		February		March		April		May		June		July		August		September		October		November		December	
(mm)*	85.1		51.7		46.5		9.4		5.5		0.5		1.5		0		4.5		25.5		45.8		39.5	

Symbols: Ca=Calcium; K=Potassium; N=Nitrogen; P=Phosphorus; S=Sulphur; Cl=Chlorine; Mg=Magnesium; NO_3=Nitrate; Na=Sodium; %=Percentage; DM=Dry Matter; mg/kg=milligramme per kilogramme; S.D=standard deviation; mm=millimetre; *=Rainfall data for Musina Nature Reserve (2014).

Table 7.2: Monthly effect of pruning on the concentration of macronutrients in mopane leaves.

	February		May		June		August		October		December	
Macronutrients	*t Stat*	*P-value*	*t Stat*	*P-value*	*t Stat*	*P-value*	*t Stat*	*P-value*	*t Stat*	*P-value*	*t Stat*	*P-value*
Ca (% DM)	-1.258	0.297^{a}	-0.932	0.450^{a}	-1.096	0.387^{a}	0.021	0.985^{a}	1.649	0.241^{a}	1.728	0.226^{a}
K (% DM)	0.552	0.611^{a}	-0.932	0.404^{a}	-1.674	0.193^{a}	-1.835	0.208^{a}	-0.959	0.439^{a}	0.046	0.965^{a}
N (% DM)	0.651	0.551^{a}	-2.199	0.115^{a}	-0.595	0.594^{a}	-1.140	0.318^{a}	-0.506	0.663^{a}	-0.289	0.787^{a}
P (% DM)	-1.014	0.385^{a}	-0.426	0.711^{a}	-1.472	0.238^{a}	-2.038	0.111^{a}	-0.269	0.801^{a}	-0.870	0.476^{a}
S (% DM)	0.326	0.766^{a}	-0.238	0.824^{a}	-0.147	0.890^{a}	-2.686	0.075^{a}	-0.837	0.491^{a}	-0.678	0.568^{a}
Cl (% DM)	-0.266	0.803^{a}	-0.246	0.818^{a}	-0.510	0.637^{a}	-0.071	0.947^{a}	-0.638	0.589^{a}	-0.053	0.961^{a}
Mg (% DM)	-0.395	0.719^{a}	1.854	0.205^{a}	0.266	0.804^{a}	0.498	0.645^{a}	0.497	0.669^{a}	-0.924	0.424^{a}
NO_3 (mg/kg DM)	1.039	0.357^{a}	0.690	0.540^{a}	1.573	0.256^{a}	0.503	0.665^{a}	0.754	0.506^{a}	1.073	0.396^{a}
Na (mg/kg DM)	-0.465	0.674^{a}	0.081	0.941^{a}	0.417	0.717^{a}	2.415	0.137^{a}	0.982	0.429^{a}	1.240	0.283^{a}
Protein (% DM)	0.976	0.384^{a}	-1.951	0.146^{a}	-1.046	0.405^{a}	-2.302	0.083^{a}	-3.588	0.070^{a}	-1.883	0.200^{a}
Fibre (% DM)	-0.869	0.476^{a}	-2275	0.085^{a}	10.530	0.002^{b}	1.228	0.287^{a}	-0.518	0.656^{a}	0.237	0.825^{a}

Symbols: Ca=Calcium; K=Potassium; N=Nitrogen; P=Phosphorus; S=Sulphur; Cl= Chlorine; Mg=Magnesium; NO_3=Nitrate; Na=Sodium; %=Percentage; DM=Dry Matter; mg/kg=milligramme per kilogramme. **Note:** ^{a}=Not significant at $P < 0.05$, ^{b}=Significant at $P < 0.05$. Statistical superscripts refer to rows in the table.

Table 7.3: Seasonal effect of pruning on the concentration of macronutrients in mopane leaves. Seasons used in the analysis were the wet (February, October and December) and dry (May, June and August) seasons.

	Wet season		**Dry season**	
Macronutrients	*F-value*	*P-value*	*F-value*	*P-value*
Ca (% DM)	1.759	0.203^{a}	0.853	0.369^{a}
K (% DM)	0.176	0.680^{a}	5.076	0.039^{b}
N (% DM)	0.181	0.676^{a}	2.386	0.142^{a}
P (% DM)	0.767	0.394^{a}	1.287	0.273^{a}
S (% DM)	0.501	0.489^{a}	0.403	0.535^{a}
Cl (% DM)	0.263	0.615^{a}	0.233	0.636^{a}
Mg (% DM)	0.003	0.959^{a}	0.736	0.404^{a}
NO_3 (mg/kg DM)	1.088	0.312^{a}	0.754	0.398^{a}
Na (mg/kg DM)	0.613	0.445^{a}	0.947	0.345^{a}
Protein (% DM)	3.114	0.097^{a}	2.712	0.119^{a}
Fibre (% DM)	0.161	0.693^{a}	2.464	0.136^{a}

Symbols: Ca=Calcium; K=Potassium; N=Nitrogen; P=Phosphorus; S=Sulphur; Cl=Chlorine; Mg=Magnesium; NO_3=Nitrate; Na=Sodium. **Note:** ^{a}=Not significant at $P < 0.05$, ^{b}=Significant at $P < 0.05$. Statistical superscripts refer to rows in the table.

Table 7.4: Annual effect of pruning on the concentration of macronutrients in mopane leaves.

	Pruned versus Control	
Macronutrients	*F-value*	*P-value*
Ca (% DM)	0.570	0.456[a]
K (% DM)	1.052	0.312[a]
N (% DM)	1.039	0.315[a]
P (% DM)	1.739	0.196[a]
S (% DM)	0.957	0.335[a]
Cl (% DM)	0.520	0.476[a]
Mg (% DM)	0.503	0.483[a]
NO_3 (mg/kg DM)	1.265	0.269[a]
Na (mg/kg DM)	1.586	0.216[a]
Protein (% DM)	4.983	0.032[b]
Fibre (% DM)	0.001	0.976[a]

Symbols: Ca=Calcium; K=Potassium; N=Nitrogen; P=Phosphorus; S=Sulphur; Cl= Chlorine; Mg=Magnesium; NO_3= Nitrate; Na=Sodium. **Note:** [a]=Not significant at $P < 0.05$, [b]=Significant at $P < 0.05$. Statistical superscripts refer to rows in the table.

7.4 DISCUSSION

7.4.1 Role of macronutrients to herbivores

Mopane leaves contain various macronutrients (Table 7.1). These macronutrients are required in the diet of herbivores in relatively large amount because they play a critical role in building healthy bodies (Warlaw & Smith 2011). They also enhance animal's performance and proper functioning of metabolism (Ormsbee *et al*. 2014). Protein, fibre, NO_3 and Na are present in high concentrations in mopane leaves (Table 7.1).

The high amount of protein in mopane leaves plays an important role in the diet of browsers (Bonsma 1942; Hooimeijer *et al*. 2005). According to Owen-Smith and Cooper (1989), protein requirements for the greater kudu range from 9% at the end of the dry season to between 12% and 14% in the late wet season. The average level of protein obtained in this study ranged from 7% during the dry season to 14% during the wet season (Table 7.1), which is essential in meeting the dietary requirements of the greater kudu. Protein also contains different amino acids that protect animal cell walls and serve as active enzymes, hormones and antibiotics (Robbins 1983), which assist in enhancing the immune response, cellular repair, and formation of blood cells as well as tissues (FAO 2004).

Fibre, for instance, influences the digestibility as well as acceptability of the leaves for browsers (Cooper & Owen-Smith 1985). Fibre also plays a role in improving gut health (Montagne *et al*. 2003). However, the high intake of fibre, especially during summer, may enhance gut perturbation and cause subsequent diarrhoea in calves (Montagne *et al*. 2003). The high quantity of fibre during the wet season implies that mopane leaves will not be easily digested, as opposed to the dry season, where the concentration of fibre is relatively low (Figure 7.11).

Other macronutrients found in mopane leaves at high concentration are NO_3 and Na (Table 7.1). Nitrates plays a role in increasing gastric mucosal blood flow (Petersson *et al*. 2007), protects animals against injuries and cardiovascular disorders, and enables optimal performance (Lundberg *et al*. 2011). Sodium is found in a high concentration in mopane leaves, but the plant only needs small quantities of it. It is the herbivores that need a large amount of Na, because it plays a role in the generation of nerve impulses, maintenance of electrolyte balance, fluid balance, heart activity and certain metabolic functions (Pohl *et al*. 2013).

The concentration of Ca, K, N, P, S, Cl, and Mg in mopane leaves was less than 5% (Table 7.1). Despite the low concentration of these nutrients in the leaves, they are required by browsers at that level, and play a critical role in ensuring that browsers are healthy. The nutritional value of mopane makes it one of the more important quality fodder species in the mopane woodland. Browsers such as elephants (Ben-Shahar & MacDonald 2002) and greater kudu (Hooimeijer *et al*. 2005) feed on mopane leaves, as they are attracted by their nutritional value (Hooimeijer *et al*. 2005), especially during the dry season (Curlewis 2014). The availability of mopane leaves during the dry season when most species in the mopane woodland are leafless increases its acceptability to browsers (Makhado *et al*. 2016). In addition, mopane leaves are highly browsed during the dry season when secondary metabolites such as tannins and phenols are at lower concentration (Wessels *et al*. 2007; Kohi *et al*. 2010).

7.4.2 Effect of pruning on the concentration of macronutrients

This study showed that <10% pruning does not have an effect on the amount of macronutrients between treatments (Table 7.2). However, Du Toit *et al*. (1990) are of the opinion that pruning ultimately improves the quality of forage for ungulates. Hrabar (2005), Wessels *et al*. (2007) and Hrabar *et al*. (2009) also stated that it seems that pruning is an ideal measure to increase the number of mopane leaves and enhance leaf flush. This could be critical in ensuring that browsers in mopane woodland have enough forage, especially during the dry season.

7.4.3 Seasonal variation in the concentration of macronutrients

As also found by Hrabar (2005), the concentration of macronutrients did not differ between the pruned and control mopane trees (Table 7.3). The quantity of macronutrients in mopane leaves generally starts to increase at the onset of the growth season (October), after the first summer rains, and declines during the dry season, particularly during June, when the leaves mature and age (Table 7.1). Similar trends were observed by Wessels *et al*. (2006) and Kasale (2013). Old leaves contain essential macronutrients and relatively low concentration of secondary metabolites, making them readily available (Wessels *et al*. 2007) and highly acceptable to browsers such as the greater kudu in the mopane woodland (Hooimeijer *et al*. 2005; Curlewis 2014). The build-up of the sampled macronutrients, except for Mg and NO_3, happens at the same time as an increase in the secondary metabolites in young mopane leaves (Styles & Skinner 1997; Hooimeijer *et al*. 2005), which suggests that mopane invests its resources to protect young leaves to attain maximum growth with minimal browsing disturbance.

In addition, the increase in the concentration of macronutrients occurs during October following the first summer rains and then declines during the dry season as rainfall drops. This pattern was confirmed by various authors (Chidumayo & Frost 1996; Chidumayo 2001; Smit 2001; Wessels *et al*. 2006; Mlambo & Nyathi 2008; Wessels *et al*. 2011; Stevens *et al*. 2016), who indicated that the quality of the leaf is also triggered by rainfall. This suggests that rainfall needs to be taken into account when determining the quality of leaves. In this instance, leaf moisture can be specifically used to determine the quality of the leaf during different growing seasons.

7.5 CONCLUSION

It is concluded that mopane leaves contain essential macronutrients. These macronutrients have important role to play in building healthy body for browsers. This study showed that <10% pruning exerted in this study did not have an effect in the concentration of most macronutrients sampled. It is further concluded that the amount of macronutrients in mopane leaves is not dependent on <10% pruning, but appears to be associated with leaf growth stages. Though it need further research, this study showed that spring leaf flush triggers an increase in the concentration of most macronutrients, but declined as the leaf matures and ages. However, the amount of NO_3 and Mg shows a converse relationship with leaf flush. The amount of NO_3 and Mg built up in mature and old leaves in June, which is contrary to other macronutrinets sampled, which built up in the young leaves, particularly in October.

CHAPTER 8

EFFECTS OF PRUNING ON THE CONCENTRATION OF TRACE ELEMENTS IN *COLOPHOSPERMUM MOPANE* LEAVES[6]

8.1 INTRODUCTION

The abundance of herbivores in the African savanna is largely determined by the availability of quality forage (Fritz & Duncan 1994). Plant nutritional quality is highly variable at various spatio-temporal scales (Owen-Smith 2007; Barber & Marquis 2011), but largely determines the nutrient status of the animal living in that particular habitat (Van Rooyen 2009). The quality of forage also controls the performance (Van Soest 1994), productivity, distribution and feeding pattern of herbivores (Codron 2006; Holá 2012).

Browsers prune plant shoots (Bryant *et al*. 1991), which affects the performance of plant and resource allocation (Hendrix 1988). Browsing by herbivores also results in variation in the chemical composition and the quantity of minerals in a plant as a whole (Bryant *et al*. 1991; Lukhele & Van Ryssen 2000). Poor quality forage can reduce animal productivity (Odenyo *et al*. 1997). In general, herbivores prefer browse with high nutritional content (Villalba & Provenza 1999), and avoid forage with a high concentration of secondary metabolites (Holá 2012), such as tannins and phenols (Wessels *et al*. 2007). Knowledge of the effect of pruning on plant resource allocation and responses is necessary, in order to gain a better understanding of the distribution of herbivores, and their feeding patterns as determined by forage quality (Hester *et al*. 2006).

The savanna biome is characterised by tree-grass co-existence and support grazers and browsers with forage (Scholes & Walker 1993). *Colophospermum mopane* is a dominant tree or shrub in the low-lying areas of southern Africa's

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[6] Makhado, R.A., Potgieter, M.J., Luus-Powell, W.J. & Mapaure, I. (2017) Effects of pruning on the concentration of trace elements in *Colophospermum mopane* leaves. *African Journal of Ecology* 55(4): 600–608.

mopane woodland (Werger & Coetzee 1978; Mapaure 1994). Mopane plays an important role in supplying browsers and ungulates with nutritious fodder (Kos *et al.* 2012), especially during the dry season (Makhado *et al*. 2016). High intake of dry mopane browse during the dry season is mainly a result of its nutritional value (Hooimeijer *et al*. 2005), availability on the ground (Makhado *et al*. 2016), and a relatively low concentration of secondary compounds in the forage (Wessels *et al*. 2007).

Considering the nutritional value of dry mopane leaves to browsers' diet, their high consumption rate, during the dry season, as well as the large area covered by this tree species, it is surprising that there is such limited information on the concentration of trace elements in mopane leaves and the effect of browsing on leaf quality. The available and accessible literature on mopane leaf trace elements is limited to publications by Lukhele (2002), Lukhele and Van Ryssen (2000), Wessels *et al*. (2006) and Lundu (2012). As a result, data and information on the nutritional value of mopane are scanty, and do not cover trace elements such as boron (B), fluoride (F) and molybdenum (Mo). In addition, the available data is sometimes based on one or two sampling points, which does not properly reflect seasonal leaf quality variations. Lack of data and information therefore makes it difficult to understand the seasonal variation in the amount of trace elements in mopane leaves, and their nutritional contribution to the diet of browsers in the mopane woodland ecosystem. It further limits understanding of the factors influencing the distribution of browsers in the mopane woodland during various seasons.

This study has been conducted to close the knowledge gap that currently exists, by determining the concentration of trace elements such as iron (Fe), manganese (Mn), boron (B), molybdenum (Mo), copper (Cu), zinc (Zn), cobalt (Co), fluoride (F) and selenium (Se) in mopane leaves. The study further determined the effect of pruning on the concentration of trace elements from mopane leaves. The pruning experiment was intended to simulate the effect of browsing by large herbivores (Wessels *et al*. 2007), such as the greater kudu, on mopane leaf quality. This study therefore contributes to better understanding of the effect of simulated browsing on the monthly, seasonal and annual concentration of trace elements in mopane leaves, which is necessary for understanding the distribution of browsers in relation to leaf quality, and the effective management of mopane as an important dry season browsing species.

8.2 METHODOLOGY

8.2.1 Study area

This study was conducted in the Musina Nature Reserve, northern Limpopo Province, South Africa. The reserve is situated 5 km south-east of the town of Musina at 22°24’36”S, 30°03’00”E, and covers 4976 hectares. The altitude of the reserve ranges from 400 to 750 m above sea level. Rainfall in Musina typically starts in late September to early October and reaches its maximum in November, December, January and February. The average rainfall is 331 mm per annum and typically ranges between 300 and 400 mm per annum. The mean annual temperature is 16ºC in winter and can reach a maximum of 45ºC in summer. The annual average maximum temperature is 30ºC. The relative humidity of the area is very low, ranging from 12% in September to 28% in February (SA Weather Services 1981–2014).

The geology is underpinned by the Archaean Beit Bridge Complex, comprising of gneisses and meta-sediments. Soils range from deep red/brown clays at the bottom of slopes to freely drained sandy soils at the top of slopes. The soil has high sodium content and is alkaline (Mucina & Rutherford 2006).

Musina Nature Reserve is located within the Musina Mopane Bushveld and Limpopo Ridge Bushveld of the Mopane bioregion (Mucina & Rutherford 2006). The experimental site (1 hectare) is located in the Musina Mopane Bushveld. The dominant species is mopane (Rutherford *et al.* 2006), with an estimated density of 1 344 trees per hectare (Wessels *et al*. 2007). The grass layer is poorly developed, but dominated by *Schmidtia pappophoroides* (LEDET 2012–2017).

The reserve has a diverse range of antelope including *Tragelaphus strepsiceros*, *Taurotragus oryx*, *Oryx gazelle*, Tragelaphus angasii, *Hippotragus niger*, *Connochaetes taurinus*, *Sylvicapra grimmia*, *Aepyceros melampus*, *Oreotragus oreotragus* and *Raphicerus campestris* (LEDET 2012–2017).

8.2.2 Sampling procedures

8.2.2.1 Pruning experiment

Pruning and control experiments were conducted, following the procedures of Wessels *et al*. (2007), during the wet season of February 2014 in a homogenous stand of similar sized (3 m high) mopane trees. The wet (October–April) and dry (May–September) seasons in South Africa are important periods for determining leaf quality. During the sampling period in 2014, the average rainfall in Musina Nature Reserve was 316 mm. Rainfall started in September (5 mm), reached its maximum in January (85 mm) and thereafter declined to 0 mm in August (Table 8.1). The leaves began to flush in October, most likely in response to temperature.

Seven healthy tertiary side branches, near the main stem, of relatively equal circumference (20 mm), from each of 40 mopane trees, were randomly selected from different sides of the tree (north, south, east and west). The twigs were pruned back 50 mm by hand shears. The selected branches were marked to assist with future identification in this longitudinal study. Pruning was conducted in order to simulate the effects of browsing by large herbivores (Wessels *et al*. 2007), such as the greater kudu, on mopane leaf quality. The total amount of leaf and shoot biomass removed was less than 10% from the selected branch, which is a reasonable approximation of what is taken by herbivores (Scholes & Walker 1993) such as the greater kudu in a single visit. Forty trees were not treated and used as controls. These control trees were interspersed with experimental trees within the same red/brown oakleaf soil form. The experimental area was excluded from further browsing through fencing.

8.2.2.2 Leaf sampling and analysis

Mature mopane leaves, including petioles, were randomly collected at intervals of 55 days from the experimental and control mopane trees. Mopane leaf samples were collected from treated and control branches during February, May, June, August, October and December of the same year. The first samples were collected after the treatment was administered. Three independent samples composed of seven mopane leaves per 40 mopane trees were randomly collected from the canopies of experimental and control per sampling event, and transported to the laboratory in sealed transparent plastic bags in a cooler box. The samples were dried in plant presses at room temperature. The dried leaves from each three independent samples were mixed separately and a pooled sample of 10 g per treatment per sample cycle (55 days) was sent to the Agricultural Research Council (ARC), Institute for Soil, Climate and Water for the determination of Fe, Mn, B, Mo, Cu, Zn, Co, F and Se content. Each trace element was analysed three times, per sample cycle, which totalled to 18 samples per treatment per trace element. Trace elements were determined using the inductively coupled plasma atomic emission spectrometry techniques (ICP-AES, iCAP 600 Series, Thermo Scientific, Cambridge, UK).

8.2.3 Statistical analysis

Collected datasets were analysed using descriptive and inferential statistical analysis. Descriptive statistical analysis was used to determine the mean and standard deviation for the sampled trace elements. The effect of pruning on the monthly concentration of trace elements in mopane leaves was tested using a two-tailed t-Test: Two-Sample Assuming Equal Variance. The seasonal and annual effect of pruning on the concentration of trace elements in mopane leaves was tested using One-Way Anova (IBM SPSS Statistics 24, USA). A significant difference was accepted when $P < 0.05$.

8.3 RESULTS

8.3.1 Iron

Pruned trees showed to have low amount of Fe, but levelled during June and split thereafter (Figure 8.1). The concentration of Fe was lowest during December at 49.67 mg/kg±1.53 mg/kg on average in the pruned trees, while in the control trees the lowest level was during May at 71.33 mg/kg±22.50 mg/kg on average. The concentration of Fe in the leaves reached a maximum level during October at 151.67 mg/kg±41.63 mg/kg and 161.00 mg/kg±87.64 mg/kg on average in the pruned and control trees, respectively (Figure 8.1; Table 8.1). The amount of Fe between the pruned and control mopane trees statistically differed significantly in August (*P*=0.001), but was not significant at *P*<0.05 in most of the sampling months (Table 8.2). In addition, the concentration of Fe during wet (*P*=0.567) and dry (*P*=0.292) seasons did not differed significantly (Table 8.3). This study also found that the annual amount of Fe between pruned and control trees was statistically insignificant (*P*=0.339) (Table 8.4).

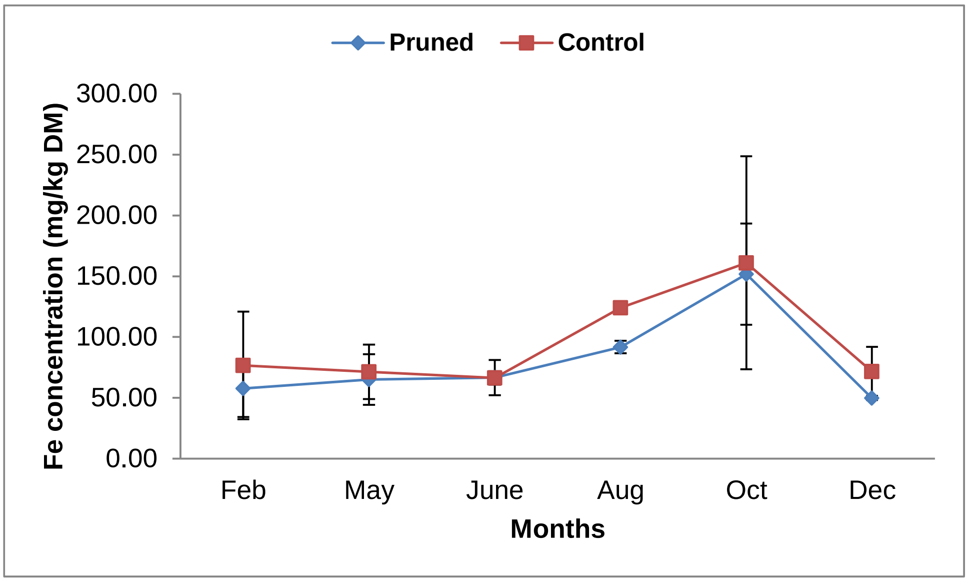

Figure 8.1: Average Fe concentration in the pruned and control mopane trees. Bars indicate standard deviation.

8.3.2 Manganese

The concentration of Mn started to increase during February at 15.33 mg/kg±6.07 mg/kg and 19.57 mg/kg±6.41 mg/kg and reached maximum levels during the leaf flush period in October at 29.00 mg/kg±2.65 mg/kg and 31.00 mg/kg±2.65 mg/kg on average in pruned and control trees, respectively (Figure 8.2; Table 8.1). The level of Mn thereafter started to decline during December (Figure 8.2). The concentration of Mn between the pruned and control mopane trees was not statistically significant at *P*<0.05 in all sampling months (Table 8.2). The concentration of Mn during wet (*P*=0.442) and dry (*P*=0.115) seasons was also insignificant (Table 8.3). In addition, the annual concentration of Mn in mopane trees did not differed significantly (*P*=0.148) (Table 8.4).

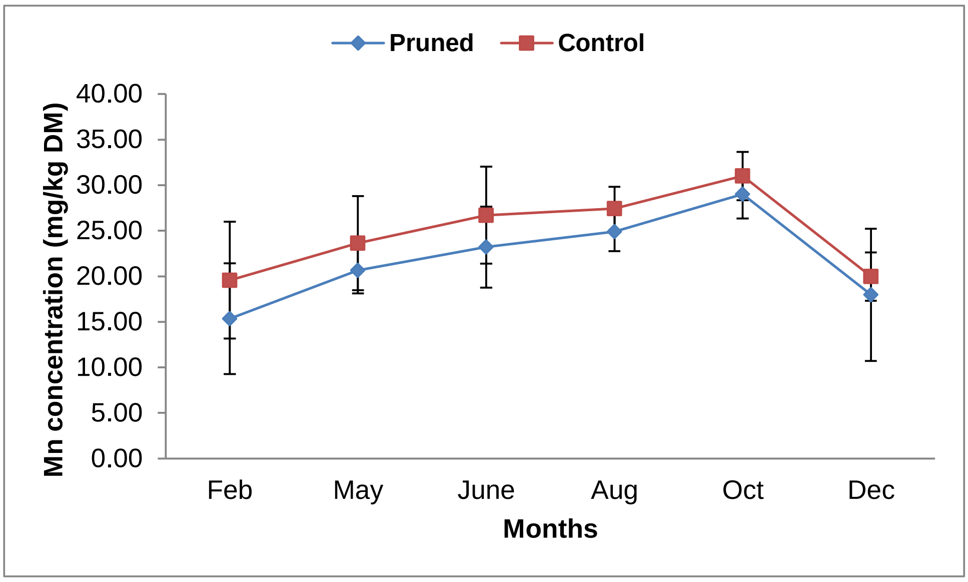

Figure 8.2: Average Mn concentration in the pruned and control mopane trees. Bars indicate standard deviation.

8.3.3 Boron

The amount of B in the pruned trees was slightly lower compared to control trees, but levelled during December. The concentration of B in the pruned and control trees increased during the dry season but declined slightly during the wet season (Figure 8.3). The highest concentration of B was in mature and senescent leaves. The maximum level of B was reached during August at 102.67 mg/kg±2.08 mg/kg and 110.33 mg/kg±10.50 mg/kg on average in the pruned and control trees, respectively (Figure 8.3; Table 8.1). The concentration of B in the pruned and control mopane trees was statistically significant in May (*P*=0.046), but was insignificant at *P*<0.05 in most sampling months (Table 8.2). In addition, the concentration of B was statistically insignificant during the wet season (*P*=0.616), but differed significantly during the dry season (*P*=0.031) (Table 8.3). The results further showed that the annual amount of B between pruned and control mopane trees did not differed significantly (*P*=0.334) (Table 8.4).

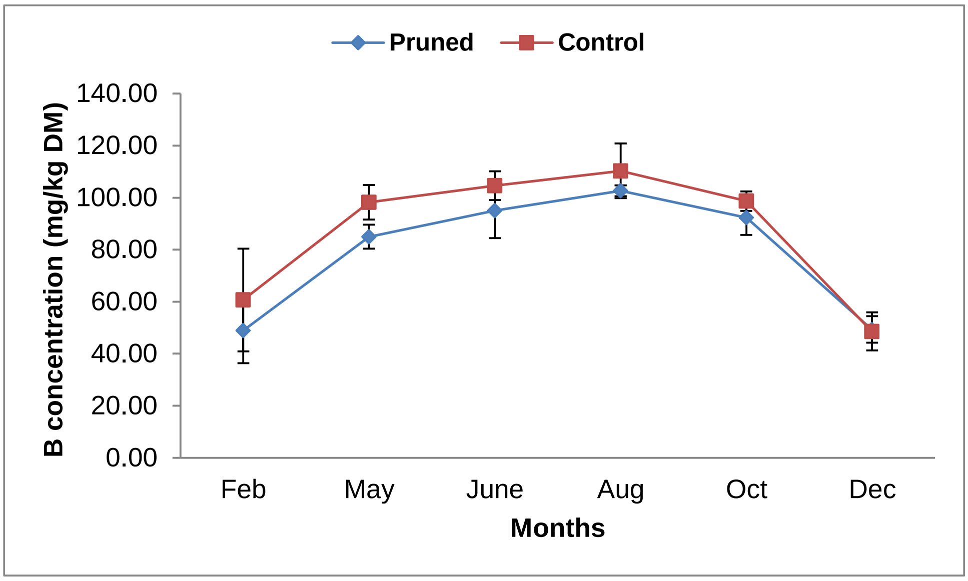

Figure 8.3: Average B concentration in the pruned and control mopane trees. Bars indicate standard deviation.

8.3.4 Molybdenum

The concentration of Mo was less than 0.95 mg/kg on average in the pruned and control trees. Pruning initially proved to reduce the amount of Mo slightly, but the level of Mo in the pruned trees exceeded that in the control trees over time, particularly in December (Figure 8.4). The concentration of Mo started to increase in June from an average minimum of 0.53 mg/kg±0.28 mg/kg and 0.62 mg/kg±0.36 mg/kg in the pruned and control trees, respectively. The average maximum level of Mo was reached during December at 0.94 mg/kg±0.06 mg/kg and 0.82 mg/kg±0.15 mg/kg in the pruned and control trees, respectively (Figure 8.4; Table 8.1). The concentration of Mo between pruned and control trees was statistically insignificant at *P*<0.05 in all sampling months (Table 8.2). In addition, the amount of Mo during the wet (*P*=0.878) and dry (*P*=0.549) seasons did not differed significantly (Table 8.3). Similarly, the annual concentration of Mo between pruned and control mopane trees was insignificant (*P*=0.679) (Table 8.4).

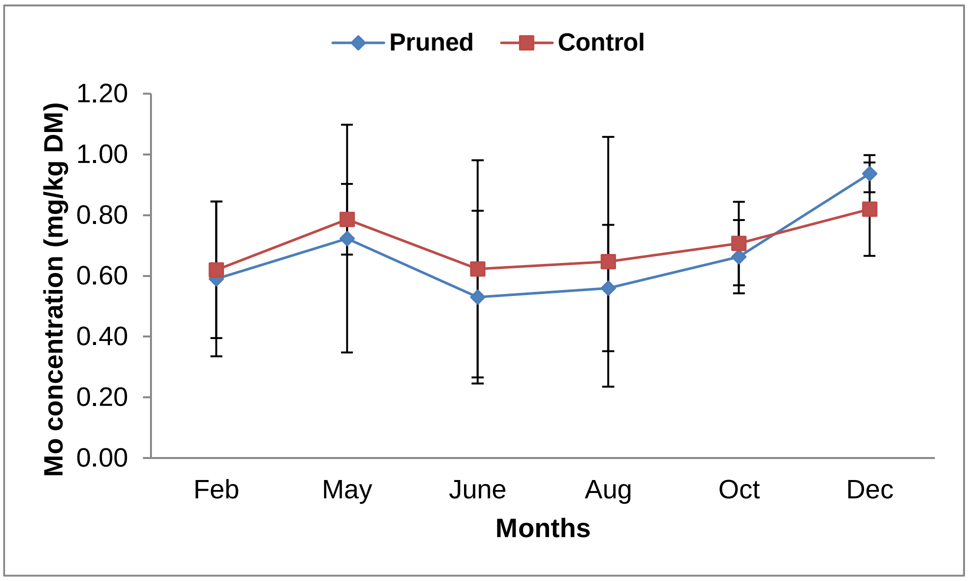

Figure 8.4: Average Mo concentration in the pruned and control mopane trees. Bars indicate standard deviation.

8.3.5 Copper

The level of Cu in the leaves was low during the dry season, particularly in August, but increased with leaf flush in October, and reached the maximum level during December/January (Figure 8.5). During August, the average Cu concentration in the leaves was low at 4.00 mg/kg±1.23 mg/kg and 4.69 mg/kg±0.45 mg/kg in the pruned and control trees, respectively. The highest average concentration of Cu in the control trees was reached during December at 8.20 mg/kg±0.60 mg/kg, while the maximum level in the pruned trees was reached in February at 7.33 mg/kg±1.46 mg/kg on average (Figure 8.5; Table 8.1). Over time, pruned leaves showed a slight reduction in the concentration of Cu when compared to those of control trees (Figure 8.5). However, the concentration of Cu in the pruned and control mopane trees was statistically insignificant at *P*<0.05 during all the sampling months (Table 8.2). In addition, the amount of Cu between pruned and control mopane trees during wet (*P*=0.334) and dry (*P*=0.624) seasons was statistically insignificant (Table 8.3). The annual concentration of Cu between pruned and control mopane trees was also insignificant (*P*=0.370) (Table 8.4).

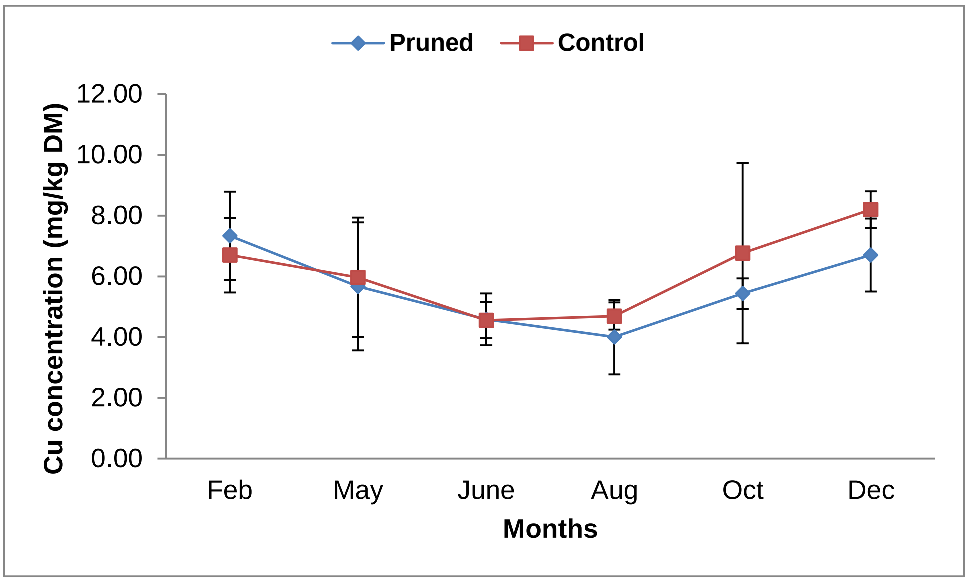

Figure 8.5: Average Cu concentration in the pruned and control mopane trees. Bars indicate standard deviation.

8.3.6 Zinc

The amount of Zn was slightly high in the pruned trees, but declined over time (Figure 8.6). The amount of Zn was lowest during August at 20.00 mg/kg±2.65 mg/kg and 21.40 mg/kg±4.69 mg/kg on average in the pruned and control trees, respectively. The Zn concentration in the leaves reached a maximum level during October at 33.33 mg/kg±12.86 mg/kg on average in the control trees, while the Zn level in pruned trees reached its average maximum during May at 28.47 mg/kg±4.72 mg/kg (Figure 8.6; Table 8.1). However, the concentration of Zn in the pruned and control mopane trees was not significant at *P*<0.05 in all the sampling months (Table 8.2). The concentration of Zn during the wet season was statistically near significant (*P*=0.064), but insignificant during the dry season (*P*=0.573) (Table 8.3). Futhermore, the annual amount of Zn between pruned and control mopane trees was statistically insignificant (*P*=0.165) (Table 8.4).

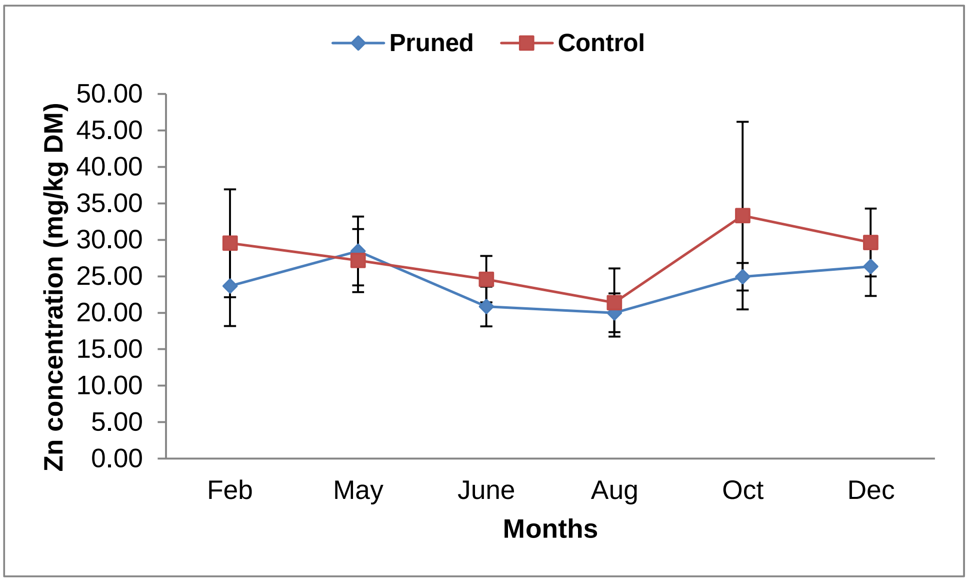

Figure 8.6: Average Zn concentration in the pruned and control mopane trees. Bars indicate standard deviation.

8.3.7 Cobalt

The concentration of Co was lowest during June at 0.44 mg/kg±0.29 mg/kg and 0.41 mg/kg±0.31 mg/kg on average in the pruned and control trees, respectively. The highest concentration of Co in the control trees was reached during August at 3.34 mg/kg±4.81 mg/kg on average, while the maximum level of Co in pruned trees was reached in December at 3.64 mg/kg±2.91 mg/kg on average (Figure 8.7; Table 8.1). The concentration of Co between the pruned and control mopane trees was not statistically significant at $P<0.05$ in all sampling months (Table 8.2). In addition, the amount of Co in the pruned and control mopane trees during the wet ($P=0.488$) and dry ($P=0.739$) seasons did not differed significantly (Table 8.3). The results further showed that the annual concentration of Co in the pruned and control mopane trees did not differed significantly ($P=0.807$) (Table 8.4).

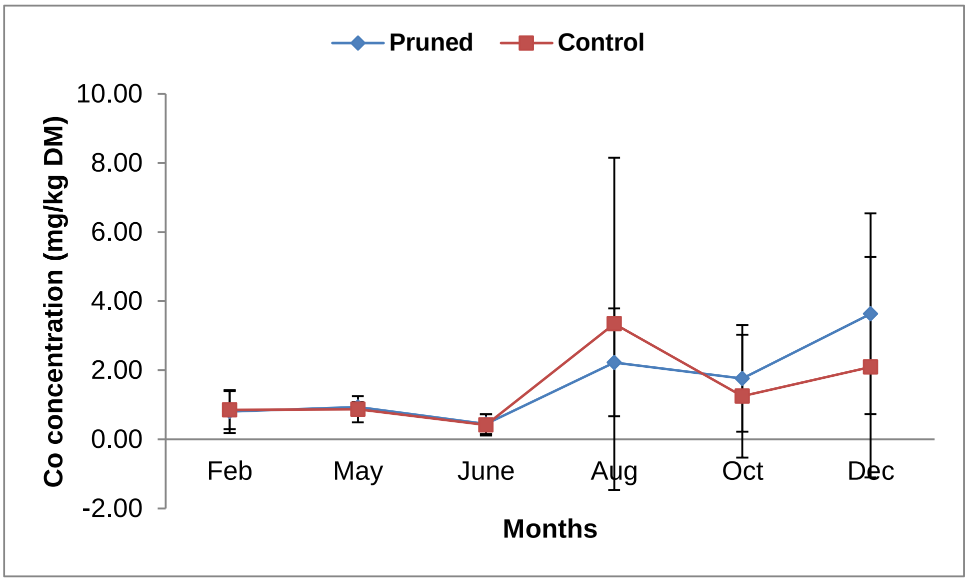

Figure 8.7: Average Co concentration in the pruned and control mopane trees. Bars indicate standard deviation.

8.3.8 Fluoride

The amount of F was lowest during February at 71.59 mg/kg±51.86 mg/kg and 69.53 mg/kg±36.61 mg/kg on average in the pruned and control trees, respectively. The concentration of F in the leaves reached its maximum level at 258.43 mg/kg±237.58 mg/kg and 302.83 mg/kg±224.10 mg/kg on average during June in the pruned and control trees, respectively (Figure 8.8; Table 8.1). The concentration of F between pruned and control trees was not statistically significant at $P<0.05$ in all the sampling months (Table 8.2). In addition, the amount of F during the wet ($P=0.742$) and dry ($P=0.894$) seasons was statistically insignificant (Table 8.3). This study further showed that the annual amount of F between pruned and control mopane trees was statistically insignificant ($P=0.964$) (Table 8.4).

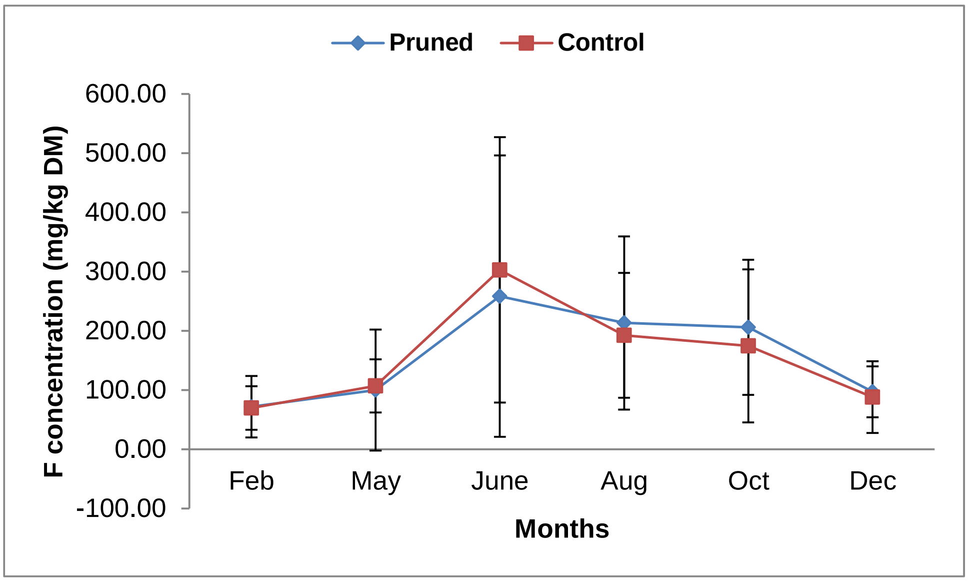

Figure 8.8: Average F concentration in the pruned and control mopane trees. Bars indicate standard deviation.

8.3.9 Selenium

The amount of Se was lowest during June at 0.80 mg/kg ±0.26 mg/kg and 1.11 mg/kg ±0.89 mg/kg on average in the pruned and control trees, respectively. The concentration of Se in the leaves reached its maximum level at 5.85 mg/kg ±5.40 mg/kg and 4.03 mg/kg ±3.74 mg/kg on average during December in the pruned and control trees, respectively (Figure 8.9; Table 8.1). However, the amount of Se between pruned and control mopane trees was not significant at *P*<0.05 in all the sampling months (Table 8.2). In addition, the concentration of Se during the wet (*P*=0.780) and dry (*P*=0.989) seasons did not differed significantly (Table 8.3). The results further showed that the annual amount of Se between pruned and control mopane trees did not differed significantly (*P*=0.7796) (Table 8.4).

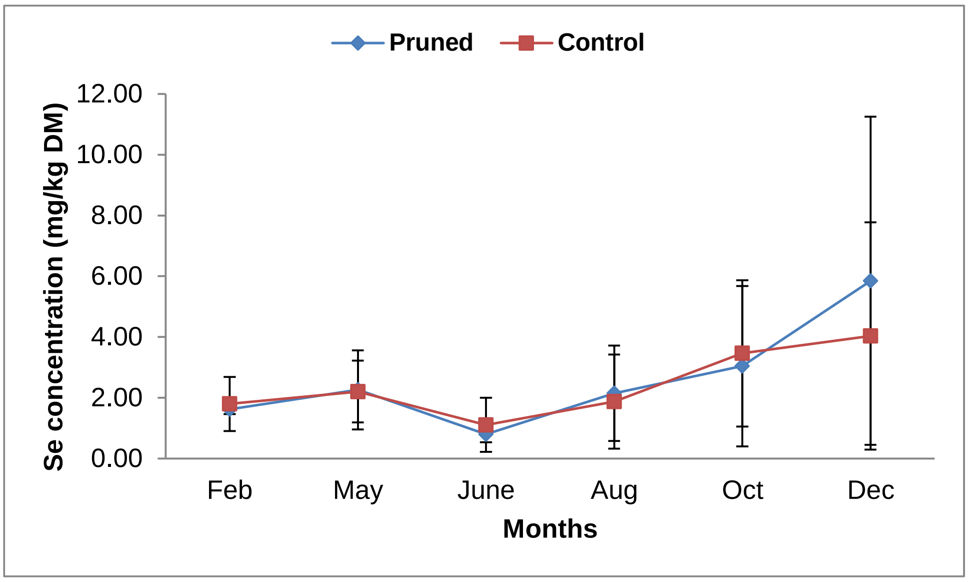

Figure 8.9: Average Se concentration in the pruned and control mopane trees. Bars indicate standard deviation.

Table 8.1: Mean (±S.D) trace elements concentration in mopane leaves in the pruned (*n*=18) and control (*n*=18) trees.

	February				May				June				August				October				December			
	Pruned		Control		Pruned		Control		Pruned		Control		Pruned		Control		Pruned		Control		Pruned		Control	
Trace elements	mean	S.D.	mean	S.D	mean	S.D	mean	S.D	mean	S.D	mean	S.D	mean	S.D	mean	S.D	mean	S.D	mean	S.D	mean	S.D	mean	S.D
Fe (mg/kg DM)	57.67	23.46	76.53	44.25	65.00	20.81	71.33	22.50	66.67	14.50	66.33	5.51	91.67	5.13	124.00	4.58	151.67	41.63	161.00	87.64	49.67	1.53	71.67	20.11
Mn (mg/kg DM)	15.33	6.07	19.57	6.41	20.63	2.51	23.63	5.17	23.20	4.45	26.70	5.32	24.90	2.15	27.43	2.38	29.00	2.65	31.00	2.65	17.97	7.27	19.97	2.65
B (mg/kg DM)	48.93	12.54	60.67	19.73	85.00	4.58	98.27	6.63	95.00	10.54	104.63	5.56	102.67	2.08	110.33	10.50	92.33	6.66	98.67	3.79	49.33	5.13	48.60	7.29
Mo (mg/kg DM)	0.59	0.26	0.62	0.23	0.72	0.38	0.79	0.12	0.53	0.28	0.62	0.36	0.56	0.21	0.65	0.41	0.66	0.12	0.71	0.14	0.94	0.06	0.82	0.15
Cu (mg/kg DM)	7.33	1.46	6.70	1.23	5.67	2.11	5.97	1.96	4.58	0.86	4.56	0.60	4.00	1.23	4.69	0.45	5.43	0.50	6.77	2.97	6.70	1.20	8.20	0.60
Zn (mg/kg DM)	23.67	5.51	29.53	7.42	28.47	4.72	27.17	4.32	20.87	2.73	24.60	3.18	20.00	2.65	21.40	4.69	24.93	1.90	33.33	12.86	26.33	4.04	29.63	4.65
Co (mg/kg DM)	0.80	0.62	0.85	0.55	0.94	0.15	0.87	0.38	0.44	0.29	0.41	0.31	2.23	1.56	3.34	4.81	1.76	1.55	1.25	1.78	3.64	2.91	2.09	3.20
F (mg/kg DM)	71.59	51.86	69.53	36.61	99.90	102.3	106.8	44.89	258.4	237.6	302.8	224.1	213.2	146.3	192.3	105.6	205.7	114.2	174.4	129.2	97.00	43.03	88.07	60.60
Se (mg/kg DM)	1.62	0.16	1.79	0.89	2.26	1.30	2.20	1.02	0.80	0.26	1.11	0.89	2.15	1.57	1.87	1.55	3.04	2.64	3.46	2.41	5.85	5.40	4.03	3.74
Mean Rainfall	January		February		March		April		May		June		July		August		September		October		November		December	
(mm)*	85.1		51.7		46.5		9.4		5.5		0.5		1.5		0		4.5		25.5		45.8		39.5	

Symbols: Fe=Iron; Mn=Manganese; B=Boron; Mo=Molybdenum; Cu=Copper; Zn=Zinc; Co=Cobalt; F=Fluoride; Se=Selenium; DM=Dry Matter; mg/kg=milligramme per kilogramme; S.D=standard deviation; mm=millimetre; *=Rainfall Data for Musina Nature Reserve (2014).

Table 8.2: Monthly effect of pruning on the concentration of trace elements in mopane leaves.

	February		May		June		August		October		December	
Trace elements	*t-Stat*	*P-value*	*t-Stat*	*P-value*	*t-Stat*	*P-value*	*t-Stat*	*P-value*	*t-Stat*	*P-value*	*t-Stat*	*P-value*
Fe (mg/kg DM)	-0.652	0.550^a	-0.358	0.738^a	0.037	0.972^a	-8.140	0.001^b	-0.167	0.876^a	-1.890	0.132^a
Mn (mg/kg DM)	-0.830	0.453^a	-0.904	0.417^a	-0.873	0.432^a	-1.368	0.243^a	-0.926	0.407^a	-0.448	0.677^a
B (mg/kg DM)	-0.870	0.434^a	-2.850	0.046^b	-1.401	9.234^a	-1.240	0.283^a	-1.432	0.225^a	0.143	0.894^a
Mo (mg/kg DM)	-0.153	0.886^a	-0.279	0.794^a	-0.353	0.742^a	-0.325	0.761^a	-0.410	0.703^a	1.220	0.289^a
Cu (mg/kg DM)	0.575	0.596^a	-0.182	0.864^a	0.044	0.967^a	-0.918	0.410^a	-0.766	0.487^a	-1.936	0.125^a
Zn (mg/kg DM)	-1.010	0.333^a	0.352	0.742^a	-1.543	0.198^a	-0.451	0.676^a	-1.119	0.326^a	-0.928	0.406^a
Co (mg/kg DM)	-0.091	0.932^a	0.299	0.780^a	0.124	0.907^a	-0.382	0.722^a	0.378	0.725^a	0.620	0.569^a
F (mg/kg DM)	0.056	0.958^a	-0.107	0.920^a	-0.235	0.825^a	0.201	0.851^a	0.314	0.769^a	0.208	0.845^a
Se (mg/kg DM)	-0.325	0.762^a	0.056	0.958^a	-0.572	0.598^a	0.217	0.839^a	-0.205	0.847^a	0.480	0.657^a

Symbols: Fe=Iron; Mn=Manganese; B=Boron; Mo=Molybdenum; Cu=Copper; Zn=Zinc; Co=Cobalt; F=Fluoride; Se=Selenium; DM=Dry Matter; mg/kg=milligram per kilogram. **Note**: ^{a}=Not significant at *P* < 0.05, ^{b}=Significant at *P* < 0.05. Statistical superscripts refer to rows in the table.

Table 8.3: Seasonal effect of pruning on the concentration of trace elements in mopane leaves. Seasons used in the analysis were the wet (February, October and December) and dry (May, June and August) seasons.

	Wet season		**Dry season**	
Trace elements	*F-value*	*P-value*	*F-value*	*P-value*
Fe (mg/kg DM)	0.341	0.567^a	1.185	0.292^a
Mn (mg/kg DM)	0.622	0.442^a	2.776	0.115^a
B (mg/kg DM)	0.261	0.616^a	5.609	0.031^b
Mo (mg/kg DM)	0.024	0.878^a	0.374	0.549^a
Cu (mg/kg DM)	0.993	0.334^a	0.250	0.624^a
Zn (mg/kg DM)	3.960	0.064^a	0.331	0.573^a
Co (mg/kg DM)	0.503	0.488^a	0.115	0.739^a
F (mg/kg DM)	0.112	0.742^a	0.018	0.894^a
Se (mg/kg DM)	0.081	0.780^a	0.000	0.989^a

Symbols: Fe=Iron; Mn=Manganese; B=Boron; Mo=Molybdenum; Cu=Copper; Zn=Zinc; Co=Cobalt; F=Fluoride; Se=Selenium; DM=Dry Matter; mg/kg=milligram per kilogram. **Note**: ^{a}=Not significant at *P* < 0.05, ^{b}=Significant at *P* < 0.05. Statistical superscripts refer to rows in the table.

Table 8.4: Annual effect of pruning on the concentration of trace elements in mopane leaves.

	Pruned versus Control	
Trace elements	*F-value*	*P-value*
Fe (mg/kg DM)	0.941	0.339
Mn (mg/kg DM)	2.197	0.148
B (mg/kg DM)	0.960	0.334
Mo (mg/kg DM)	0.174	0.679
Cu (mg/kg DM)	0.825	0.370
Zn (mg/kg DM)	3.296	0.078
Co (mg/kg DM)	0.061	0.807
F (mg/kg DM)	0.002	0.964
Se (mg/kg DM)	0.068	0.796

Symbols: Fe=Iron; Mn=Manganese; B=Boron; Mo=Molybdenum; Cu=Copper; Zn=Zinc; Co=Cobalt; F=Fluoride; Se=Selenium; DM=Dry Matter; mg/kg=milligram per kilogram.

8.4 DISCUSSION

8.4.1 Desirable level of trace elements in diet of herbivores

Mopane leaves contain various trace elements (Table 7.1), but required in the diet of herbivores in small quantities (Suttle 2010). Trace elements play a role in enhancing tissue function and proper functioning of metabolism (Lundu 2012).

The desirable level of Fe in the forage for ruminants is 50 mg/kg DM (Roosendaal 1992). The level of Fe in this study ranged from 50 to161 mg/kg DM on average in the pruned and control trees (Table 8.1), which was within the desirable level of 50 mg/kg DM, and not at toxic levels of >435 mg/kg DM (Lukhele & Van Ryssen 2003). This shows that mopane leaves contain an acceptable concentration of Fe, which plays an essential role in the formation of red blood cells (Hart 2008) and proper functioning of tissues (Soetan *et al*. 2010).

The concentration of Mn in this study ranged from 15 to 31 mg/kg DM on average in the control and pruned trees (Table 8.1), which was below the desirable level of 60 mg/kg DM (Webb *et al*. 2016). Deficiency of Mn might negatively impact on normal skeletal development, nervous and muscular system functions (Hart 2008). This implies that any supplementary forage should contain Mn, in order to improve skeletal development, and proper muscular function (Hart 2008).

The level of Co, Cu and Se in this study ranged from 0.4 to 4 mg/kg DM, 4 to 8 mg/kg DM and 0.8 to 6 mg/kg DM on average in the control and pruned trees, respectively (Table 8.1), which was within the desirable level of 0.15 mg/kg DM (Webb *et al*. 2016), 5 mg/kg DM and 0.15 mg/kg DM for ruminants (Roosendaal 1992), respectively.

In addition, the level of Zn in this study ranged from 20 to 33 mg/kg DM on average in the pruned and control trees (Table 8.1), which was below the desirable level of 60 mg/kg DM (Webb *et al*. 2016), but within the deficient level of 25 mg/kg DM (MacPherson 2000). This suggests that any supplementary forage should contain Zn. This is important because forage intake with desirable Zn can improve the formation of red blood cells (Hart 2008).

Browsers such as *Loxodonta africana* and *Tragelaphus strepsiceros* feed on mopane leaves, attracted by their nutritional value (Mosimanyana & Kiflewahid 1988; Macala *et al*. 1992; Hooimeijer *et al*. 2005), especially during the dry season (Curlewis 2014). The consumption of the leaves is reduced during summer owing to the high concentration of secondary metabolites such as tannins and phenols (Styles & Skinner 1997; Hooimeijer *et al*. 2005; Wessels *et al*. 2007; Kohi *et al*. 2010). For instance, forage containing more than 5% leaf dry weight of condensed tannins (Cooper & Owen-Smith 1985) reduces the crude protein digestibility of browse (Wessels *et al*. 2007) and has a bitter taste (Macala *et al*. 1992). The increase in secondary metabolites during the leaf flush period seems to be a natural adaptation mechanism of mopane to inhibit herbivores from browsing the leaves during the growing season (Wessels *et al*. 2007).

8.4.2 Seasonal variation in the concentration of trace elements

As suggested by various authors (Hrabar 2005; Wessels *et al*. 2006; Hrabar *et al*. 2009; Lundu 2012), this study also found that the concentration of trace elements in the pruned and control trees did not differed significantly (Table 8.2). It was further reported from the current study that the nutritional value of the leaves decreased as the leaf matured and aged. The amount of Fe, Mn, Mo, Cu, Zn and Se in the leaves generally increased during the leaf flush (October), after the first summer rains, and declined during the dry season, particularly in June (Table 8.1), when the leaves matured and aged. Similar trends have been observed by MacPherson (2000), Wessels *et al*. (2006) and Kasale (2013).

However, the amount of B, Co and F does not decline with leaf age, but increased in old and mature leaves, particularly during the dry season (Table 8.1). This finding is comparable to that of Lukhele (2002), in that the levels of minerals such as Co in *Combretum apiculatum* leaves were high during the dry season. This implies that the amount of B, Co and F is low in green leaves but increased in dry leaves possibly when moisture and other elements have leached-out.

The build-up of Mo, Fe, Mn, Cu, Zn and Se occurs during October (Table 8.1). This happens at the same time as the increase in secondary metabolites in the mopane leaves (Styles & Skinner 1997; Hooimeijer *et al*. 2005). High concentration of secondary metabolites deters herbivores from browsing the leaves (Wessels *et al*. 2007), which enables leaves to grow with minimal browsing disturbance. The increase in the concentration of Fe, Mn, Mo, Cu, Zn and Se during October occurs after the first summer rains, and then declines during the dry season (Wessels *et al*. 2006).

8.4.3 Effect of pruning on the concentration of trace elements

Results from the current study reported that <10% pruning had no significant effect on the concentration of trace elements in mopane leaves, except for B and Fe during May and August, respectively (Table 8.2). In addition, the seasonal effect of pruning on the concentration of trace elements in the leaves was found to be statistically insignificant, except for Zn during the wet season (Table 8.3). In addition, <10% pruning did not have an effect on the annual concentration of trace elements in the leaves (Table 8.4). This study therefore confirms the findings of Wessels *et al*. (2006) that pruning of mopane trees at <10% teatment does not significantly affect the variations in the amount of trace elements. This suggests that <10% pruning, simulating the browsing of large herbivores (Wessels *et al*. 2007), such as the greater kudu, does not have an impact on the concentration of trace elements in mopane leaves. However, du Toit *et al*. (1990) are of the opinion that pruning ultimately improves the quality of browse for ungulates. As indicated by Hrabar (2005), Wessels *et al*. (2007) and Hrabar *et al*. (2009), pruning increases the number of mopane leaves and enhance leaf flush. This is necessary to ensure that there is availability of browse, especially during the dry season, when most savanna species have shed their leaves.

8.5 CONCLUSION

It is concluded that <10% pruning does not have an effect on the concentration of most trace elements in the mopane leaves. This suggests that the amount of trace elements in the leaves is independent of simulated browsing at that level. The concentration of trace elements therefore seems to be mainly related to leaf growth stages. This could be the case because spring leaf flush triggers an increase in the concentration of Fe, Mn, Mo, Cu, Zn and Se in the leaves, but these trace elements declined as the leaf matures and ages. Nevertheless, the amount of B, Co and F shows a converse relationship with leaf flush.

CHAPTER 9

EFFECTS OF PRUNING ON THE CONCENTRATION OF SECONDARY METABOLITES IN *COLOPHOSPERMUM MOPANE* LEAVES[7]

9.1 INTRODUCTION

Plants and herbivores of the African savanna have coexisted for millions of years (Scholes & Walker 1993). Consequently, plants produce secondary metabolites or chemical compounds as a defence mechanism against herbivory (Mazid *et al*. 2011), while some browsers can overcome the build-up of secondary metabolites (Scholes & Walker 1993). High levels of secondary metabolites in plants can have significant negative effects on herbivory as well as on animal distribution and productivity (Lundberg & Åström 1990).

Although the production of secondary metabolites such as tannins and phenols is initially costly (Hartmann 1991), plants growing in nutrient-poor environments invest heavily in defence (Scholes & Walker 1993). Plants take this investment risk in order to avoid a significant loss of nutrients and carbon through herbivory (Scholes & Walker 1993). According to Van der Waal (2010), the loss of nutrients and carbon may reduce the growth and production of a plant. Consequently, a plant produces defence chemicals when browsed, which is an essential survival strategy (Stock *et al*. 1993).

Wild animals such as *Giraffa camelopardalis* and *Tragelaphus strepsiceros* prune shoot ends of plants while browsing (Du Toit *et al*. 1990). Pruning by herbivores may have a detrimental effect on plant resource allocation and performance (Hendrix 1988). It may also result in a variation in the amount of chemical

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[7] Makhado, R.A., Potgieter, M.J. & Luus-Powell, W.J. 2018. Effects of pruning on the concentration of secondary metabolites in *Colophospermum mopane* leaves. *Southern Forests: A Journal of Forest Science* 81(2): 123–128.

composition and minerals (Lukhele & Van Ryssen 2000). Herbivores prefer browse with a high nutritional content (Villalba & Provenza 1999) and avoid forage with deterrence chemicals, such as tannins and phenols (Provenza *et al*. 1990). Knowledge of the effect of pruning on the concentration of secondary metabolites is necessary, in order to understand better why some plant species are accepted by browsers in certain seasons, and rejected in other seasons in the mopane woodland.

Savanna species such as *Colophospermum mopane* dominate the low-lying areas of southern Africa's mopane woodland (Werger & Coetzee 1978). Considerable parts of the largest and best-known national parks in southern Africa are located within mopane woodland. These include, most notably, the Limpopo Transfrontier Park between South Africa, Mozambique and Zimbabwe and the Mapungubwe-Tuli-Shashe Transfrontier Park between Botswana, South Africa and Zimbabwe. Parts of national parks such as the Kruger National Park and Mapungubwe National Park and reserves such as Timbavati Game Reserve, Makuya Nature Reserve and Musina Nature Reserve are also found within mopane woodland areas.

Mopane trees or shrubs provide nutritional browse to a wide range of herbivores (Hooimeijer *et al*. 2005). Although mopane leaves are rich in proteins (Hooimeijer *et al*. 2005), deterrent chemicals such as tannin and phenols are also high, particularly during the wet season (Wessels *et al*. 2007), which effectively deters browsers during that period (Styles & Skinner 1997). The high levels of secondary metabolites tend to diminish in older leaves (Wessels *et al*. 2007), rendering the leaves more acceptable to browsers during the dry season (Makhado *et al*. 2016).

Considering the nutritional value of mopane to browsers, especially during the dry season, and its ability to produce secondary metabolites, particularly during the wet season, it is surprising that there is such a lack of studies on determining the deterrents in mopane forage and the effect of browsing on forage quality. The available and accessible literature on mopane leaf secondary metabolites is limited to the work of Coley (1988), Styles and Skinner (1997), Lukhele (2002), Lukhele and Van Ryssen (2000), Hooimeijer *et al*. (2005), Ferwerda (2005), Ferwerda *et al*. (2005), Wessels *et al*. (2007) and Kos *et al*. (2011). Furthermore, data and information on seasonal variations in mopane leaf secondary metabolites remains limited (Wessels *et al*. 2007). In some instances, the available data is based on one or two sampling points, which does not properly reflect seasonal leaf quality variations. Lack of data and information therefore makes it difficult to understand the seasonal variation in the amount of secondary metabolites in mopane leaves, and its influence on animals' browsing behaviour during different seasons. It further limits understanding of the factors influencing the distribution of browsers in the mopane woodland during various seasons.

This study aims to address the knowledge gap that currently exists by determining the concentration of secondary metabolites, such as total phenols (TP), condensed tannins (CT) and protein-precipitating tannins (PPT) in mopane leaves during different seasons. The study has further determined the effect of management control measures, such as pruning, on the concentration of secondary metabolites from mopane leaves. The pruning experiment was intended to simulate the effect of browsing by large herbivores (Wessels *et al*. 2007), such as the greater kudu, on mopane leaf quality. This study therefore contributes to better understanding of the effect of simulated browsing on the concentration of secondary metabolites in mopane leaves. This is necessary for understanding the distribution of browsers in relation to leaf quality, and the effective management of mopane as an important dry season browse species.

9.2 METHODOLOGY

9.2.1 Study area

This study was conducted in the Musina Nature Reserve, northern Limpopo Province, South Africa. The reserve is situated 5 km south-east of the town of Musina at 22°24'36"S, 30°03'00"E, and covers 4 976 hectares. The altitude of the reserve ranges from 400–750 m above sea level. The slope of the experimental site is relatively flat. Rainfall in Musina typically starts in late September to early October, and reaches its maximum in November, December, January and February. The average rainfall is 331 mm per annum, and typically ranges from 300 to 400 mm per annum. The mean annual temperature is 16^{o}C in winter and can reach a maximum of 45^{o}C in summer. The annual average maximum temperature is 30^{o}C. The relative humidity of the area is very low, ranging from 12% in September to 28% in February (SA Weather Services 1981–2014).

The Archaean Beit Bridge Complex provides the geological foundation, and comprises of gneisses and meta-sediments. Soils range from deep red/brown clays at the bottom of slopes to freely drained sandy soils at the top of slopes. The soil has high sodium content and is alkaline (Mucina & Rutherford 2006). Musina Nature Reserve is located within the Musina Mopane Bushveld and Limpopo Ridge Bushveld of the Mopane bioregion (Mucina & Rutherford 2006). The experimental site (1 hectare) is located in the Musina Mopane Bushveld and is dominated by mopane (Rutherford *et al.* 2006), with an estimated density of 1 344 trees per hectare (Wessels *et al*. 2007). The grass layer is poorly developed, but dominated by *Schmidtia pappophoroides* (LEDET 2012–2017). The reserve has a diverse range of antelope including the *Tragelaphus strepsiceros*, *Taurotragus oryx*, *Oryx gazelle*, *Tragelaphus angasii*, *Hippotragus niger*, *Connochaetes taurinus*, *Sylvicapra grimmia*, *Aepyceros melampus*, *Oreotragus oreotragus* and *Raphicerus campestris* (LEDET 2012–2017).

9.2.2 Sampling procedures

9.2.2.1 Pruning experiment

Pruning and control experiments were conducted in accordance with the procedures of Wessels *et al*. (2007). These were initiated in the same soil strata during the wet season of February 2014 in a homogenous stand of similar-sized (3 m high) mopane trees. The wet (October–April) and dry (May–September) seasons in South Africa are critical periods for determining leaf quality. During the sampling period in 2014, the average rainfall in Musina Nature Reserve was 316 mm. Rainfall started in September (5 mm) and reached its maximum in January (85 mm), thereafter declining to 0 mm in August (Table 9.1). The leaves started to flush in October, possibly in response to temperature.

Seven healthy tertiary side branches, near the main stem, of relatively equal circumference (20 mm), from each of 40 mopane trees, were randomly selected from different sides of the tree (north, south, east and west). The twigs were pruned back 50 mm using hand shears. The selected branches were marked to assist with future identification in this longitudinal study. Pruning was conducted to simulate the effects of browsing by large herbivores (Wessels *et al*. 2007), such as the greater kudu, on mopane leaf quality. The total amount of leaf and shoot biomass removed was less than 10% from the selected branch, which is a reasonable approximation of what is taken by herbivores (Scholes & Walker 1993) in a single visit. Forty trees were not treated and used as controls. These control trees were interspersed with experimental trees within the red/brown oakleaf soil form. The experimental area was excluded from further browsing through fencing.

9.2.2.2 Leaf sampling and analysis

Mature mopane leaves, including petioles, were randomly collected at intervals of 55 days from the experimental and control mopane trees. Mopane leaf samples were collected from treated and control branches during February, May, June, August, October and December of the same year. The first samples were collected after the treatment was administered. Three independent samples composed of seven mopane leaves per 40 mopane trees were randomly collected from the canopies of experimental and control per sampling event, and transported to the laboratory in sealed transparent plastic bags in a cooler box. The samples were dried in plant presses at room temperature following the procedures outlined by Hagerman (2011). The dried leaves from each three independent samples were then mixed separately and a pooled sample of 10 g per treatment per sample cycle (55 days) was sent to the Botany Department, University of Cape Town, for the determination of TP, CT and PPT. Total phenols content was determined based on gallic acid equivalents, while CT and PPT were determined based on sorghum tannin equivalents, as described by Hagerman (2011). The samples were replicated three times, which totalled to 18 samples per treatment per secondary metabolite.

9.2.3 Statistical analysis

Collected datasets were analysed using descriptive and inferential statistical analysis. Descriptive statistical analysis was used to determine the mean and standard deviation for the sampled secondary metabolites. The effect of pruning on the monthly concentration of secondary metabolites in mopane leaves was tested using a two-tailed t-Test: Two-Sample Assuming Equal Variance. The seasonal and annual effect of pruning on the concentration of secondary metabolites in mopane leaves was tested using One-Way Anova (IBM SPSS Statistics 24, USA). A significant difference was accepted when $P < 0.05$.

9.3 RESULTS

9.3.1 Total phenols

This study showed that the concentration of TP decreases in the mature and aged leaves during the dry season. The lowest concentration of TP was 47.67 mg g^{-1}±35.74 mg g^{-1} and 42.35 mg g^{-1}±29.59 mg g^{-1} during August in the pruned and control trees, respectively. The amount of TP slightly increased during leaf flush in October, reaching their maximum level in December. The average concentration of TP in December was 91.34 mg g^{-1} ±21.25 mg g^{-1} and 86.00 mg g^{-1}±28.58 mg g^{-1} in the pruned and control trees, respectively (Figure 9.1; Table 9.1). The concentration of TP in the pruned and control mopane trees was statistically insignificant at $P<0.05$ in all the sampling months (Table 9.2). The amount of TP in the pruned and control mopane trees did not differed significantly during the wet ($P=0.731$) and dry ($P=0.806$) seasons (Table 9.3). In addition, the annual quantity of TP in the pruned and control mopane trees did not differed significantly ($P=0.690$) (Table 9.4).

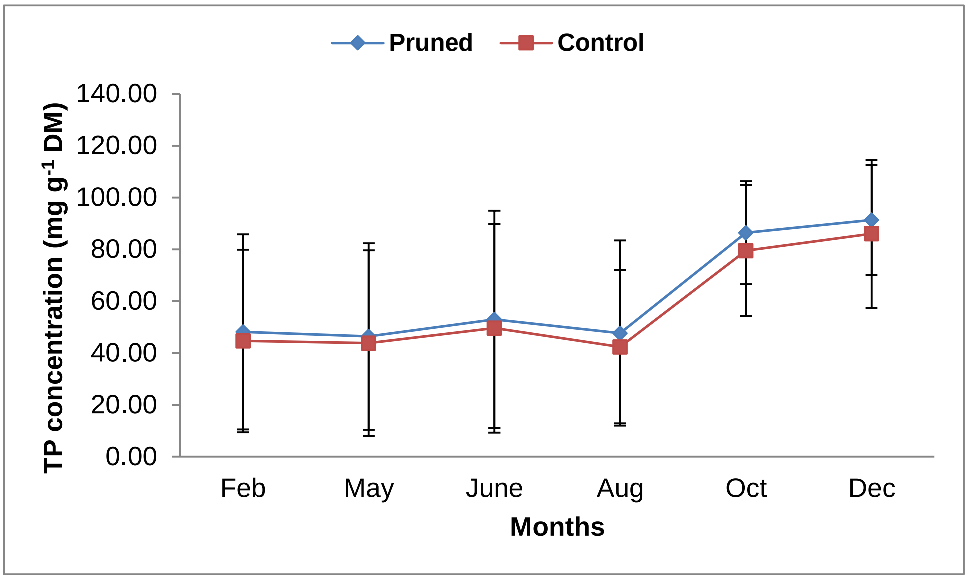

Figure 9.1: Average TP concentration in the pruned and control mopane trees. Bars indicate standard deviation.

9.3.2 Condensed tannins

The amount of CT was relatively low in the mature and aged leaves during the dry season. The lowest concentration of CT was 52.84 mg g^{-1}±38.11 mg g^{-1} and 44.91 mg g^{-1}±30.45 mg g^{-1} during August in the pruned and control trees, respectively. The amount of CT slightly increased during leaf flush in October, reaching its maximum in December. The average concentration of CT in December was 110.38 mg g^{-1}±32.35 mg g^{-1} and 97.28 mg g^{-1}±29.72 mg g^{-1} in the pruned and control trees, respectively (Figure 9.1; Table 9.1). The concentration of CT in the pruned and control mopane trees was not statistically significant at P<0.05 in all the sampling months (Table 9.2). The amount of CT in the pruned and control mopane trees did not differed significantly during the wet (P=0.619) and dry (P=0.662) seasons (Table 9.3). In addition, the annual quantity of CT in the pruned and control mopane trees did not differed (P=0.527) (Table 9.4).

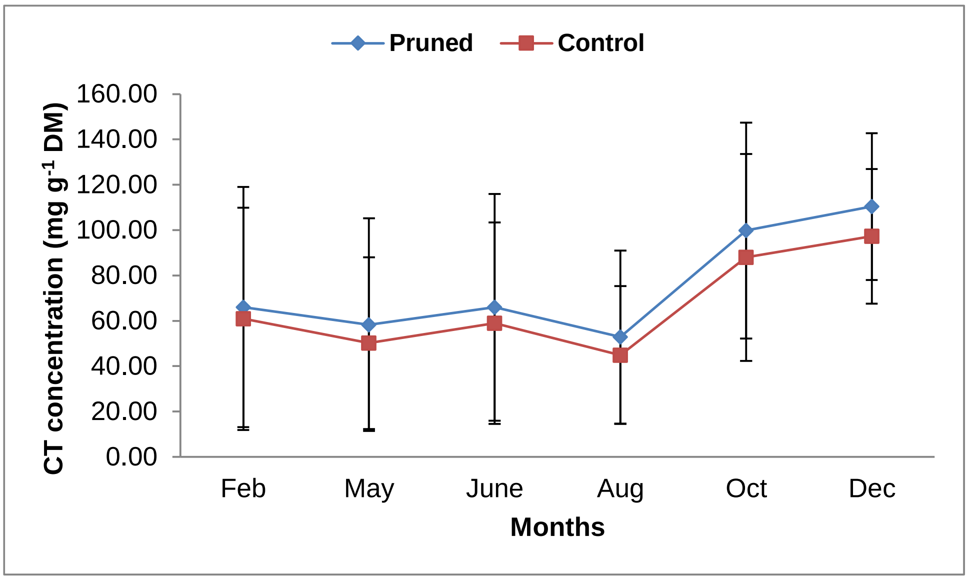

Figure 9.2: Average CT concentration in the pruned and control mopane trees. Bars indicate standard deviation.

9.3.3 Protein-precipitating tannins

The concentration of PPT was moderately low in the mature and aged leaves during the dry season. The lowest amount of PPT was 58.27 mg g^{-1}±46.59 mg g^{-1} and 48.17 mg g^{-1}±36.81 mg g^{-1} during August in the pruned and control trees, respectively. The amount of PPT increased during leaf flush in October, reaching its maximum level in December. The average concentration of PPT in December was 115.65 mg g^{-1}±35.24 mg g^{-1} and 99.68 mg g^{-1}±14.28 mg g^{-1} in the pruned and control trees, respectively (Figure 9.1; Table 9.1). The concentration of PPT in the pruned and control mopane trees was not statistically significant at $P<0.05$ in all the sampling months (Table 9.2). The amount of PPT in the pruned and control mopane trees did not differed significantly during wet ($P=0.586$) and dry ($P=0.454$) seasons (Table 9.3). In addition, the annual amount of PPT in the pruned and control mopane trees did not differed significantly ($P=0.379$) (Table 9.4).

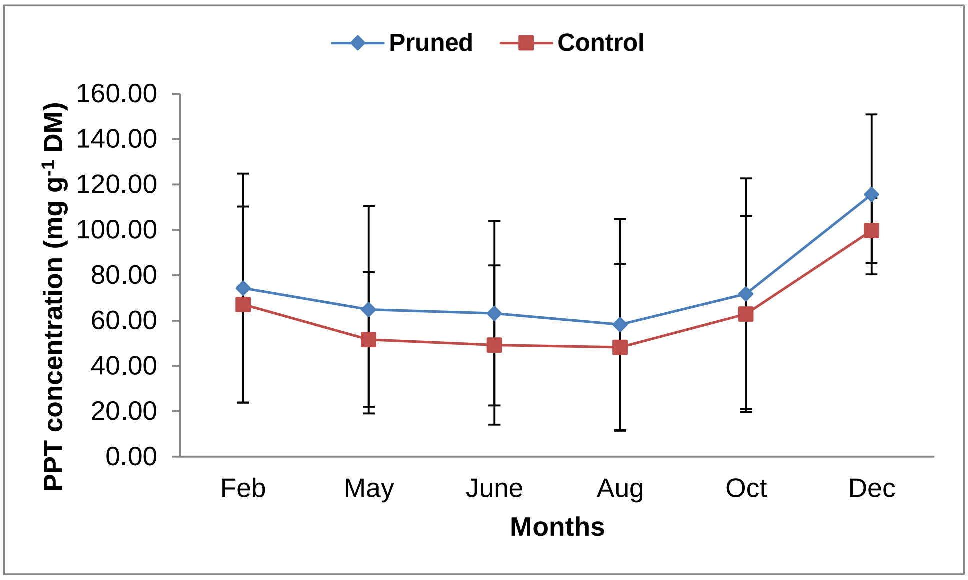

Figure 9.3: Average PPT concentration in the pruned and control mopane trees. Bars indicate standard deviation.

Table 9.1: Mean (±S.D) concentration of secondary metabolites in mopane leaves in the pruned (*n*=18) and control (*n*=18) trees.

		TP		CT		PPT		Mean Rainfall	
		mean	S.D	mean	S.D	mean	S.D	(mm)*	
February	Pruned	48.12	37.63	66.05	52.94	74.37	50.50	Jan	85.1
	Control	44.63	35.28	60.87	48.97	67.10	43.26	Feb	51.7
May	Pruned	46.37	36.00	58.29	46.91	64.83	45.76	Mar	46.5
	Control	43.80	35.82	50.16	37.85	51.68	29.71	Apr	9.4
June	Pruned	52.98	41.91	65.99	50.00	63.24	40.75	May	5.5
	Control	49.55	40.27	58.92	44.42	49.20	35.07	Jun	0.5
August	Pruned	47.67	35.74	52.84	38.11	58.27	46.59	Jul	1.5
	Control	42.35	29.59	44.91	30.45	48.17	36.81	Aug	0
October	Pruned	86.39	19.82	99.84	47.60	71.84	50.83	Sep	4.5
	Control	79.46	25.29	87.95	45.65	62.94	43.15	Oct	25.5
December	Pruned	91.34	21.25	110.38	32.35	115.65	35.24	Nov	45.8
	Control	86.00	28.58	97.28	29.72	99.68	14.28	Dec	39.5

Symbols: TP=total phenols; CT=condensed tannins; PPT=protein-precipitating tannins; DM=dry matter; mg/kg=milligramme per kilogramme; S.D=standard deviation; mm=millimetre; *=rainfall data for Musina Nature Reserve (2014).

Table 9.2: Monthly effect of pruning on the concentration of secondary metabolites in mopane leaves.

Secondary metabolites	February		May		June		August		October		December	
	t Stat	*P-value*	*t Stat*	*P-value*	*t Stat*	*P-value*	*t Stat*	*P-value*	*t Stat*	*P-value*	*t Stat*	*P-value*
TP (mg g^{-1} DM)	0.117	0.912	0.088	0.934	0.102	0.924	0.198	0.852	0.374	0.728	0.260	0.808
CT (mg g^{-1} DM)	0.124	0.907	0.234	0.827	0.183	0.864	0.282	0.792	0.312	0.771	0.516	0.633
PPT (mg g^{-1} DM)	0.189	0.859	0.417	0.698	0.452	0.675	0.295	0.783	0.231	0.829	0.728	0.507

Symbols: TP=total phenols; CT=condensed tannins; PPT=protein-precipitating tannins; mg g^{-1}=milligramme per gramme; DM=dry matter.

Table 9.3: Seasonal effect of pruning on the concentration of secondary metabolites in mopane leaves. Seasons used in the analysis were the wet (February, October and December) and dry (May, June and August) seasons.

	Wet season		**Dry season**	
	F-value	*P-value*	*F-value*	*P-value*
TP (mg g^{-1} DM)	0.122	0.731	0.062	0.806
CT (mg g^{-1} DM)	0.257	0.619	0.199	0.662
PPT (mg g^{-1} DM)	0.310	0.586	0.589	0.454

Symbols: TP=total phenols; CT=condensed tannins; PPT=protein-precipitating tannins; mg g^{-1}=milligramme per gramme; DM=dry matter.

Table 9.4: Annual effect of pruning on the concentration of secondary metabolites in mopane leaves.

	Pruned versus Control	
	F-value	*P-value*
TP (mg g^{-1} DM)	0.162	0.690
CT (mg g^{-1} DM)	0.409	0.527
PPT (mg g^{-1} DM)	0.793	0.379

Symbols: TP=total phenols; CT=condensed tannins; PPT=protein-precipitating tannins; mg g^{-1}=milligramme per gramme; DM=dry matter.

9.4 DISCUSSION

9.4.1 Seasonal variation in the concentration of secondary metabolites

As observed in various studies (Styles & Skinner 1997; Lukhele 2002; Wessels *et al*. 2007), the concentrations of secondary metabolites are high during the wet season and decline during the dry season as the mopane leaf matures and ages.

The quality of mopane foliage undergoes seasonal changes (Styles & Skinner 1997), possibly in response to many factors, including climatic variability (Van Soest 1987; Stevens *et al*. 2016), browsing by herbivores (Coley 1988), level of nitrogen in the soil (Ferwerda *et al*. 2005), and growth of the leaf (Kasale 2013). The concentration of secondary metabolites, CT in particular, increases with increasing leaf longevity, decreases with increasing growth rate and increases with increasing herbivore pressure (Coley 1988) and soil nitrogen (Ferwerda *et al*. 2005). In addition, climatic changes affect vegetation quality, particularly in areas with erratic rainfall (Ferwerda 2005), a phenomenon which regularly occurs in the study area and most parts of southern Africa's savanna (Scholes & Walker 1993). It therefore suggests that the variations in the concentration of secondary metabolites determine the amount and duration or season in which the foliage can be browsed. Mopane forage is mainly browsed during the dry season (Hooimeijer *et al*. 2005; Makhado *et al*. 2016) when the concentration of secondary metabolites is relatively lower (Wessels *et al*. 2007; Kos *et al*. 2011), and rejected during the wet season, owing to high amounts of secondary metabolites (Hooimeijer *et al*. 2005).

According to Ferwerda *et al*. (2005), plants respond to browsing by producing shoots with well-developed chemical defences. The highest concentration of secondary metabolites was PPT, followed by CT and lastly TP (Table 9.1). The concentration of PPT ranged from a minimum of 48 mg g^{-1} and 58 mg g^{-1} in August to a maximum of 100 mg g^{-1} and 116 mg g^{-1} in December in the control and pruned trees, respectively (Table 9.1). As indicated by Wessels *et al*. (2007), the relatively large increase in PPT predicts a significantly lower intake of mopane. This was expected because tannin deters herbivores from browsing the plant (Scholes & Walker 1993). For instance, forage containing >5% (Cooper & Owen-Smith 1985) or >20 g/kg (McDowell & Valle 2000) of leaf dry weight of condensed tannins lowers the digestibility of forage. As a result, the forage is avoided by browsers such as the greater kudu (Cooper & Owen-Smith 1985).

An increase in the amount of tannins (Robbins *et al*. 1987) and phenolic compounds (Cooper & Owen-Smith 1985) makes the leaves less palatable to herbivores. The consumption of browse with high concentrations of phenols and tannins may cause loss of appetite in browsers (Van Soest 1987; Van Hoven 1991). A reduction in forage intake could further reduce the growth rate of animals, which happens as a result of a lack of nutrients (Woodward & Reed 1989). Therefore, the concentration of secondary metabolites determines the amount of forage that can be consumed by herbivores in a particular season (Owen-Smith & Cooper 1987). The high levels of tannins and phenols observed in this study during the wet season suggests that mopane forage will be rejected in that season, but more accepted during the dry season (Hooimeijer *et al*. 2005) when secondary metabolites are at low levels. The increased levels of secondary metabolites during the wet season therefore suggest that browsed plants, such as mopane, increase herbivore deterring substances in order to reduce browsing pressure during the growing season (Wessels *et al*. 2007). This mechanism allows mopane to grow with minimal browsing disturbance, which thus partly explains its survival in the savannas.

Regardless of the build-up of secondary metabolites in mopane leaves during the growing season, some browsers seem to tolerate them slightly. For instance, the diet of *Loxodonta africana* (Smallie & O'Connor 2000), *Taurotragus oryx* (Styles and Skinner, 1997) and *Tragelaphus strepsiceros* (Hooimeijer *et al*. 2005) relatively contain mopane forage even during the wet season. Browsers such as the *T. strepsiceros* seem to select for diet quality but their choice can be restricted based on the availability of species within their habitat (Hooimeijer *et al*. 2005). This was confirmed by Owen-Smith (2002) who indicated that plants with high protein content are likely to be browsed, though in small quantities, regardless of their deterrent chemicals. Mopane leaves have a high crude protein content (Bonsma 1942), ranging from 6% during the dry season to 13% during the wet season (Hooimeijer *et al*. 2005). As a result, the nutritional value of mopane could justify its relatively low consumption during the wet season even when the secondary metabolites are high.

Browsers such as the greater kudu seem to tolerate the effects associated with an increased intake of secondary compounds by diversifying their diet so as to satisfy their protein requirements while reducing potential toxic effects associated with the high concentration of secondary metabolites (Hooimeijer *et al*. 2005). Havenga (2014) added that herbivores that can produce proline-rich glycoproteins in their saliva are capable of deactivating tannins and prohibiting them from having a negative effect. This could increase nitrogen production and digestibility of forage (Havenga 2014). These browsing strategies may be responsible for the ability of browsers such as the greater kudu, elephant and giraffe to keep the intake of plant chemical compounds to sub-critical levels (Scholes & Walker 1993). As indicated also by Owen-Smith (2002), the current study therefore confirms that diet selection by herbivores in the savannas is a trade-off between nutritional benefits against various costs and rates of restriction.

9.4.2 Effect of pruning on the concentration of secondary metabolites

This study showed that <10% pruning has no effect on the amount of secondary metabolites in the leaves (Tables 9.2-9.4). However, the ability of mopane to release secondary metabolites seems to be a good defence mechanism against browsers (Wessels *et al*. 2007). As also confirmed by Hooimeijer *et al*. (2005), Ferwerda (2005), Wessels *et al*. (2006) and Kohi *et al.* (2010), the present study found that the concentration of secondary metabolites in the pruned and control trees did not differ significantly (Table 9.2). This could be because the concentration of phenols and tannins in mopane foliage follows the same trend as crude protein (Hooimeijer *et al*. 2005). Therefore, the amount of secondary metabolites as observed in this study cannot be attributed to <10% foliage removal, but may have occurred as a result of leaf flush (Ferwerda 2005; Wessels *et al*. 2006). Depending on treatment intensity, pruning could improves the quality of browse for ungulates (Du Toit *et al*. 1990). In addition, pruning has the potential to increase the number of mopane leaves and could enhance leaf flush (Hrabar 2005; Wessels *et al*. 2007; Hrabar *et al*. 2009).

9.5 CONCLUSION

It is concluded that the concentration of secondary metabolites in mopane leaves is not related to <10% pruning exerted, but appears to be associated with leaf growth stages. The amount of tannins and phenols in mopane leaves increases during the growing season, but declined with leaf senescence during the dry season. It seems that leaf flush during October triggers the production of secondary metabolites, which appears to be a natural defence strategy by mopane. The production of secondary metabolites is a useful mechanism to deter browsers from foraging on the leaves, particularly during the growing season.

CHAPTER 10

TRAGELAPHUS STREPSICEROS BROWSE DURING THE DRY SEASON IN THE MOPANE WOODLAND OF LIMPOPO PROVINCE, SOUTH AFRICA[8]

10.1 INTRODUCTION

Mopani veld (Acocks 1988), also known as mopane woodland (Low & Rebelo 1996) or mopane bioregion (Rutherford *et al.* 2006), is an extensive vegetation type that dominates low-lying areas of southern Africa. This vegetation type is characterised by the dominant tree *Colophospermum mopane*. Mopane woodland is distributed in the northern part of the Limpopo Province in South Africa stretching from Musina to Phalaborwa, mainly dominating the hot dry valley bottoms and adjacent plains (Acocks 1988). Mopane woodland as referred to in this study provides important forage and habitat for many wild animals. Most of the parks (such as the Kruger National Park and Mapungubwe National Park), reserves (for example, Musina Nature Reserve and Makuya Nature Reserve) and game farms (for example, the Sandown Game Farm) in the northern part of the Limpopo Province are found in mopane woodland.

The greater kudu is distributed predominantly in the southern and eastern regions of Africa (Skinner & Chimimba 2005) and is adapted to live in mopane woodland (Curlewis 2014). *Colophospermum mopane* is an important forage plant for the greater kudu (Hooimeijer *et al*. 2005; Curlewis 2014), as well as for a variety of wild animals, including elephants (Kos *et al*. 2012). *Colophospermum mopane* has a high nutritional value (Ben-Shahar & MacDonald 2002), with crude protein values averaging 11% (Bonsma 1942; Macala *et al*. 1992), but it also has high levels of tannins and other phenolics, especially during summer (Wessels *et al*.

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[8] Makhado, R., Potgieter, M., Luus-Powell, W., Cooper, S., Oppong, C., Kopij, G., Mutisi, C. & Makhabu, S. 2016. *Tragelaphus strepsiceros* browse during the dry season in the mopani veld of Limpopo Province, South Africa. *Transactions of the Royal Society of South Africa* 71(1): 17–21.

2007). Tannins and phenols can reduce the digestibility of forages by binding with proteins to render them less palatable. Without adequate additional browse species in the diet, excessive consumption of plants with high tannin content can eventually result in the death of the animal (Furstenburg 2010). Kudu browse mopane all year round, but consumption typically increases during the dry season (Hooimeijer *et al*. 2005; Curlewis 2014), possibly because of a decreased concentration of secondary metabolites in older foliage and shed leaves (Wessels *et al*. 2007). However, the greater kudu is adapted to survive in mopane woodland and changes its dietary mix to survive changes in food quantity and quality that accompany the various seasons (Wessels *et al*. 2007; Curlewis 2014).

It should be taken into consideration that greater kudu are specialist browsers that feed mainly on leaves, shoots, pods and fruits of a wide range of shrubs, trees, forbs and succulents, but they rarely eat grass (Owen-Smith 1979, 1993; Furstenburg 2010; Curlewis 2014). However, greater kudu in the Eastern Cape valley bushveld have been observed accepting small quantities of grasses (Furstenburg 2010). In the Limpopo Province, in mopane woodland, the diet of the greater kudu, especially during the dry season, is dominated by mopane forage (Hooimeijer *et al*. 2005; Curlewis 2014).

Despite the reported value of mopane as a source of browse for the greater kudu, and other ungulates feeding on mopane, especially during the dry season, there is still limited information on the diet composition and selection of browse of the greater kudu in mopane woodland. In addition, lack of knowledge on differences in browse selection between male and female greater kudu necessitated the need to undertake this study. This deficiency in the current knowledge is hampering effective management of habitat for the greater kudu, especially during times of food scarcity. The purpose of this chapter was therefore to identify plant species, types and parts that are mostly browsed by the greater kudu in mopane woodland during the dry season. The study also compares the diet selected by male versus female greater kudu. Results of this study are essential because they will enable game farmers, ranchers and reserve managers in mopane woodland to understand the diet requirements of the greater kudu better and adjust their management interventions, especially during the dry season.

10.2 METHODOLOGY

10.2.1 Study area

This study was conducted at the Sandown Game Farm in the Musina Local Municipality. The farm was conducting culling programme during the study period, hence the reason for chossing it as the study area. The Sandown Game Farm is situated in the far northern part of the Limpopo Province, South Africa at 22°28'S, 29°29E. The Sandown Game Farm covers 2070 hectares of pristine and unspoilt environment. Its altitude ranges from 400 to 750 m above sea level.

Sandown Game Farm is in an arid to semi-arid environment where rainfall typically occurs in summer and declines drastically in winter. The average rainfall of the area is 331 mm per annum, and it typically ranges between 300 and 400 mm per annum (SA Weather Services 1981–2014). The area is characterised by high summer temperatures. The annual average maximum temperature is 30^{o}C. The average annual minimum temperature is 16^{o}C and there is zero probability of snow occurrence. Relative humidity is less than 30% (SA Weather Services 1981–2014).

The geology of the area consists mostly of rocks of the Beit Bridge Complex (Swazian Erathem), as well as sediments (including sandstones of the Clarens Formation) and basalt (particularly in the east) of the Karoo Supergroup. Soils are underlain by the Archaean Beit Bridge Complex comprising of gneisses and meta-sediments. The soils are variable, ranging from deep red/brown clays to freely drained sandy soils and calcareous clayey soils (Mucina & Rutherford 2006).

The Sandown Game Farm is located within the Musina Mopane Bushveld of the Mopane Bioregion. The Musina Mopane Bushveld vegetation unit is the most widespread in the northern part of South Africa, and is dominated by *C. mopane* on clayey lowlands and *Combretum apiculatum* on the hills. The tree and shrub component is dominated by *C. mopane*, but other species such *C. apiculatum*, *Terminalia prunioides*, *Adansonia digitata*, *Sclerocarya birrea*, *Commiphora*, *Vachellia* and *Senegallia* species are also found (Mucina & Rutherford 2006).

The fauna at the Sandown Game Farm consists of a variety of species. These include *Giraffa camelopardalis*, *Tragelaphus strepsiceros*, *Connochaetes taurinus*, *Aepyceros melampus*, *Taurotragus oryx*, *Kobus ellipsiprymnus*, *Oryx gazelle*, *Raphicerus campestris*, *Equus quagga burchellii* and *Sylvicapra grimmia*, amongst others.

10.2.2 Greater kudu rumen content analysis procedure

The parts (leaves, twigs, flowers, pods and fruits) of major plant species browsed by the greater kudu, as identified by Curlewis (2014), were collected from Musina Nature Reserve. The parts were individually placed in labelled and sealed transparent plastic bags and transported to the University of Limpopo in a cooler box. The collected plant materials were preserved in 70% ethanol for later use. Plant parts were fixed as a reference collection of slides in order to assist in the identification of what is contained in the greater kudu rumen (Figure 10.1). Photographs of these parts were also taken in the field to assist in the identification of plant fragments in the rumen.

In total, five samples were collected from three adult male and two adult female greater kudu culled during the dry season on 29 and 30 June 2014. The dry season in South Africa starts in May and ends in September. The wet mass of collected samples ranged from 938 g to 2990 g, with an average of 1730 g. Individual rumen contents were thoroughly mixed in a plastic container and washed several times with tap water until the particulates in the samples were clean. A 2x2 mm sieve was used to sift particulates (plant materials) from water. Using the reference collection, the sifted materials were grouped by plant species. The materials were identified by comparing leaf shape, structure, veins, hairs, stomata, fruits, barks, seeds, pods and flowers with the reference collection. A stereomicroscope (light detector) was used to identify fine plant parts that could not be identified with the naked eye.

Figure 10.1: Comparison of kudu rumen content with reference collection. The analyses were conducted at the laboratory, University of Limpopo.

10.2.2 Statistical analysis

Data were analysed using descriptive and inferential statistics. Descriptive statistics were used to determine the mean and standard deviation of species browsed by the greater kudu. The percentage contribution of each species to the greater kudu diet was calculated. The abundance of each species was calculated as a percentage of the total wet weight of particulates, identified from the rumen of each culled greater kudu. The grouped sub-samples (leaves, twigs, grass, forbs, flowers, seeds and pods) were calculated to determine the parts most often browsed. Pearson Correlation Coefficient analysis was used to compare the diets of female and male greater kudu (IBM SPSS Statistics 24, USA). A significant difference was accepted when $P < 0.05$.

10.3 RESULTS

10.3.1 Species browsed by the greater kudu

In the dry season, greater kudu in the study area mainly browsed *C. mopane*, *Dichrostachys cinerea*, *Commiphora edulis*, *Grewia bicolor*, *Grewia flava*, *C. apiculatum* and *T. prunioides* (Table 10.1). The average (± s.d.) wet weight of species comprising the analysed greater kudu rumen samples during the dry season was *C. mopane* (792 g ± 480 g), followed by *D. cinerea* (506 g ± 276 g), *C. edulis* (344 g ± 73 g) and *G. bicolor* (129 g ± 249 g). Other less frequently browsed species such as *C. apiculatum* (86 g ± 59 g), *G. flava* (5 g ± 3 g) and *T. prunioides* (4 g ± 4 g) contributed far smaller amounts to the greater kudu diet during the dry season (Table 10.1).

Table 10.1: Species and amounts browsed by the greater kudu during the dry season of 2014 in mopane woodland, Limpopo Province, South Africa (*n*=5).

Species	**Wet weight (g)**					
	Sum	Min	Average	Max	S.D	Variance
Colophospermum mopane	3961.15	226.44	792.23	1190.0	479.77	230182
Dichrostachys cinerea	2529.52	292.10	505.90	938.56	276.29	76333.5
Commiphora edulis	1032.90	260.28	344.30	386.31	72.76	5294.52
Grewia bicolor	515.14	2.86.0	128.79	501.68	248.61	61805
Combretum apiculatum	431.33	4.73	86.27	150.0	59.12	3495.01
Grewia flava	10.18	2.90	5.09	7.28	3.10	9.5922
Terminalia prunioides	11.15	0.04	3.72	7.05	3.52	12.37

Symbols: Min=Minimum, Max=Maximuim, S.D=standard deviation.

Proportionally, *C. mopane* contributed most (47% ± 6%) to the diet of the greater kudu in mopane woodland. This was followed by *D. cinerea* (30% ± 24%), *C. edulis* (12% ± 6%), *G. bicolor* (6% ± 22%), *C. apiculatum* (5% ± 5%); the remaining species such as *T. prunioides* and *G. flava* contributed 0.12% ± 0.27% and 0.13% ± 0.31%, respectively, to the diet of the greater kudu, which is insignificant (Figure 10.1).

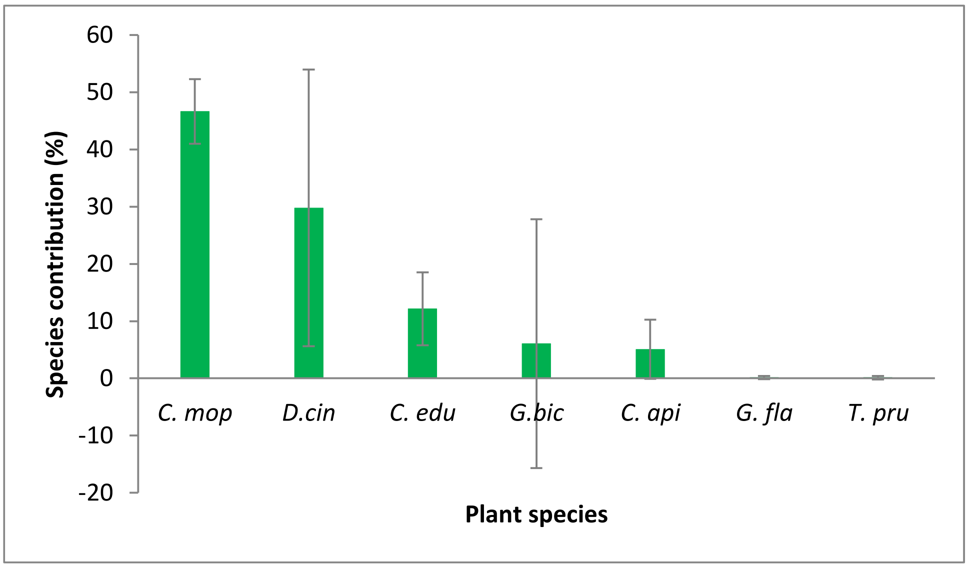

Figure 10.2: Species contribution to the greater kudu diet during the dry season in mopane woodland, Limpopo Province, South Africa (*n*=5). ***Note***: *C. mop* = *Colophospermum mopane*, *D. cin* = *Dichrostachys cinerea*, *C. edu* = *Commiphora edulis*, *G. bic* = *Grewia bicolor*, *C. api* = *Combretum apiculatum*, *G. fla* = *Grewia flava* and *T. pru* = *Terminalia prunioides*.

Foliage from trees contributed more (57%) to the greater kudu diet composition than shrubs (43%). The parts of trees and shrubs mostly consumed by the greater kudu during the dry season were leaves, followed by pods, seeds and twigs (Table 10.2). Leaves contributed 75% to the diet, while pods, seeds and twigs contributed the remaining 25%. The pods and seeds were mainly browsed from *D. cinerea*. This study further indicates that the greater kudu consumes the leaves of *G. flava* and *G. bicolor*, while in most other plant species identified, a combination of leaves and twigs were consumed (Table 10.2).

Table 10.2: Type of plants and parts browsed by greater kudu during the dry season of 2014 in mopane woodland, Limpopo Province, South Africa (*n*=5).

Species	**Type of plant**	**Parts browsed**	**Dominant parts**
Colophospermum mopane	tree	leaves and twigs	leaves
Dichrostachys cinerea	shrub	leaves, twigs, pods and seeds	pods and seeds
Commiphora edulis	tree	leaves and twigs	leaves
Grewia bicolor	shrub	leaves	leaves
Combretum apiculatum	tree	leaves and twigs	leaves
Grewia flava	shrub	leaves	leaves
Terminalia prunioides	tree	leaves and twigs	leaves
	Tree 57.14%		Leaves 75.00%
	Shrub 42.86%		Pods, seeds and twigs 25.00%

10.3.2 Comparison of diet composition of male and female greater kudu

The diets of female and male greater kudu were slightly different. Five species (*C. mopane*, *D. cinerea*, *G. bicolor*, *C. apiculatum* and *T. prunioides*) were browsed by female greater kudu during the dry season, while seven species (*C. mopane*, *D. cinerea*, *C. edulis*, *G. bicolor*, *G. flava*, *C. apiculatum* and *T. prunioides*) were browsed by male greater kudu (Table 10.3). Therefore, two species, *G. flava* and *C. edulis,* were browsed by male greater kudu, but were not recorded in the diet of female greater kudu (Table 10.3). This study further shows that 93% of the female greater kudu diet consisted of forage from just two species, *C. mopane* (71% ± 46%) and *D. cinerea* (22% ± 25%). On the other hand, 64% of the male greater kudu diet was comprised of *D. cinerea* (33% ± 24%) and *C. mopane* (31% ± 39%). *Commiphora edulis* and *G. bicolor* contributed 18% ± 5% and 14% ± 26%, respectively, to the male greater kudu diet. Despite the variance in preference for species in the diet of female and male greater kudu, the difference in browsing selection between female and male greater kudu proves to be positively correlated (*r*=0.69; Table 10.3; Figure 10.3).

Table 10.3: Browsing selectivity between female (*n*=2) and male (*n*=3) greater kudu during the dry season of 2014 in mopane woodland, Limpopo Province, South Africa.

	Wet weight of amount browsed					
	Female			**Male**		
Plant species	**Average (g)**	**S.D**	**%**	**Average (g)**	**S.D**	**%**
Colophospermum mopane	1115.41	105.49	71.22±45.56	576.78	529.83	30.79±39.40
Dichrostachys cinerea	338.855	57.78	21.64±24.96	617.27	323.25	32.95±24.04
Grewia bicolor	2.955	0.13	0.19±0.06	254.62	349.40	13.59±25.95
Combretum apiculatum	103.325	66.01	6.60±28.51	74.89	65.78	4.00±4.89
Terminalia prunioides	5.555	2.11	0.35±0.91	0.46	0.59	0.02±0.04
Grewia flava	-	-	-	5.09	3.10	0.27±0.23
Commiphora edulis	-	-	-	344.30	72.76	18.38±5.41
Pearson correlation	*r*=0.691					

Symbols: g=gramme, S.D=standard deviation, %=percent.

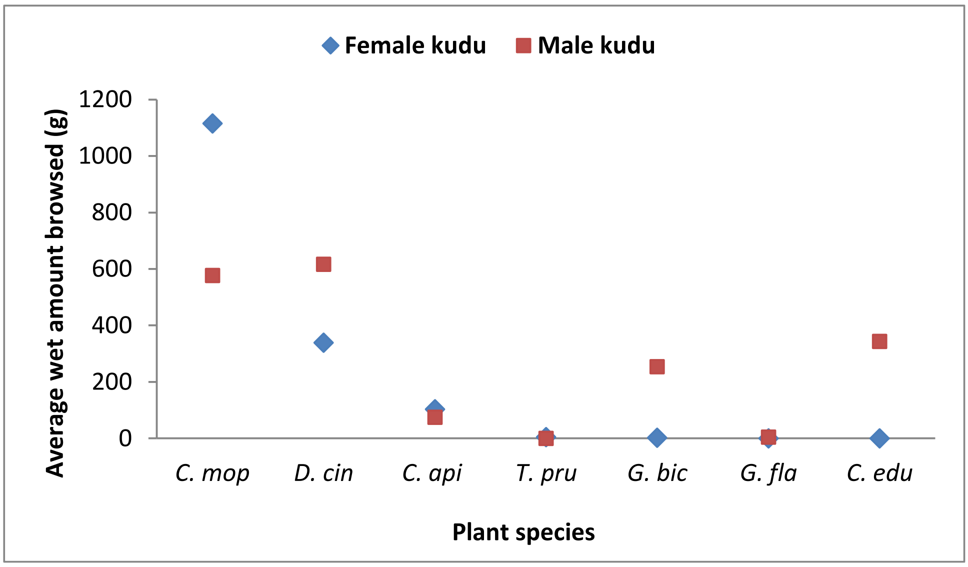

Figure 10.3: Species browsed by female (*n*=2) and male (*n*=3) greater kudu during the dry season of 2014 in mopane woodland, Limpopo Province, South Africa. ***Note***: *C. mop* = *Colophospermum mopane*, *D. cin* = *Dichrostachys cinerea*, *C. edu* = *Commiphora edulis*, *G. bic* = *Grewia bicolor*, *C. api* = *Combretum apiculatum*, *G. fla* = *Grewia flava* and *T. pru* = *Terminalia prunioides*.

10.4 DISCUSSION

The current findings (Figures 10.2-10.3) concur with various studies across the mopane areas that indicated that *C. mopane* provides essential forage for animals (Hooimeijer *et al*. 2005), especially during the dry season (Styles & Skinner 1997) and drought years (Mosimanyana & Kiflewahid 1988). Hooimeijer *et al*. (2005) and Curlewis (2014) confirm that much of the diet of the greater kudu in mopane woodland is comprised of *C. mopane* foliage, especially during the dry season. The extensive use of this abundant species as an essential browse plant for the greater kudu may explain the common distribution of greater kudu in mopane woodland.

The dependency of the greater kudu on *C. mopane* browse is influenced by various factors. It is the nutritional value of *C. mopane* that attracts many browsers, including the greater kudu, to forage on the leaves, twigs and barks, particularly during the dry season when other forage is very scarce. The crude-protein content of *C. mopane* dry leaves averages around 11% (Bonsma 1942), while it is between 15% and 16% in *C. mopane* pods with seeds (Macala *et al.* 1992). Browsers make more use of *C. mopane* leaves during the dry season, when the foliar chemical deterrents, such as tannins and phenols, are at a lower concentration compared to their levels at other times of the year (Styles & Skinner 1997; Wessels *et al.* 2007). Furthermore, *C. mopane* is the dominant tree species in the study area. In the dry season when the availability of other forage is low, *C. mopane* sheds its leaves, which had previously not been within reach for most animals. The dry leaves are thus readily available on the ground during the dry season for browsers. The combination of nutritional value in *C. mopane* with its availability and acceptability to browsers makes *C. mopane* an important dry season browse species throughout extensive areas of southern Africa.

In addition to *C. mopane*, greater kudu also browse the leaves and twigs of a variety of woody plants. Curlewis (2014) suggests that the greater kudu in mopane woodland prefers to browse trees without thorns in winter, but the current study found that *D. cinerea* was readily browsed, mainly by male greater kudu, regardless of the presence of thorns (Table 10.3). This implies that the greater kudu will also browse thorny species despite their physical defence (Owen-Smith & Cooper 1983). The animals may be attracted by high concentrations of protein and minerals and low concentrations of fibre, lignin and condensed tannins in this species (Cooper & Owen-Smith 1985; Owen-Smith & Cooper 1987; Cooper *et al.* 1988). As indicated by Owen-Smith (2002), diet selection is therefore a trade-off between nutritional benefits against various costs of ingestion of secondary chemicals and feeding rate restrictions created by structural defences of the plants. The two female greater kudu browsed on a more restricted variety of plants than the three males (Table 10.3). These dietary variances may be associated with the difference in body size and nutrient requirements of male and female greater kudu (Furstenburg 2005), but a greater sample size would be required to give a conclusive answer. It may merely be that the larger size body of male greater kudu enables them to browse from a higher stratum than females (Curlewis 2014), and that they thereby have a greater variety of plants from which to choose.

10.5 CONCLUSION

During the dry season in mopane woodland, fewer species are available to be browsed by the greater kudu. Therefore, *C. mopane* contributes significantly to the diet of the greater kudu. High consumption of *C. mopane* by the greater kudu during the dry season in mopane woodland can be associated with the availability of *C. mopane* browse, its nutritional value and a lowered concentration of secondary metabolites such as tannins and phenols in older or shed leaves. Other important dry season food plants include pods and seeds of *D. cinerea*. Male greater kudu appear to have a wider diet than females, which are more selective feeders. The dependency on *C. mopane* as main source of browse, particularly during the dry season, indicates the importance of this species to the diet of the greater kudu in the mopane woodland.

CHAPTER 11

TRAGELAPHUS STREPSICEROS BROWSE DURING THE WET SEASON IN THE MOPANE WOODLAND OF LIMPOPO PROVINCE, SOUTH AFRICA[9]

11.1 INTRODUCTION

Tragelaphus strepsiceros Pallas, 1766, commonly known as the greater kudu (Ansell 1972), is widely distributed in southern and eastern Africa. It is highly adapted to a diverse range of habitats in those areas (Skinner & Chimimba 2005). It is one of the valued antelope in game reserves in South Africa's mopane woodland (Curlewis 2014), attracting many tourists. It is also sought after in the dried meat industry and for trophy hunting (Bonsma & Du Toit 2009; Taylor *et al*. 2016).

The mopane woodland is an extensive vegetation type that dominates the hot dry valleys and adjacent plains in southern Africa (Werger & Coetzee 1978; Timberlake *et al.* 2010). Its distribution ranges from southern Angola and northern Namibia across Botswana and Zimbabwe to central and southern Mozambique and from the Luangwa Valley in Zambia and central Malawi to northern South Africa (Mapaure 1994). Tree and shrub forms of *Colophospermum mopane* dominate this vegetation type (Mapaure 1994; Timberlake *et al.* 2010; Siebert 2012).

Various authors indicated that mopane provides essential forage for browsers (Mosimanyana & Kiflewahid 1988; Macala *et al*. 1992; Styles & Skinner 1997) such as the greater kudu (Hooimeijer *et al*. 2005; Curlewis 2014) especially during the dry season (Makhado *et al*. 2016). The selection of mopane browse by the

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[9] Makhado, R.A., Potgiter, M.J., Luus-Powell, W.J., Cooper, S.M. & Kopij, G. 2016. *Tragelaphus strepsiceros* browse during the wet season in the mopani veld of Limpopo Province, South Africa. *Rangeland Ecology & Management* 69(5): 408–413.

greater kudu, particularly during the dry season, is mainly due to the availability of this forage, when most other savanna species are leafless (Kos *et al.* 2012). In addition, the nutritional value of mopane browse causes it to be habitually selected by the greater kudu during the dry period (Bonsma 1942; Hooimeijer *et al*. 2005), when concentrations of secondary metabolites such as tannins and phenols are relatively low in leaf tissues (Wessels *et al*. 2007; Kohi *et al*. 2010). Browsing of mopane by the greater kudu is limited during the wet season (Hooimeijer *et al*. 2005; Curlewis 2014), mainly because of a high concentration of secondary metabolites (Wessels *et al*. 2007; Kohi *et al*. 2010). The consumption of browse with high concentrations of secondary metabolites can cause digestion challenges to herbivores (Van Hoven 1991) and loss of appetite (Bailey 1978), because such forage is of low palatability to the animals (Cooper & Owen-Smith 1985).

Despite the reported nutritional value of mopane (Bonsma 1942; Hooimeijer *et al*. 2005) and other species such as *Combretum apiculatum* and *Dichrostachys cinerea* as a source of browse for the greater kudu and other ungulates feeding in mopane woodland (Curlewis 2014; Makhado *et al*. 2016), there is limited information on the diet composition and selection of browse of the greater kudu in mopane woodland, particularly during the wet season when mopane contains high levels of secondary metabolites. In addition, there is lack of data on browse selection between male and female greater kudu, which is critical to any management plan. This deficiency in the current knowledge is hampering understanding of ecological requirements and adaptation mechanisms of the greater kudu against the build-up of secondary metabolites in browsing plants during the wet season.

The purpose of this study is therefore to identify the species, types and parts of plants that are mostly browsed by the greater kudu in mopane woodland during the wet season. The study also compares the diet selected by female versus male greater kudu. The results of this study should be of significance to game farmers, ranchers and reserve managers in the extensive mopane woodland, by enabling them to better understand the diet requirements of the greater kudu during the wet season and to adjust their management interventions to favour browse species needed for best year-round nutrition of the greater kudu.

11.2 METHODOLOGY

11.2.1 Study area

This study was conducted at the Sandown Game Farm in the Musina Local Municipality. The farm was conducting culling programme during the study period, hence the reason for choosing it as the study area. The farm is situated in the northern part of the Limpopo Province, South Africa at 22°28'S, 29°29’E. It covers 2070 hectares of pristine environment. The altitude ranges from 400 to 750 m above sea level. The Sandown Game Farm is in an arid to semi-arid environment where rainfall typically occurs in summer and declines significantly in winter. The average annual rainfall of the area is 331 mm, and it typically ranges between 300 mm and 400 mm per annum (SA Weather Services 1981–2014). The area is characterised by high summer temperatures. The annual average maximum temperature is 30^{o}C. The average annual minimum temperature is 16^{o}C, and there is zero probability of snow occurrence. Relative humidity is less than 30% (SA Weather Services 1981–2014).

The geology of the area consists mostly of rocks of the Beit Bridge Complex (Swazian Erathem), as well as sediments (including sandstones of the Clarens Formation) and basalt (particularly in the east) of the Karoo Supergroup. Soils are underpinned by the Archaean Beit Bridge Complex, which consists of gneisses and meta-sediments. The soils are variable, ranging from deep red/brown clays to freely drained sandy soils and calcareous clayey soils (Mucina & Rutherford 2006).

The Sandown Game Farm is located within the Musina Mopane Bushveld of the Mopane Bioregion. The Musina Mopane Bushveld vegetation unit is the most widespread vegetation unit in the northern part of South Africa. The tree and shrub component is dominated by *C. mopane*. Species such as *Combretum* *apiculatum*, *Terminalia prunioides*, *Adansonia digitata*, *Commiphora mollis, Sclerocarya birrea* and *Senegallia* species add to the mix of this vegetation (Mucina & Rutherford 2006).

The fauna at the Sandown Game Farm consists of a variety of species, which include *Giraffa camelopardalis*, *Tragelaphus strepsiceros*, *Connochaetes taurinus*, *Aepyceros melampus*, *Taurotragus oryx*, *Kobus ellipsiprymnus*, *Oryx gazelle*, *Raphicerus campestris*, *Equus quagga burchellii* and *Sylvicapra grimmia*, amongst others.

11.2.2 Greater kudu rumen content analysis procedure

The parts (leaves, twigs, flowers, pods, barks and fruits) of major plant species browsed by the greater kudu, as identified by Curlewis (2014), were collected from Musina Nature Reserve. The parts were individually placed in labelled and sealed transparent plastic bags and transported to the University of Limpopo in a cooler box. The collected plant materials were preserved in 70% ethanol for later use. Plant parts were fixed as a reference collection of slides, in order to assist in the identification of what is contained in the greater kudu rumen. Photographs of these parts were also taken in the field to assist in the identification of plant fragments in the rumen.

In total, eight samples were collected from four adult male and four adult female greater kudu culled during the late wet season on 22–24 March 2015. The wet season in South Africa starts in October and ends in April. The wet mass of collected samples ranged from 982 g to 3021 g, with an average of 1705 g. Individual rumen contents were thoroughly mixed in a plastic container and washed several times with tap water until the particulates in the samples were clean. A 2x2 mm sieve was used to sift particulates (plant materials) from water. Using the reference collection, the sifted materials were grouped by plant species. The materials were identified by comparing leaf shape, structure, veins, hairs, stomata, fruits, barks, seeds, pods and flowers with the reference collection. A stereomicroscope (light detector) was used to identify fine plant parts that could not be identified with the naked eyes.

11.2.3 Statistical analysis

Datasets were analysed using descriptive and inferential statistics. Descriptive statistics were used to determine the mean and standard deviation of species browsed by the greater kudu. The percentage contribution of each species to the greater kudu diet was calculated. The abundance of each species was calculated as a percentage of the total wet weight of particulates, identified from the rumen of each culled kudu. The grouped sub-samples (leaves, twigs, grass, forbs, flowers, seeds and pods) were calculated in order to determine the parts most often browsed. Pearson Correlation Coefficient analysis was used to compare the diets of female and male greater kudu (IBM SPSS Statistics 24, USA). Significant difference was accepted when $P < 0.05$.

11.3 RESULTS

11.3.1 Species browsed by the greater kudu

During the wet season, the greater kudu diet in the study area was composed of a variety of species. Sixteen plant species were browsed by the greater kudu during that period, including *C. apiculatum*, *S. birrea*, *C. mopane*, *Senegalia nigrescens*, *T. prunioides*, *C. mollis*, *D. cinerea*, *Indigofera* spp., *Boscia albitrunca*, *Solanum panduriforme*, *Maerua parvifolia*, *Grewia* spp., *Vachelia erioloba* and *Vachellia tortilis* (Table 11.1). The average (± s.d.) wet weight of species mainly found in the greater kudu rumen samples during the wet season were *C. apiculatum* (656 g ± 459 g), *S. birrea* (483 g ± 452 g), *C. mopane* (246 g ± 290 g), *S. nigrescens* (127 g ± 120 g), *T. prunioides* (66 g ± 61 g), *C. mollis* (77 g ± 23 g), *D. cinerea* (43 g ± 28 g), *Indigofera* spp. (37 g ± 26 g), *B. albitrunca* (28 g ± 32 g), *S. panduriforme* (52 g ± 0.4 g), *M. parvifolia* (30 g ± 50 g) and *Grewia* spp. (27 g ± 39 g). Other less frequently browsed species such as *V. erioloba* (0.02 g ± 0.01 g) and *V. tortilis* (0.03 g ± 0.01 g) contributed far smaller amounts to the greater kudu diet (Table 11.1).

Table 11.1: Species and amount browsed by the greater kudu during the wet season of 2015 in mopane woodland, Limpopo Province, South Africa (*n*=8).

Species	**Wet weight (g)**					
	Sum	Min	Average	Max	S.D	Variance
Combretum apiculatum	5245.83	224.20	655.73	1719.05	459.06	210734.70
Sclerocarya birrea	2899.08	98.75	483.18	1228.73	451.92	204228.60
Colophospermum mopane	1474.73	56.07	245.79	822.70	289.87	84023.04
Senegalia nigrescens	1014.63	0.23	126.83	270.91	119.73	14335.17
Terminalia prunioides	462.18	1.67	66.03	170.24	60.80	3696.16
Commiphora mollis	306.97	52.87	76.74	105.51	22.71	515.58
Dichrostachys cinerea	214.04	0.03	42.81	71.07	27.57	760.19
Indigofera spp.	185.31	13.82	37.06	79.81	26.02	676.91
Boscia albitrunca	113.86	0.32	28.47	57.4	32.45	1052.91
Solanum panduriforme	104.59	52.03	52.30	52.56	0.37	0.14
Maerua parvifolia	86.87	0.05	28.96	86.74	50.04	2504.19
Grewia spp.	81.01	0.33	27.00	71.86	39.08	1527.11
Vachellia erioloba	0.03	0.01	0.02	0.02	0.01	0.0001
Vachellia tortilis	0.05	0.02	0.03	0.03	0.01	0.00001
Unidentified fruit	0.08	0.03	0.04	0.05	0.01	0.0002
Unidentified forb	0.04	0.01	0.02	0.03	0.01	0.0002

Symbols: g=gramme, Min=Minimum, Max=Maximum, S.D=standard deviation.

Combretum apiculatum, *S. birrea*, *C. mopane* and *S. nigrescens* are the four tree species mostly browsed. Proportionally, *C. apiculatum* contributed most (43% ± 29%) to the diet of the greater kudu in mopane woodland. This was followed by *S. birrea* (24% ± 29%), *C. mopane* (12% ± 18%) and *S. nigrescens* (8% ± 8%). The contribution of the remaining species such as *T. prunioides*, *C. mollis*, *D. cinerea*, *Indigofera* spp., *B. albitrunca*, *S. panduriforme*, *M. parvifolia*, *Grewia* spp., *V. erioloba* and *V. tortilis* to the diet of the greater kudu was less than 5%, which is insignificant (Figure 11.1).

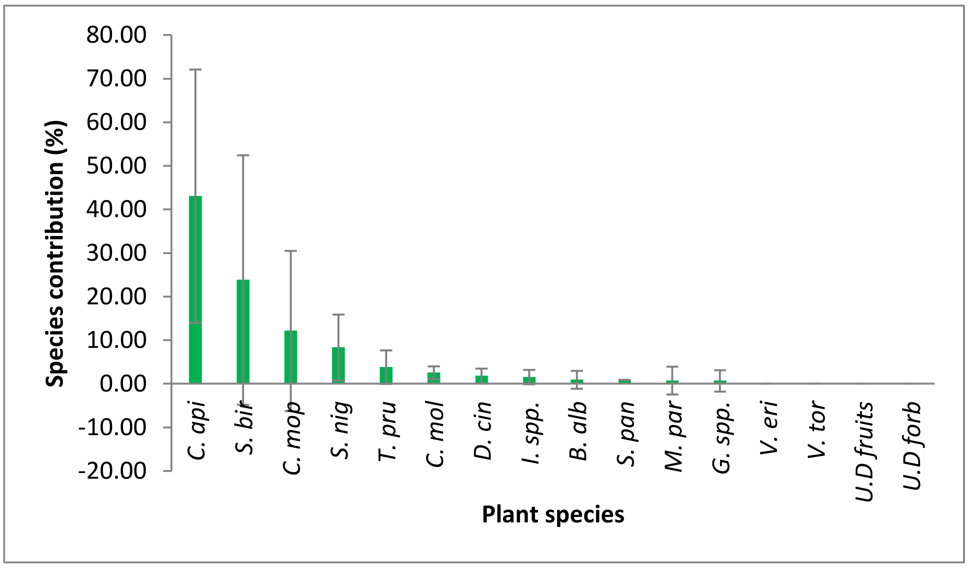


Figure 11.1: Species contribution to the greater kudu diet during the wet season in mopane woodland, Limpopo Province, South Africa (*n*=8). ***Note***: *V. eri = Vachellia erioloba*, *S. nig = Senegalia nigrescens*, *V. tor = Vachellia tortilis*, *B. alb = Boscia albitrunca*, *C. mop = Colophospermum mopane*, *C. api = Combretum apiculatum*, *C. mol = Commiphora mollis*, *D. cin = Dichrostachys cinerea*, *I*. spp.= *Indigofera* species, *G*. spp. = *Grewia* species, *M. par = Maerua parvifolia*, *S. bir = Sclerocarya birrea*, *S. pan = Solanum panduriforme*, *T. pru = Terminalia prunioides* and U.D = Unidentified.

Foliage from trees contributed significantly more (71%) to the greater kudu diet composition as compared to shrubs (14%) and forbs (14%). The parts of trees, shrubs and forbs mostly consumed by the greater kudu during the wet season were leaves, followed by fruits (Table 11.2). Leaves contributed most (81%) to the diet, while fruit contributed the remaining 19%. The fruit browsed was mainly from *S. birrea*. This study further showed that the greater kudu also consume seeds, twigs and pods from species such as *S. nigrescens*, *Indogofera* spp*.* and to a lesser extent *S. panduriforme* (Table 11.2).

Table 11.2: Type of plants and parts browsed by greater kudu during the wet season of 2015 in mopane woodland, Limpopo Province, South Africa (*n*=8).

Species	Type of plant	Parts browsed	Dominant parts
Vachellia erioloba	tree	leaves	leaves
Senegalia nigrescens	tree	seeds, pods and leaves	leaves
Vachellia tortilis	tree	leaves	leaves
Boscia albitrunca	tree	leaves	leaves
Colophospermum mopane	tree	leaves	leaves
Combretum apiculatum	tree	leaves	leaves
Commiphora mollis	tree	leaves	leaves
Dichrostachys cinerea	shrub	leaves	leaves
Grewia spp.	shrub	leaves	leaves
Indogofera spp.	forb	flowers, twigs, pods, seeds and leaves	leaves
Maerua parvifolia	tree	leaves	leaves
Sclerocarya birrea	tree	fruit	fruits
Solanum panduriforme	forb	fruit, seeds, pods and twigs	fruits
Terminalia prunioides	tree	leaves	leaves
Unidentied fruits	-	fruit and seeds	fruits
Unidentified forb	forb	leaves	leaves
	Tree 71.43%		Leaves 81.25%
	Shrubs 14.29%		Fruits 18.75%
	Forbs 14.29%		

11.3.2 Comparison of diet composition of male and female greater kudu

The diets of female and male greater kudu were slightly different. Sixteen plant species (*V. erioloba*, *S. nigrescens*, *V. tortilis*, *B. albitrunca*, *C. mopane*, *C. apiculatum*, *C. mollis*, *D. cinerea*, *Grewia* spp., *Indogofera* spp., *M. parvifolia*, *S. birrea*, *S. panduriforme*, *T. prunioides*, unidentified fruits and unidentified forbs) were browsed by females during the wet season, while nine plant species (*S. nigrescens*, *C. mopane*, *C. apiculatum*, *C. mollis*, *D. cinerea*, *Grewia* spp., *Indogofera* spp., *S*. *birrea* and *T. prunioides*) were browsed by males (Table 11.3). Therefore, seven species (*S. panduriforme*, *M. parvifolia*, *B. albitrunca*, *V. tortilis*, *V. erioloba*, unidentified fruits and unidentified forbs) were browsed by females, but were not recorded in the diet of males (Table 11.3). This study further identified that 64% of the female diet consisted of forage from just two species: *C. apiculatum* (44% ± 48%) and *C. mopane* (20% ± 24%). *Senegalia nigrescens*, *S. birrea* and *C. mollis* contributed 8% ± 10%, 7% ± 2% and 6% ± 1%, respectively to the female diet. In contrast, 71% of the male greater kudu diet comprised of *S. birrea* (38% ± 54%) fruits and leaves of *C. apiculatum* (34% ± 9%). *Senegalia nigrescens*, *T. prunioides* and *C. mopane* contributed 7% ± 13%, 6% ± 8% and 5% ± 5%, respectively, to the male diet. The remaining plant species contributed less than 5% to the diets of females and males (Table 11.3). However, despite the difference in preference for particular species in the diet of females and males greater kudu, the browsing selection between female and male proved to be positively correlated (*r*=0.68; Table 11.3) in view of the great importance of *C. apiculatum* in the diets of greater kudu of both genders (Table 11.3 and Figures 11.2).

Table 11.3: Browsing selectivity between female (*n*=4) and male (*n*=4) greater kudu during the wet season of 2015 in mopane woodland, Limpopo Province, South Africa.

	Wet weight of amount browsed					
	Female			**Male**		
Plant species	**Average (g)**	**S.D**	**%**	**Average (g)**	**S.D**	**%**
Combretum apiculatum	709.72	691.29	44.01±48.45	601.74	77.85	33.88±9.27
Colophospermum mopane	325.66	337.52	20.19±23.66	86.05	42.39	4.85±5.05
Sclerocarya birrea	116.48	25.07	7.22±1.76	666.53	453.54	37.53±53.98
Senegalia nigrescens	125.36	145.36	7.77±10.19	128.30	110.97	7.22±13.21
Terminalia prunioides	34.81	40.18	2.16±2.82	107.65	64.17	6.06±7.64
Commiphora mollis	94.05	16.21	5.83±1.14	67.15	14.89	3.78±1.77
Solanum panduriforme	52.3	0.37	3.24±0.03	-	-	-
Indigofera spp.	46.82	46.66	2.90±3.27	30.56	10.33	1.72±1.23
Dichrostachys cinerea	36.83	35.59	2.28±2.49	51.77	15.49	2.92±1.84
Maerua parvifolia	28.96	50.04	1.80±3.51	-	-	-
Boscia albitrunca	28.47	32.45	1.77±2.27	-	-	-
Grewia spp.	4.58	6.00	0.28±0.42	36.10	50.58	2.03±6.02
Vachellia tortilis	0.03	0.01	0.00±0.00	-	-	-
Unidentified fruit	0.04	0.01	0.00±0.00	-	-	-
Vachellia erioloba	0.02	0.01	0.00±0.00	-	-	-
Unidentified forb	0.02	0.01	0.00±0.00	-	-	-
Pearson correlation	*r*=0.675					

Symbols: g=gramme, S.D=standard deviation, %=percent.

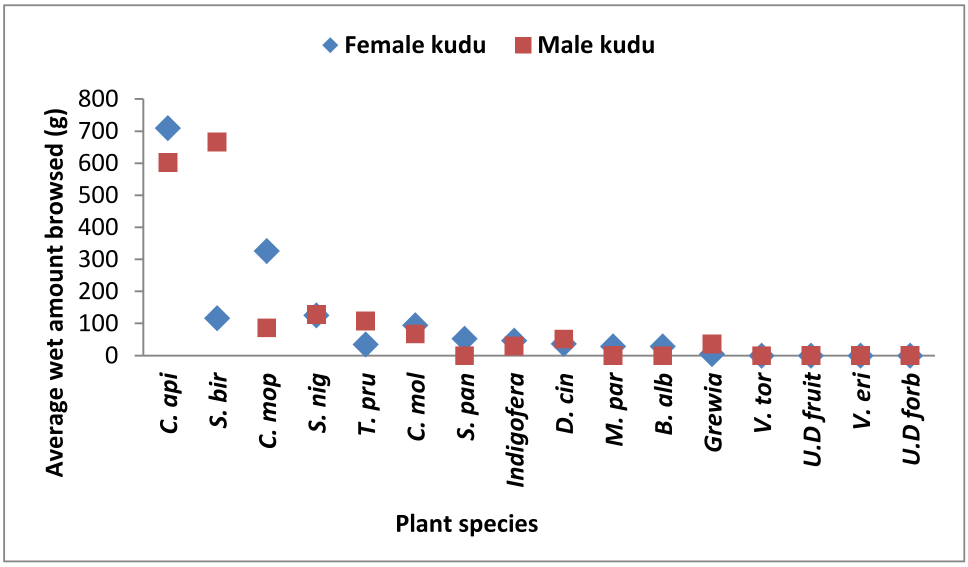


Figure 11.2: Species browsed by female (*n*=4) and male (*n*=4) greater kudu during the wet season of 2015 in mopane woodland, Limpopo Province, South Africa. ***Note***: *V. eri* = *Vachellia erioloba*, *S. nig* = *Senegalia nigrescens*, *V. tor* = *Vachellia tortilis*, *B. alb* = *Boscia albitrunca*, *C. mop* = *Colophospermum mopane*, *C. api* = *Combretum apiculatum*, *C. mol* = *Commiphora mollis*, *D. cin* = *Dichrostachys cinerea*, *M. par* = *Maerua parvifolia*, *S. bir* = *Sclerocarya birrea*, *S. pan* = *Solanum panduriforme*, *T. pru* = *Terminalia prunioides* and U.D = Unidentified.

11.4 DISCUSSION

The wet season is usually accompanied by rain in the savannas, which promotes the growth and development of plant species (Scholes & Walker 1993). This study shows that during the wet season, an abundance of diverse plant species of presumed high nutritional quality is readily available to browsers (Table 11.1). Curlewis (2014) indicates that the availability of diverse and palatable plant species during the wet season allows the greater kudu to select a diet composed of many different species. The forage choices for greater kudu during this period range from trees and shrubs to forbs. Grasses were not recorded in the greater kudu rumen, which confirms the findings of Curlewis (2014) that the diet of the greater kudu in mopane woodland does not include grass. However, previous studies in the same locality record that a small proportion of grass, ranging from 2.9% (Hooimeijer *et al*. 2005) to 7% (Cooper 1985; Owen-Smith & Cooper 1985), was consumed by the greater kudu during the early wet season. In addition, Furstenburg (2010) indicates that 5%–12% of grasses were consumed by the greater kudu in the Eastern Cape Valley Bushveld of South Africa. Though the greater kudu seems to accept small quantities of grasses, especially new growth during the early wet season (Cooper 1985; Hooimeijer *et al*. 2005; Furstenburg 2010), its digestive anatomy is not designed to handle high-fibre forages such as grasses. Greater kudu therefore reject the mature grasses available during the late wet and dry seasons (Hofmann & Stewart 1972). The sampling period of the current study was late wet season, which could be the main reason the grasses were not found in the greater kudu rumen. As also found in this study, greater kudu are predominantly selective browsers, mainly feeding on leaves, twigs, pods, seeds and fruits of a wide range of trees, shrubs, forbs and succulents (Furstenburg 2010; Curlewis 2014).

Various researchers indicated that *C. mopane* is an essential browse to the greater kudu (Hooimeijer *et al*. 2005; Curlewis 2014), particularly during the dry season (Macala *et al.* 1992; Mosimanyana & Kiflewahid 1988; Makhado *et al*. 2016). However, this study shows that during the wet season, the greater kudu selected mainly *C. apiculatum* leaves and *S. birrea* fruits (Figures 11.1 and 11.2). Although *C. mopane* is a dominant (Mapaure 1994) and nutritious species in mopane woodland (Hooimeijer *et al*. 2005), it was not highly browsed during the wet season. However, *C. mopane* was eaten in limited amounts during the wet season, especially by the female greater kudu. This study therefore concurs with the findings of Styles and Skinner (1997) and Hooimeijer *et al*. (2005), that the greater kudu still browse *C. mopane*, though in limited quantities, during the wet season regardless of the higher concentration of chemical defences (Owen-Smith & Cooper 1983), such as tannins and phenols, in the non-senescent leaves (Styles & Skinner 1997; Wessels *et al.* 2007; Kohi *et al*. 2010). Plants that contain more than 5% of condensed tannins are rejected by ungulates (Cooper & Owen-Smith 1985) because these tannins reduce the crude protein digestibility of browse (Cooper & Owen-Smith 1985; Provenza *et al*. 2003; Wessels *et al*. 2007). However, *C. mopane* was browsed by the greater kudu during the wet season when secondary metabolites were at high levels, which proves that tannin-rich species are not totally rejected, but rather consumed in limited quantity. It appears that consumption of limited amounts of dry season browse species during the wet months may be a sampling behaviour allowing the animals to monitor the changing dietary quality of the leaves throughout the seasons. Alternatively, the greater kudu inhabiting the mopane woodland may be metabolically adapted to coping with the tannins present in this widespread and abundant plant species. However, the ability of the greater kudu to diversify its diet selection seems to be a critical mechanism to limit the quantity of secondary metabolites ingested in the diet. Consumption of limited quantities of a wide variety of plants most likely ensures that the level of secondary metabolites does not exceed safety levels (Westoby 1978).

Sclerocarya birrea fruits, commonly known as marula, appear to be one of the favourite options of the greater kudu, mainly browsed by the males (Table 11.3), which may be due to the behavioural dominance of the males. Marula fruits ripen towards the end of the wet season and are readily consumed by ungulates during that period. The selection of marula fruits could be due to the energy-providing sugars and their high vitamin C content. Fresh marula fruits contain up to 180 mg per 100 g of vitamin C (Shackleton *et al*. 2002), attracting not only the greater kudu (Hooimeijer *et al*. 2005), but also other browsers such as *Loxodonta africana* (Morris *et al*. 2006), *Giraffa camelopardalis*, *Kobus ellipsiprymnus* and *Taurotragus oryx* (Venter & Venter 1996). During the wet season the greater kudu mainly browses the leaves (Table 11.2), probably because other plant parts such as pods and seeds are still unripe. Leaves thus contribute significantly to the diet of ungulates in the wet season (Owen-Smith 1993). In addition, thorn species such as *S. nigrescens* and *D. cinerea*, which are an integral part of the greater kudu’s diet during the dry season (Curlewis 2014; Makhado *et al*. 2016), are not often browsed during the wet season. This implies that the greater kudu selectively avoids thorn species during the wet season (Curlewis 2014), which could be due to the availability and accessibility of thorn-less species during that period. This would provide a higher rate of food intake and also avoid the physical challenge associated with browsing thorn species (Cooper & Owen-Smith 1986).

During the wet season, females browsed a greater variety of plant species than males (Table 11.3). This suggests that female greater kudu develop more appetite for food when it is abundant during the wet season, leading to consumption of a variety of species. This study further found that females browsed ripe fruits of *S. panduriforme*, which are generally considered inedible. However, Pooley (1998) indicates that they are also browsed by nyala (*Tragelaphus angasii*) and black rhino (*Diceros bicornis*). Most *S. panduriforme* fruits are swallowed without being chewed, which suggests that it could be a mechanism employed by the female greater kudu to avoid the unpalatable taste of the fruits when chewed. Green *S. panduriforme* fruits are toxic and were not recorded in the rumen, but have high medical value in the treatment of infections, sores and pain in animals (Madzimure *et al*. 2013).

11.5 CONCLUSION

During the wet season, broad mixtures of plant species are available to be browsed by the greater kudu. This is reflected in the wide dietary selection of these animals in the wet season. In mopane woodland, the diet of the greater kudu was mainly composed of leaves from trees. The leaves of the deciduous tree, *C. apiculatum*, contributed significantly to the diet of both male and female greater kudu. Seasonably available fruits of *S. birrea* were also important food items, particularly to the males. In addition, to a lesser extent, the greater kudu browsed species such as *C. mopane*, *D. cinerea*, *S. nigrescens* and *Vachellia* spp., which are important dry season food plants, but may have more chemical and physical defences against herbivores. Female greater kudu appeared to have a wider diet selection than males during the wet season, although the dominance of a limited number of species in the diet of both genders rendered the difference statistically non-significant. The dependency of the greater kudu on species such as *C. mopane* and *C. apiculatum* as main sources of browse indicates the importance of these species to the diet of the greater kudu in the mopane woodland.This chapter was based on a small sample size which therefore requires further studies to be undertaken in order to validate the current findings.

CHAPTER 12

SUMMARY, CONCLUSION AND RECOMMENDATIONS

12.1 SUMMARY OF RESULTS

This section provides a summary of results derived from Chapters 6 to 11. This study showed that <10% pruning has a seasonal effect on mopane leaf phenology and production. The concentration of macronutrients, trace elements and secondary metabolites in mopane leaf increased during the wet season and then deteriorates during the leaf senescence period. The leaves are nutritious and extensively consumed by browsers, especially during the dry season, when secondary metabolites are at low concentration. The amount of macronutrients, trace elements and secondary metabolites in mopane leaves is not influenced by <10% pruning, but seems to be associated with leaf growth stages. The sections that follow provide a summary of results in relation to the study objectives.

12.1.1 Mopane leaf phenology and production

Chapter 6 provides the results on the rate of mopane leaf phenology and production. The effect of pruning on mopane leaf phenology and production was also determined. It was found that mopane leaf green-up starts in October and the tree attains its maximum greenness from December to February. Leaf greenness was lowest during the dry season, particularly in August. Pruning resulted in a decline in the number of leaves during the initiation of the experiment, but increases during the next growing season.

12.1.2 Concentration of macronutrients and trace elements in mopane leaves

Chapters 7 to 8 provide the results on the concentration of mopane leaf macronutrients and trace elements. The monthly, seasonal and annual effect of pruning on the amount of mopane leaf macronutrients and trace elements was also determined.

Mopane leaves contain macronutrients such as calcium (Ca), potassium (K), nitrogen (N), phosphorus (P), sulphur (S), chlorine (Cl), magnesium (Mg), nitrate (NO_3), sodium (Na), protein and fibre. They also contain trace elements such as iron (Fe), manganese (Mn), boron (B), molybdenum (Mo), copper (Cu), zinc (Zn), cobalt (Co), fluoride (F) and selenium (Se). These elements play a critical role in the healthy growth and development of browsers. Most of these elements were within the desirable level for consumption by ruminants. This study showed that the concentration of these elements in mopane leaves is not dependent on <10% pruning, but seems to be associated with leaf growth stages. The level of most elements sampled increased during leaf flush in October and then declined as the leaves matured and aged.

12.1.3 Chemical deterrence in mopane leaves

The concentration of secondary metabolites was determined in chapter nine. Mopane produces chemical compounds such as tannins and phenols. The monthly, seasonal and annual effect of pruning on the concentration of secondary metabolites in mopane leaves was also determined. This study found that <10% pruning does not have an effect on the amount of secondary metabolites. The amount of total phenols (TP), condensed tannins (CT) and protein-precipitating tannins (PPT) increased during leaf flush in October, and then declined as the leaves matured and aged (Tables 9.2-9.4).

12.1.4 Greater kudu browse in the mopane woodland

Mopane leaves provide essential browse to the greater kudu, particularly during the dry season. Species composition in the diet and parts browsed by the greater kudu during the dry and wet seasons were determined and reported on in Chapters 10 and 11. This study found that during the dry season, greater kudu mainly browsed *Colophospermum mopane*. Other important dry season browse species included *Dichrostachys cinerea*, *Commiphora edulis*, *Grewia bicolor*, *Grewia flava*, *Combretum apiculatum* and *Terminalia prunioides*. During the wet season, the greater kudu seemed to change its diet requirements. The most browsed species during the wet season was *C. apiculatum*. Other browse plant species consumed during the wet season were *Sclerocarya birrea*, *C. mopane* and *Senegalia nigrescens*.

Foliage from trees contributed more to the greater kudu diet composition than shrubs and forbs. Leaves were the main parts browsed by the greater kudu during the dry and wet seasons. The diets of female and male greater kudu were slightly different. During the dry season, five species (*C. mopane*, *D. cinerea*, *G. bicolor*, *C. apiculatum* and *T. prunioides*) were browsed by female greater kudu, while seven species (*C. mopane*, *D. cinerea*, *C. edulis*, *G. bicolor*, *G. flava*, *C. apiculatum* and *T. prunioides*) were browsed by male greater kudu. During the wet season, 16 plant species (*Vachellia erioloba*, *S. nigrescens*, *Vachellia tortilis*, *Boscia albitrunca*, *C. mopane*, *C. apiculatum*, *Commiphora mollis*, *D. cinerea*, *Grewia* spp., *Indogofera* spp., *Maerua parvifolia*, *S. birrea*, *Solanum panduriforme*, *T. prunioides*, unidentified fruits and unidentified forbs) were browsed by female greater kudu, while nine plant species (*Senegalia nigrescens*, *C. mopane*, *C. apiculatum*, *C. mollis*, *D. cinerea*, *Grewia* spp., *Indogofera* spp., *S*. *birrea* and *T. prunioides*) were browsed by the males.

12.2 GENERAL CONCLUSION

The leaves of mopane are nutritious and thus regarded as an important browse, particularly during the dry season. Mopane leaves contain essential macronutrients, trace elements and also secondary metabolites such as tannins and phenols. Mopane leaf production and phenology were studied to determine the greenness and availability of the leaves. It is concluded that <10% pruning has a seasonal effect on mopane leaf phenology and production. It appears that <10% pruning reduces the number of leaves during the initiation of the experiment, but triggers vigorous flush of mopane leaves in the following season, which result in a prolonged growing season. The increase in the number of leaves in the following season and prolonged leaf carriage enables mopane to supply browsers with forage, particularly during the dry season, when forage is limited in the mopane woodland.

Mopane leaves contain macronutrients and trace elements, which are essential for the healthy growth and development of browsers. It is concluded that the concentration of macronutrients and trace elements in the leaves is not dependent on <10% pruning, but seems to be associated with leaf growth stages. This could be the case because the amount of macronutrients and trace elements increased during spring leaf flush and declined as the leaf matured and aged during the dry season.

This study concluded that the amount of secondary metabolites in mopane leaves is not dependent on <10% pruning, but appeared to be associated with leaf growth stages. It seems that spring leaf flush triggers the production of secondary metabolites, which deteriorates during leaf senescence stage, especially during the dry season. The production of secondary metabolites appears to be a chemical defence strategy exerted by mopane to deter browsers from consuming the leaves, particularly during the growing season.

It is further concluded in this study that mopane contributes significantly to the diet of the greater kudu, especially during the dry season. High consumption of mopane forage during the dry season is associated with the availability of mopane browse, its nutritional value and a lowered concentration of secondary metabolites in older or shed leaves. Male greater kudu appear to have a wider diet than females, which are more selective feeders. During the wet season, the leaves of *C. apiculatum* contribute significantly to the diet of both male and female greater kudu. The fruits of *S. birrea* are also important seasonal food items, particularly for the males. The dependency of the greater kudu on *C. mopane* and *C. apiculatum* as sources of browse during dry season indicates the importance of these species to the diet of the greater kudu in the mopane woodland.

12.3 RECOMMENDATIONS

This study demonstrated that mopane leaves contribute significantly to the diet of the greater kudu in the study area, especially during the dry season. In addition, mopane leaves are nutritious and contain vital elements needed for the body of browsers. The availability of mopane forage and its nutritional value makes it an important dry season browse, particularly for browsers such as the greater kudu. A pruning experiment was employed in this study to simulate the effect of browsers on mopane leaf phenology, production, macronutrients, trace elements and secondary metabolites. Based on the findings of this study, the following recommendations were proposed.

12.3.1 Control of mopane leaf quality

Pruning resulted in a decline in the rate of phenology and number of leaves during the initiation of the experiment, but level during the end of the experiment. This study recommends that <10% pruning increases browse in the following season, whilst reducing it for the current season.

The effect of <10% simulated browsing employed in this study resulted to insignificant difference in the amount of most macronutrients, trace elements and all secondary metabolites in the pruned and control trees. It is therefore recommended that other pruning intensities, such as 25%, 50%, 75% and 100%, be tested to simulate the effect of medium to heavy browsing on mopane trees.

The amount of macronutrients, trace elements and secondary metabolites increases during leaf flush and deteriorates as the leaf ages and matures. This study therefore recommended that leaf flush has an important role to play in influencing the amount of macronutrients, trace elements and secondary metabolites in mopane leaf. Other important parameters that need to be taken into consideration include the availability of soil moisture.

12.3.2 Mopane-greater kudu relationship

Mopane is a dominant tree species at Musina Nature Reserve and contribute significantly to the diet of the greater kudu, particularly during the dry season. This study showed that the greater kudu changes its diet requirements in response to seasonal changes. It seems that the greater kudu diversifies its diet in the wet season in order to reduce the toxic effects of secondary metabolites. Considering the harsh conditions in the study area and the adaptability of the greater kudu to that habitat, this study recommends that the area could be used for goat or game farming. This study further recommends that the desirable stock in the area could be browsers.

12.4 HYPOTHESES TESTING

Research hypotheses, as outlined in section 1.4.3 of this thesis, were tested using inferential statistical analyses. The hypotheses were addressed in Chapters 6 to 11 and tested as follows:

Hypothesis 1: Pruning has no effect on seasonal leaf phenology and production of C. mopane. This hypothesis was tested in Chapter 6. This study proved that <10% pruning results in variations in the rate of mopane leaf phenology (Table 6.2) and production (Table 6.4). This study conclusively showed that <10% pruning has significant effect on seasonal leaf phenology and production of mopane. This hypothesis is therefore rejected.

Hypothesis 2: Pruning has no effect on seasonal leaf quality of C. mopane. This hypothesis was tested in Chapters 7 to 9. Chapter 7 showed that <10% pruning has no effect in the amount of macronutrients in mopane leaves (Table 7.3), except for K (P=0.039) during the dry season. Chapter 8 also proved that <10% pruning did not result in a statistical difference in the amount of trace elements in mopane leaves (Table 8.3). Chapter 9 further showed that <10% pruning does not have an effect in the concentration of secondary metabolites in mopane leaves (Table 9.3). This study thus showed that <10% pruning does not have an effect on the concentration of macronutrients, trace elements and secondary metabolites in mopane leaves. Accordingly, the hypothesis is accepted.

Hypothesis 3: Seasonal changes have an influence on the diet composition and browse selection of T. strepsiceros in the mopane woodland. This hypothesis was tested in Chapters 10 to 11. Chapter 10 attested that during the dry season, seven species were browsed. *Colophospermum mopane* leaves contributed the most to the diet of the greater kudu during the dry season (Table 10.1). In addition, Chapter 11 proved that during the wet season, 16 species were browsed. *Combretum apiculatum* leaves contributed the most to the diet of the greater kudu during the wet season (Table 11.1). This study indicated that seasonal changes from dry to wet have an influence on the diet composition and browse selection of *T. strepsiceros* in the mopane woodland. This hypothesis is therefore accepted.

12.5 RESEARCH QUESTIONS ANSWERED

Research questions, as outlined in section 1.4.4 of this thesis, were addressed in Chapters 6 to 11, and thus answered as follows:

Question 1: What is the effect of pruning on mopane leaf phenology and production?

Answer: Less than 10% has an effect on the rate of mopane leaf phenology. It also resulted in the decline of mopane leaf production during the initiation of the experiment, but level during the end of the experiement.

Question 2: What is the effect of pruning on mopane leaf quality?

Answer: Less than 10% pruning does not have an effect on the concentration of macronutrients, trace elements and secondary metabolites in mopane leaves.

Question 3: Which parts of mopane (leaf, twigs, pods, flowers, fruit and bark) constitute the highest proportion of the diet of the greater kudu during the different seasons?

Answer: The greater kudu mainly browsed the leaves of *C. mopane*, especially during the dry season. During the wet season, the greater kudu diet is mainly constituted by *C. apiculatum* leaves.

Question 4: What is the diet composition for greater kudu in different seasons?

Answer: *Colophospermum mopane* leaves contributed the most to the diet composition of the greater kudu during the dry season. However, during the wet season, *C. apiculatum* leaves contributed the most to the diet composition of the greater kudu.

12.6 FUTURE RESEARCH

This study has contributed to improved understanding of the effect of pruning on mopane leaf nutritional and chemical composition, and the role played by mopane in the diet of the greater kudu in the mopane woodland. The study was, however, limited to mopane leaf quality and greater kudu diet composition during different seasons in the mopane woodland. As a result, there is a need for a comprehensive approach to understand the leaf quality of plant species found in mopane woodland and their contribution to the diet of browsers in that ecosystem. In addition, the application of only <10% pruning intensity is not adequate for simulating the effect of browsers on mopane leaf quality. Future research in mopane woodland should therefore close the current research gaps and focus on the following research areas:

- Assessment of forage quality and browsers' response to variations in forage quality in the mopane woodland. The study will be essential for better understanding of the quality of species browsed and distribution of browsers in relation to forage quality in the mopane woodland.

- Simulating the effects of browsers using 25%, 50%, 75% and 100% browsing intensities on forage quality in the mopane woodland. The study is important in understanding the effect of browsers on forage quality. This could contribute to an improved understanding of the browsing behaviour of different wild animals in mopane woodland.

- Inventory on species consumed by browsers in the mopane woodland. The study is essential for the identification of species selected for browse during different seasons. The information generated will be important for effective conservation of mopane woodland and animal species supported with forage in that ecosystem.

- Investigation into the capability of the greater kudu to cope with the build-up of secondary metabolites during the wet season in mopane woodland. Greater kudu accept, though in small quantities, forage containing secondary metabolites. This study will be important in seeking to understand the response strategy of browsers to chemical deterrence in the forage.

REFERENCES

Acocks, J.H.P. 1988. Veld types of South Africa. 3rd Edition. *Memoirs of the Botanical Survey of South Africa* 57: 1–146.

Adelabu, A.S. 2013. The remote sensing of insect defoliation in mopane woodland. PhD Thesis. College of Agriculture, Engineering and Science, University of KwaZulu-Natal, Pietermaritzburg.

Agrawal, A.A. & Spiller, D.A. 2004. Polymorphic buttonwood: Effects of disturbance on resistance to herbivores in green and silver morphs of abahamian shrub. *American Journal of Botany* 91: 1990–1997.

Anderson, G.D. & Walker, B.H. 1974. Vegetation composition and elephant damage in the Sengwa Wildlife Research Area, Rhodesia. *Journal of the South African Wildlife Management Association* 4: 1–14.

Ansell, W.F.H. 1972. Family Artiodactyla. In: Meesterand, J. & Setzer, H.W. (Eds). The Mammals of Africa: An Identification Manual. Smithsonian Institution Press, Washington D.C. pp. 1–84.

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

Bailey, E.M. 1978. Physiologic response of livestock to toxic plants. *Journal of Range Management* 31: 343–347.

Barber, N.A. & Marquis, R.J. 2011. Leaf quality, predators, and stochastic processes in the assembly of a diverse herbivore community. *Ecology* 92: 699–708.

Ben-Shahar, R. 1993. Patterns of elephant damage to vegetation in northern Botswana. *Biological Conservation* 65: 249–256.

Ben-Shahar, R. & MacDonald, D.W. 2002. The role of soil factors and leaf protein in the utilization of mopane plants by elephants in northern Botswana. *BMC Ecology* 2(3): 1–6.

Bergström, R., Skappe, C. & Danell, K. 2000. Plant responses and herbivory following simulated browsing and stem cutting of *Combretum apiculatum*. *Journal of Vegetation Science* 11: 409–414.

Bonsma, J.C. 1942. Useful Bushveld Trees and Shrubs: Their Value to the Stock Farmer. *Farming in South Africa* 17: 226–239.

Bonsma, J.C & Du Toit, J.D. 2010. Game Ranch Management. 5th Edition. Van Schaik Publishers, Pretoria.

Boomker, E.A. 1987. Fermentation and digestion in the kudu. D.Sc. Thesis. University of Pretoria, Pretoria.

Brophy, J.J., Boland, D.J. & Van Der Lingen, S. 1992. Essential oils in the leaf, bark and seed of mopane (*Colophospermum mopane*). *South African Forestry Journal* 161: 23–25.

Bryant, J.P., Kuropat, P.J., Reichardt, P.B. & Clausen, T.P. 1991. Controls over the allocation of resources by woody plants to chemical antiherbivore defense. In: Palo, R.T. & Robbins, C.T. (Eds). Plant Defense against Mammalian Herbovory. CRC Press, London. pp. 83–102.

Burke, A. 2006. Savanna trees in Namibia–Factors controlling their distribution at the arid end of the spectrum. *Flora* 201: 189–201.

Chagonda, L.S., Makanda, C. & Chalchat, J.C. 2011. Essential oils of four wild and semi-wild plants from Zimbabwe: *Colophospermum mopane* (Kirk ex Benth.) Kirk ex Léonard, *Helichrysum splendidum* (Thunb.) Less, *Myrothamnus flabellifolia* (Welw.) and *Tagetes minuta* L. *Journal of Essential Oil Research* 11: 573–578.

Chaturvedi, R.K. & Raghubanshi, A.S. 2016. Leaf life-span dynamics of woody species in tropical dry forests of India. *International Journal of Tropical Plant Research* 3: 199–212.

Chen, H. & Jianga, J. 2010. Osmotic adjustment and plant adaptation to environmental changes related to drought and salinity. *Environmental Reviews* 18: 309–319.

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

Chidumayo, E. & Frost, P. 1996. Population biology of miombo trees. In: Campbell, B. (Ed.). The Miombo in Transition: Woodlands and Welfare in Africa. Center for International Forestry Research, Malaysia. pp. 56–72.

Childes, S.U. 1989. Phenology of nine common woody species in semi-arid, deciduous Kalahari sand vegetation. *Plant Ecology* 79: 151–163.

Choinski, J.S. Jr. & Tuohy, J.M. 1991. Effect of water potential and temperature on the germination of four species of African savanna trees. *Annals of Botany* 68: 227–233.

CICA. 1996. Africa’s shrinking savannas. Centro Informatico Cientifico de Andalucia (CICA). http://www.ibiblio.org/london/agriculture/forums/sustainable-agriculture2/msg00402.html [Accessed: 26 March 2017].

Cleland, E.E., Chuine, I., Menzel, A., Mooney, H.A. & Schwartz, M.D. 2007. Shifting plant phenology in response to global change. *Trends in Ecology and Evolution* 22: 357–365.

Codron, D. 2006. The ecological and evolutionary significance of browsing and grazing in savanna ungulates. PhD Thesis. University of Cape Town, Cape Town.

Codron, D., Lee-Thorp, J.A., Sponheimer, M. & Codron, J. 2007. Nutritional content of savanna plant foods: Implications for browser/grazer models of ungulate diversification. *European Journal of Wildlife Research* 53: 100–111.

Coe, K.H. 1991. Effects of thinning on *Colophospermum mopane* in an indigenous woodland setting. *Journal of Forestry Association of Botswana* 9: 47–57.

Cole, M.M. 1986. The savannas: Biogeography and Geobotany. Academic Press, London.

Coley, P.D. 1988. Effects of plant growth rate and leaf lifetime on the amount and type of anti-herbivore defense. *Oecologia* 74: 531–536.

Cooper, S.M. 1985. Factors influencing the utilization of woody plants and forbs by ungulates. PhD. Thesis. University of the Witwatersrand, Johannesburg.

Cooper, S. & Owen-Smith, N. 1985. Condensed tannins deter feeding by browsing ruminants in a South African savanna. *Oecologia* 67:142–146.

Cooper, S.M. & Owen-Smith, N. 1986. Effects of plant spinescence on large mammalian herbivores. *Oecologia* 68: 446–455.

Cooper, S.M., Owen-Smith, N. & Bryant, J.P. 1988. Foliage acceptability to browsing ruminants in relation to seasonal changes in the leaf chemistry of woody plants in a South African savanna. *Oecologia* 75: 336–342.

Cornelissen, J.H.C., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., Ter Steege, H., Morgan, H.D., Van der Heijden, M.G.A., Pausas, J.G. & Poorter, H. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51: 335–380.

Curlewis, B.J. 2014. The seasonal feeding composition of kudu (*Tragelaphus strepsiceros*) and movement of kudu, eland and nyala in the mopani veld of the Limpopo Province. PhD Thesis. University of Limpopo, Mankweng.

Dekker, B. 1996. Ecological separation of large herbivores of the Messina Experimental Farm, Limpopo Valley. MSc Dissertation. University of Pretoria, Pretoria.

Dekker, B. & Smit, G.N. 1996. Browse production and leaf phenology of some trees and shrubs in different C*olophospermum* mopane savanna communities. *African Journal of Range & Forest Science* 13: 15–23.

DHV. 1979. Countrywide animal and range assessment project. Volume 5. Government of Botswana, Gaborone.

Do, F.C., Goudiaby, V.A., Gimenez, O., Diagne, A.L., Mayecor, D., Rocheteau, A. & Akpo, L.E. 2005. Environmental influence on canopy phenology in the dry tropics. *Forest Ecology and Management* 215: 319–328.

Dreyer, J.J. & Wehmeyer, A.S. 1982. On the nutritional value of mopane worms. *South African Journal of Science* 78: 33–35.

Du Plessis, F. 2001. A phytosociological synthesis of mopaneveld. MSc Dissertation. University of Pretoria, Pretoria.

Du Toit, J.T. 1988. Patterns of resource use within the browsing ruminant guild in the Central Kruger National Park. PhD Thesis. University of the Witwatersrand, Johannesburg.

Du Toit, J.T. 2003. Large herbivores and savanna heterogeneity. In: Du Toit, J.T., Rogers, K.H. & Biggs, H.C. (Eds). The Kruger experience. Island Press, Washington DC. pp. 292–309.

Du Toit, J.T., Bryant, J. & Frisby, K. 1990. Regrowth and palatability of *Acacia* shoots following pruning by African savanna browsers. *Ecology* 71: 149–154.

Dye, P.J. & Walker, B.H. 1980. Vegetation-environment relations on sodic soils of Zimbabwe Rhodesia. *The Journal of Ecology* 68: 589–606.

Erkkilä, A. & Siiskonen, H. 1992. Forestry in Namibia. Silve Carelica 20. Faculty of Forestry, University of Joensuu, Finland.

FAO. 2004. Protein sources for the animal feed industry. Expert Consultation and Workshop, Bangkok, 29 April – 3 May 2002. Food and Agriculture Organization of the United Nations, Rome.

February, E.C., Higgins, S.I., Newton, R. & West, A.G. 2007. Tree distribution on a steep environmental gradient in an arid savanna. *Journal of Biogeography* 34: 270–278.

Ferrar, A.A. & Walker, B.H. 1974. An analysis of herbivore/habitat relationships in Kyle National Park, Rhodesia. *Journal of Southern African Wildlife Management Association* 4: 137–147.

Ferwerda, J.D. 2005. Charting the quality of forage: Measuring and mapping the variation of chemical components in foliage with hyperspectral remote sensing. PhD Thesis. International Institute for Geo-information Science and Earth Observation, Wageningen University, Netherlands.

Ferwerda, J.D., Van Wieren, S.E., Skidmore, A.K. & Prins, H.H.T. 2005. Inducing condensed tannin production in *Colophospermum mopane*: Absence of response to soil N and P fertility and physical damage. *Plant and Soil* 273: 203–209.

Fox, S.C., Hoffman, M.T. & Hoare, D. 2005. The phenological pattern of vegetation in Namaqualand, South Africa and its climatic correlates using NOAA-AVHRR NDVI data. *South African Geographical Journal* 87: 85–94.

Fritz, H. & Duncan, P. 1994. On the carrying capacity for large ungulates of African savanna ecosystems. *Proceedings: Biological Sciences* 256: 77–82.

Fuller, D.O. 1999. Canopy phenology of some mopane and miombo woodlands in eastern Zambia. *Global Ecology and Biogeography* 8: 199–209.

Furstenburg, D. 2005. The kudu. In: Bonsma, J. & Van Rooyen, N. (Eds). Intensive Wildlife Production in Southern Africa. Van Schaik Publishers, Pretoria.

Furstenburg, D. 2010. The kudu *Tragelaphus strepsiceros* (Pallas, 1766). ARC-Range & Forage Institute: Grootfontein. http://gadi.agric.za/articles/Furstenburg_D/kudu.php [Accessed: 20 October 2014].

Gandiwa, E. & Kativu, S. 2009. Influence of fire frequency on *Colophospermum mopane* and *Combretum apiculatum* woodland structure and composition in northern Gonarezhou National Park, Zimbabwe. *Koedoe* 51: 36–48.

Ghazoul, J. 2006. Mopane woodlands and the mopane worm: Enhancing rural livelihoods and resource sustainability. Final Technical Report, DFID Project Reference Number R 7822. pp. 1–6.

Giesecke, D. & Van Gylswyk, N.O. 1975. A study of feeding types and certain rumen functions in six species of South African wild ruminants. *Journal of Agricultural Science* 85: 75–83.

Ginane, C., Duncan, A.J., Young, S.A., Elston, D.A. & Gordon, I.J. 2005. Herbivore diet selection in response to simulated variation in nutrient rewards and plant secondary compounds. *Animal Behaviour* 69: 541–550.

Gordon, I.J. & Illius, A.W. 1996. The nutritional ecology of African ruminants: A reinterpretation. *Journal of Animal Ecology* 65: 18–28.

Guy, P., Mahlangu, Z. & Charidza, H. 1979. Phenology of some trees and shrubs in Sengwa wildlife research area, Zimbabwe. *South African Journal of Wildlife Research* 9: 47–54.

Hagerman, A.E. 2011. Tannin Handbook. http://www.users.muohio.edu/hagermae/ [Accessed: 26 March 2017].

Hart, S. 2008. Meat goat nutrition. Proceedings of the 23rd Annual Goat Field Day, Langston University, Langston, United States of America.

Hartmann, T. 1991. Alkaloids. In: Rosenthal, G.A. & Berenbaum, M.R. (Eds). Herbivores: Their Interaction with Secondary Plant Metabolites. Academic Press, San Diego. pp. 33–85.

Harty, A. 2014. Importance of calcium and phosphorus in the ruminant diet. http://igrow.org/livestock/b.eef/importance-of-calcium-and-phosphorus-in-the-ruminant-diet/. [Accessed on: 23 April 2017].

Haugaasen, T. & Peres, C.A. 2005. Tree phenology in adjacent Amazonian flooded and unflooded forests. *Biotropica* 37: 620–630.

Havenga, L. 2014. Tannins: A review. Virbac Animal Health. http://landbou.com/wp-content/uploads/2014/03/cd54368e-8fd2-40e7-9988-e638a3697c6b.pdf. [Accessed on: 25 April 2016].

Hendrix, S.D. 1988. Herbivory and its impact on plant reproduction. In: Lovett-Doust, J. & Lovett-Doust, L. (Eds). Plant Reproductive Ecology: Patterns and Strategies. Oxford University Press, Oxford. pp. 246–263.

Henning, A.C. 1976. A study of edaphic factors influencing the growth of *Colophospermum mopane* (Kirk ex Benth.) Kirk ex J. Léonard. PhD Thesis. University of the Witwatersrand, Johannesburg.

Herremans-Tonnoeyr, D. & Herremans, M. 1995. Birds feeding on protective capsules of mopane psyllids. *Babbler* 29/30: 1949–1955.

Hester, A.J., Bergman, M., Iason, G.R. & Moen, J. 2006. Impacts of large herbivores on plant community structure and dynamics. In: Danell, K., Bergström, R., Duncan, P. & Pastor, J. (Eds). *Large Herbivore Ecology, Ecosystem Dynamics and Conservation.* Cambridge University Press, Cambridge. pp. 97–141.

Hofmann, R.R. & Stewart, D.R.M. 1972. Grazer or browser: A classification based on stomach structure and feeding habits of East African ruminants. *Mammalia* 36: 226–240.

Holá, M. 2012. Spatial and temporal variation in the quality of summer foods for herbivores along a latitudinal gradient. MSc Thesis. Swedish University of Agricultural Sciences, Uppsala, Sweden.

Hooimeijer, J.P., Jansen, F.A., De Boer, W.F., Wessels, D.C.J., Van Der Waal, C., De Jong, C.B., Otto, N.D. & Knoop, L. 2005. The diet of kudus in a mopane dominated area, South Africa. *Koedoe* 48: 93–102.

Hrabar, H.D.N.K. 2005. Indirect interaction between elephant (*Loxodonta africana*) and mopane caterpillars (*Imbrasia belina*) through their shared food resource - mopane trees (*Colophospermum mopane*). PhD Thesis. University of Pretoria, Pretoria.

Hrabar, H., Hattas, D. & Du Toit, J.T. 2009. Differential effects of defoliation by mopane caterpillars and pruning by African elephants on the regrowth of *Colophospermum mopane* foliage. *Journal of Tropical Ecology* 25: 301–309.

Hsiao, T.C., Acevedo, E., Fereres, E. & Henderson, D.W. 1976. Water stress, growth, and osmotic adjustment. *Philosophical Transactions of Royal the Society: Biological Sciences* 273: 479–500.

IPCC. 2007. Climate Change 2007: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge.

IUCN SSC Antelope Specialist Group. 2008. *Tragelaphus strepsiceros*. IUCN Red List of Threatened Species. Version 2013.2. http://www.iucnredlist.org/details/22055/0 [Accessed: 23 April 2017].

Janecke, B.B. & Smit, G.N. 2011. Phenology of woody plants in riverine thicket and its impact on browse availability to game species. *African Journal of Range & Forage Science* 28: 139–148.

Jeltsch, F., Weber, G.E. & Grimm, V. 2000. Ecological buffering mechanisms in savanna: A unifying theory of long-term tree-grass coexistence. *Plant Ecology* 150: 161–171.

Jin, C., Xiao, X., Merbold, L., Arneth, A., Veenendaal, E. & Kutsch, W.L. 2013. Phenology and gross primary production of two dominant savanna woodland ecosystems in Southern Africa. *Remote Sensing of Environment* 135: 189–201.

Johnson, J.M., Pritchard, J., Gorham, J. & Tomos, A.D. 1996. Growth, water relations and solute accumulation in osmotically stressed seedlings of the tropical tree *Colophospermum mopane*. *Tree Physiology* 16: 713–718.

Jordaan, A. & Wessels, D.C.J. 1999. The aril of *Colophospermum mopane*. Its role during seed germination and fruit opening. *South African Journal of Botany* 65: 392–397.

Kasale, F. 2013. Determination of nutritive values of browsable plants utilised by cattle during the dry season in Sibbinda Constituency of Zambezi region – Namibia. MSc Dissertation. University of Namibia, Windhoek.

Kelso, D.L. 1987. Resource partitioning between browsing ungulates: Kudu (*Tragelaphus strepsiceros*) and eland (*Taurotragus oryx*) in Pilansberg National Park, Boputhatswana. MSc dissertation. University of the Witwatersrand, Johannesburg.

Kennedy, A.D. 2000. Wildfire reduces elephant herbivory on *Colophospermum mopane* (Fabaceae). *African Journal of Ecology* 38: 175–177.

Kennedy, A.D. & Potgieter, A.L.F. 2003. Fire season affects size and architecture of *Colophospermum mopane* in southern African savannas. *Plant Ecology* 167: 179–192.

Kohi, E.M., De Boer, W.F., Slot, M., Van Wieren, S.E., Ferwerda, J.G., Grant, R.C., Heitkönig, I.M.A., De Knegt, H.J., Knox, N., Van Langevelde, F., Peel, M., Slotow, R., Van Der Waal, C. & Prins, H.H.T. 2010. Effects of simulated browsing on growth and leaf chemical properties in *Colophospermum mopane* saplings. *African Journal of Ecology* 48: 190–196.

Kos, M., Hoetmer, A.J., Pretorius, Y., De Boer, W.F., De Knegt, H., Grant, C.C., Kohi, E., Page, B., Peel, M., Slotow, R., Van Der Waal, C., Van Wieren, S.E., Prins, H.H.T. & Van Langevelde, F. 2012. Seasonal diet changes in elephant and impala in mopane woodland. *European Journal of Wildlife Research* 58: 279–287.

Kreber, R.A. & Einhellig, F.A. 1977. Effects of tannic acid on *Drosophila* larval salivary gland cells. *Journal of Insect Physiology* 18: 1089–1096.

LEDET. 2012–2017. Five-year strategic plan for Musina Nature Reserve. Limpopo Economic Development, Environment and Tourism (LEDET), Polokwane, Limpopo Province, South Africa. http://www.ncc-group.co.za/sites/default/files/u66/Musina%20NR%20-%20DSP_0.pdf [Accessed: 27 March 2017].

Léonard, J. 1949. *Colophospermum.* Notulae Systematicae IV (Caesalpiniaceae - Amherstieae Africanae Americanaeque). *Bulletin du Jardin Botanique de Létat* (*Bruxelles*) 19: 388–408.

Lewis, D.M. 1991. Observations on tree growth, woodland structure and elephant damage on *Colophospermum mopane* in Luangwa Valley, Zambia. *African Journal of Ecology* 24: 227–241.

Liengme, C.A. 1983. A study of wood use for fuel and building in an area of Gazankulu. *Bothalia* 14: 245-257.

Low, A.B. & Rebelo, A.G. 1996. Vegetation of South Africa, Lesotho and Swaziland. Department of Environmental Affairs and Tourism, Pretoria, Pretoria.

Lukhele, M.S. 2002. The chemical composition and nutritive value of leaves of indigenous fodder trees. MSc Dissertation. University of Pretoria, Pretoria.

Lukhele, M.S. & Van Ryssen, J.B.J. 2000. The chemical composition of leaves from indigenous fodder trees in South Africa. *South African Journal of Animal Science* 30: 72–73.

Lundberg, J.O., Carlström, M., Larsen, F.J. & Weitzberg, E. 2011. Roles of dietary inorganic nitrate in cardiovascular health and disease. *Cardiovascular Research* 89: 525–532.

Lundberg, P. & Åström, M. 1990. Low nutritive quality as a defense against optimally foraging herbivores. *American Naturalist* 135: 547–561.

Lundu, T. 2012. The effect of soil and plant seasonal mineral variations on goat plasma mineral status in Siavonga District of Southern Province of Zambia. MSc Dissertation. University of Zambia, Lusaka.

Luoga, E.J., Witkowski, E.T.F. & Balkwill, K. 2004. Regeneration by coppicing (resprouting) of miombo (African savanna) trees in relation to land use. *Forestry Ecology and Management* 189: 23–36.

Macala, J., Sebolai, B. & Majinda, R.R. 1992. *Colophospermum mopane* browse plant and sorghum stover as feed resources for ruminant during the dry season in Botswana. In: Stares, J.E.S., Said, A.N. & Kategile, J.A. (Eds). The Complementarity of Feed Resources for Animal Production in Africa. Proceedings of the joint feed resources networks workshop held in Gaborone, Botswana 4-8 March 1991. African Feeds Research Network. International Livestock Centre for Africa, Addis Ababa, Ethiopia.

MacPherson, A. 2000. Trace minerals status of forages. In: Givens, D.I., Owen, E., Oxford, R.F.E. & Omed, H.M. (Eds). *Forage Evaluation in Ruminant Nutrition*. CAB International, Wallingford. pp. 345–371.

Madams, R.W. 1990. The biogeography of *Colophospermum mopane* (Kirk ex Benth.) Kirk ex J. Léonard at its distribution limit in eastern Botswana. PhD Thesis. Queen Mary Westfields College, University of London, London.

Madzibane, J. & Potgieter, M.J. 1999. Uses of *Colophospermum mopane* (Leguminosae-Caesalpinioideae) by the VhaVenda. *South African Journal of Botany* 65: 440–443.

Madzimure, J., Nyahangare, E.T., Hamudikuwanda, H., Hove, T., Belmain, S.R., Stevenson, P.C. & Mvumi, B.M. 2013. Efficacy of *Strychnos spinosa* (Lam.) and *Solanum incanum* L. aqueous fruit extracts against cattle ticks. *Tropical Animal Health and Production* 45:1341–1347.

Makhado, R.A. 2008. Mopane wood utilisation and management perceptions of rural inhabitants in the Greater Giyani Municipality, Limpopo Province. MSc Dissertation. University of Limpopo, Mankweng.

Makhado, R.A., Mapaure, I., Potgieter, M.J., Luus-Powell, W.J. & Saidi, A.T. 2014. Factors influencing the adaptation and distribution of *Colophospermum mopane* in southern Africa's mopane savannas – A review. *Bothalia* 44(1). doi: 10.4102/abc.v44i1.152.

Makhado, R.A., Potgieter, M.J., Luus-Powell, W.J., Cooper, S.M., Oppong, C.K., Kopij, G., Mutisi, C. & Makhabu, S.W. 2016. *Tragelaphus strepsiceros* browse during the dry season in the mopani veld of Limpopo Province, South Africa. *Transactions of the Royal Society of South Africa.* 71:17–21.

Makhado, R.A., Von Maltitz, G.P., Potgieter, M.J. & Wessels, D.C.J. 2009. Contribution of mopane woodland products to rural livelihoods in the northeast of Limpopo Province, South Africa. *South African Geographical Journal* 91: 46–53.

Mantlana, K.B. 2002. What determine the structure of *Colophospermum mopane* under field conditions in North-Western Botswana. MSc Dissertation. University of Natal, Durban.

Mapaure, I. 1994. The distribution of *Colophospermum mopane* (Leguminosae-Caesalpinioideae) in Africa. *Kirkia* 15: 1–5.

Mapaure, I. 2013. Short-term responses of shrub layer communities to dry season fires and tree thinning in semi-arid miombo woodlands of north-western Zimbabwe. *African Journal of Plant Science* 7: 413–425.

Marais, R. 1995. A study of the ecology of the sable (*Hippotragus niger niger*, Harris 1838) to Messina Nature Reserve with special reference to the use of plants during the different seasons, as well as the optimum carrying capacity of the reserve related to sable. Deptment of Environmental Matters and Tourism, Northern Transvaal.

Mashabane, L.G., Wessels, D.C.J. & Potgieter, M.J. 2001. The utilization of *Colophospermum mopane* by the Vatsonga in the Gazankulu region (eastern Northern Province). *South African Journal of Botany* 67: 199–205.

Mazid, M., Khan, T.A. & Mohammad, F. 2011. Role of secondary metabolites in defense mechanisms of plants. *Biology and Medicine* 3: 232–249.

McDowell, L.R. & Valle, G. 2000. Major minerals in forage. In: Givens, D.I., Owen, E., Oxford, R.F.E. & Omed, H.M. (Eds). *Forage Evaluation in Ruminant Nutrition*. CAB International, Wallingford. pp. 373–397.

Menzel, A. 2002. Phenology: Its importance to the global change community. *Climatic Change* 54: 379–385.

Messina, F.J., Durham, S.L., Richards, J.H. & McArther, E.D. 2002. Trade-off between plant growth and defence? A comparison of sagebrush populations. *Oecologia* 131: 43–51.

Mlambo, D. 2006. Influence of soil fertility on the physiognomy of the African savanna tree *Colophospermum mopane*. *African Journal of Ecology* 45: 109–111.

Mlambo, D., Nyathi, P. & Mapaure, I. 2005. Influence of *Colophospermum mopane* on surface soil properties and understorey vegetation in a southern African savanna. *Forest Ecology and Management* 212: 394–404.

Mlambo, D. & Mapaure, I. 2006. Post-fire resprouting of *Colophospermum mopane* saplings in a southern African savanna. *Journal of Tropical Ecology* 22: 231–234.

Mlambo, D. & Nyathi, P. 2008. Litterfall and nutrient return in a semi-arid southern African savanna woodland dominated by *Colophospermum mopane. Plant Ecology* 196: 101–110.

Montagne, L., Pluske, J.R. & Hampson, D.J. 2003. A review of interactions between dietary fibre and the intestinal mucosa, and their consequences on digestive health in young non-ruminant animals. *Animal Feed, Science and Technology* 108: 95–117.

Morris, S., Humphreys, D. & Reynolds, D. 2006. Myth, marula, and elephant: An assessment of voluntary ethanol intoxication of the African elephant (*Loxodonta africana*) following feeding on the fruit of the marula tree (*Sclerocarya birrea*). *Physiological and Biochemical Zoology* 79: 363–369.

Mosimanyana, B.M. & Kiflewahid, B. 1988. Value of browse as ruminant feed: The case of *Colophospermum mopane*. Ministry of Agriculture, Gaborone.

Mucina, L. & Rutherford, M.C (Eds). 2006. The Vegetation of South Africa, Lesotho and Swaziland. *Strelitzia* 19, South African National Biodiversity Institute, Pretoria.

Muposhi, V.K., Gandiwa, E., Chemura, A., Bartels, P., Makuza, S.M. & Madiri, T.H. 2016. Habitat heterogeneity variably influences habitat selection by wild herbivores in a semi-arid tropical savanna ecosystem. *PLoS ONE* 11(9): e0163084. doi:10.1371/journal.pone.0163084.

Mushove, P.T. 1992. Productivity from mopane stumps and seed. *Format* 4: 4.

Mushove, P.T. & Makoni, J.T. 1993. Coppicing ability of *Colophospermum mopane*. In: Piearce, G.D. & Gumbo, D.J. (Eds). The Ecology and Management of Indigenous Forest in southern Africa. Proceedings of an International Symposium, 27-29 July 1992, Victoria Falls, Zimbabwe. The Forestry Commission Harare, Zimbabwe. pp. 226–230.

Mutakela, P.S. 2009. Biomass prediction models for *Colophospermum mopane* (mopane) in Botswana. MSc Dissertation. University of Stellenbosch, Stellenbosch.

Myre, M. & Coutinho, L.P. 1962. Tree and shrub forage, “mopane”. *Anais dos Servicos de Veterinária* 10: 1-11.

O'Connor, T.G. 1992. Woody vegetation-environment relations in semi-arid savanna in the Northern Transvaal. *South Africa Journal of Botany* 58: 268–272.

Odenyo, A.A., Osuji, P.O., Karanfil, O. & Adinew, K. 1997. Microbiological evaluation of *Acacia angustissima* as a protein supplement for sheep. *Animal Feed, Science and Technology* 65: 99–102.

Okitsu, S. 2004. The vegetation of Africa. In: Mizuno, K. (Ed.). *Natural History of Africa*. Kokon-Syoin, Tokyo. pp. 25–34.

Okitsu, S. 2005. Factors controlling geographical distribution in savanna vegetation in Namibia. *African Study Monographs* 30: 135–151.

Ormsbee, M.J., Bach, C.W. & Baur, D.A. 2014. Pre-exercise nutrition: The role of macronutrients, modified starches and supplements on metabolism and endurance performance. *Nutrients* 6: 1782–1808.

Owen-Smith, N. 1979. Assessing the foraging efficiency of a large herbivore, the kudu. *South African Journal of Wildlife Research* 9: 102–110.

Owen-Smith, N. 1993. Evaluating optimal diet models for an African browsing ruminant, the kudu: How constraining are the assumed constraints? *Evolutionary Ecology* 7: 499–524.

Owen-Smith, N. 1994. Foraging responses of kudu to seasonal changes in food resources elasticity in constraints. *Ecology* 75: 1050–1062.

Owen-Smith, N. 2000. Modeling the population dynamics of a subtropical ungulate in a variable environment: Rain, cold and predators. *Natural Resource Modelling* 13: 57–87.

Owen-Smith, N. 2002. *Adaptive Herbivore Ecology: From Resources to Populations in Variable Environments*. Cambridge University Press, Cambridge.

Owen-Smith, N. 2007. The comparative population dynamics of browsing and grazing ungulates. In: Gordon, I.J. & Prins, H.H.T. (Eds). *The Ecology of Browsing and Grazing*. Springer, Berlin. pp. 149–177.

Owen-Smith, N. & Cooper, S.M. 1983. Aspects of feeding ecology of a browsing ruminant: the kudu. *South African Journal of Animal Science* 13: 35–38.

Owen-Smith, N. & Cooper, S.M. 1987. Palatability of woody plants to browsing ruminants in a South African savanna. *Ecology* 68: 319–331.

Owen-Smith, N. & Cooper, S.M. 1989. Nutritional ecology of a browsing ruminant the kudu (*Tragelaphus strepsiceros*), through the seasonal cycle. *Journal of Zoology* 219: 29–43.

Owen-Smith, N., Fryxell, J.M. & Merrill, E.H. 2010. Foraging theory upscaled: The behavioural ecology of herbivore movement. *Philosophical Transactions of the Royal Society in Biological Sciences* 365: 2267–2278.

Owen-Smith, N., Mason, D.R. & Ogutu, J.O. 2005. Correlates of survival rates for 10 African ungulate populations: Density, rainfall and predation. *Journal of Animal Ecology* 74: 774–788.

Petersson, J., Phillipson, M., Jansson, E.A., Patzak, A., Lundberg, J.O. & Holm, L. 2007. Dietary nitrate increases gastric mucosal blood flow and mucosal defense. *American Journal of Physiology − Gastrointestinal and Liver Physiology* 292(3): G718–G724.

Pienaar, U.D.V. 1974. Habitat-preference in South Africa antelope species and its significance in natural and artificial distribution patterns. *Koedoe* 17: 185–195.

Pohl, H.R., Wheeler, J.S. & Murray, H.E. 2013. Sodium and potassium in health and disease. *Metal Ions in Life Sciences* 13: 29–47.

Pooley, E. 1998. *A field guide to wild flowers KwaZulu-Natal and the Eastern Region*. Natal Flora Publications Trust, Durban.

Porter, R.N. 1968. The distribution and ecology of *Colophospermum mopane*. B.Sc. Honours Dissertation. University of Pretoria, Pretoria.

Potgieter, M.J. & Wessels, D.C.J. 1998. The anatomy and morphology of petioles and leaflets of *Hardwickia mopane* (Leguminosae: Caesalpinioideae). *South African Journal of Botany* 64: 281–289.

Prior, J.A.B. 1991. The improved productivity of African fuelwoods by the use of trees with stress-induced adaptations. Final Report of Southern Africa Wood Studies Project, London, UK.

Prior, J. & Cutler, D. 1992. Trees to fuel Africa’s fire. *New Scientist* 1836: 35–39.

Provenza, F.D., Burrit, E.A., Clausen, T.P., Bryant, J.P., Reichardt, P.B. & Distel, R.A. 1990. Conditioned flavor aversion: A mechanism for goats to avoid condensed tannins in blackbrush. *The American Naturalist* 136: 810–828.

Provenza, F.D., Villalba, J.J. & Banner, R.E. 2003. Linking herbivore experience, varied diets, and plant biochemical diversity. *Small Ruminant Research* 49(3): 257–274.

Robbins, C.T. 1983. Wildlife feeding and nutrition. Animal Feeding and Nutrition. A Series of Monographs. Academic Press, New York.

Robbins, C.T., Hanley, T.A., Hagerman, A.E., Hjelford, O., Backer, D.L., Schwartz, C.C. & Mautz, W.W. 1987. Role of tannins in defending plants against ruminants: Reduction in protein availability. *Ecology* 68: 98–107.

Roosendaal, B. 1992. Wildlife nutrition and feeding. http://www.alzu.co.za/img/WNutrition.pdf [Accessed: 26 March 2017].

Ross, J.H. 1977. *Colophospermum*. *Flora of Southern Africa* 16: 16–19.

Rutherford, M.C., Mucina, L., Lötter, M.C., Bredenkamp, G.J., Smit, J.H.L., Scott Shaw, C.R., Hoare, D.B., Goodman, P.S., Bezuidenhout, H., Scott, L., Ellis, F., Powrie, L.W., Siebert, F., Mostert, T.H., Henning, B.J., Venter, C.E., Camp, K.G.T., Siebert, S.J., Matthews, W.S., Burrows, J.E., Dobson, L., Van Rooyen, N., Schmidt, E., Winter, P.J.D., du Preez, P.J., Ward, R.A., Williamson S. & Hurter, P.J.H. 2006. Savanna biome. In: Mucina, L. & Rutherford, M.C. (Eds). The Vegetation of South Africa, Lesotho and Swaziland. *Strelitzia* 19: 439–538. South African National Biodiversity Institute, Pretoria.

SA Weather Services. 1981-2014. Climatic data for Musina area for the period 1981-2014. Macuville Weather Station, South African Weather Services, Pretoria.

SACS (South African Committee for Stratigraphy). 1980. Stratigraphy of South Africa, Part 1 (comp. L.E. Kent). Lithography of the Republic of South Africa, South West Africa/Namibia and the Republics of Bophuthatswana, Transkei and Venda. *Handbook of Geological Survey of South Africa* 8: 1–690.

Sankaran, M. & Anderson, T.M. 2009. Management and restoration in African savanna: Interactions and feedbacks. In: Hobbs, R. & Suding, K. (Eds). *New Models for Ecosystem Dynamics*. Island Press, Washington. pp. 136–155.

Sankaran, M., Hanan, N.P., Scholes, R.J., Ratnam, J., Augustine, D.J., Cade, B.S., Gignoux, J., Higgins, S.I., Le Roux, X., Ludwig, F., Ardo, J., Banyikwa, F., Bronn, A., Bucini, G., Caylor, K.K., Coughenour, M.B., Diouf, A., Ekaya, W., Feral, C.J., February, E.C., Frost, P.G.H., Hiernaux, P., Hrabar, H., Metzger, K.L., Prins, H.H.T., Ringrose, S., Sea, W., Tews, J., Worden, J. & Zambatis, N. 2005. Determinants of woody cover in African savanna. *Nature* 438: 846–849.

Sankaran, M., Ratnam, J. & Hanan, N.P. 2004. Tree grass coexistence in savanna revisited − Insights from an examination of assumptions and mechanisms invoked in existing models. *Ecological Letters* 7: 480–490.

Scholes, R.J. 1990. The regrowth of *Colophospermum mopane* following clearing. *Journal of Grassland Society of Southern Africa* 7: 147–151.

Scholes, R.J. 1997. Savanna. In: Cowling, R.M., Richardson, D.M. & Pierce, S.M. (Eds). *Vegetation of Southern Africa*. Cambridge University Press, Cambridge. pp. 258–277.

Scholes, R.J. & Archer, S.R. 1997. Tree-grass interactions in savanna. *Annual Review of Ecology and Systematics* 28: 517–544.

Scholes, R.J. & Walker, B.K. 1993. *An African savanna: Synthesis of the Nylsvley Study*. Cambridge University Press, Cambridge.

Schroeder, L.A. & Malmer, M. 1980. Dry matter, energy and nitrogen conversion by Lepidoptera and Hymenoptera larvae fed leaves of black cherry. *Oceologia* 45: 63–61.

Sebego R.J.G. 1999. The ecology and distribution limits of C*olophospermum mopane* in southern Africa. *Botswana Notes and Records* 31: 53–72.

Sekhwela, M.B.M. 1989. The nutritive value of mophane bread – Mophane insect secretion (Maphote or Maboti). *Botswana Notes and Records* 20: 151–153.

Seloane, M.Q. 2017. The ecological impact of elephant herbivory on the vegetation of Atherstone Collaborative Nature Researve, Limpopo Province, South Africa. Msc Dissertation. University of Limpopo, Mankweng.

Seydack, A.H.W., Vermeulen, W.J., Knox, N., Govender, N., Smit, I.P.J., Grant, R.C. & MacFadyen, S. 2014. Forage quality for grazing herbivores in a semi-arid savanna system as affected by fire and rainfall (Kruger National Park). Scientific Report Number 03/2014, South African National Parks, Skukuza.

Shackleton, S.E., Shackleton, C.M., Cunningham, T.B., Sullivan, C.A. & Netshiluvi, T.R. 2002. Knowledge on *Scelocarya birrea* subsp. *caffra* with emphasis on its importance as a non-timber forest product in South and southern Africa Part 1:

Taxonomy, ecology and role in rural livelihoods. *Southern African Forestry Journal* 194: 27–41.

Short, H.L., Blair, R.M. & Segelquist, C.A. 1974. Fiber composition and forage digestibility by small ruminants. *Journal of Wildlife Management* 38: 197–209.

Siebert, F. 2012. A phytosociological synthesis of Mopaneveld vegetation at different spatial scales using various classification methods. PhD Thesis. North-West University, Mahikeng.

Skarpe, C. 1991. Impact of grazing in savanna ecosystems. *Ambio* 20: 351–356.

Skarpe, C. 1992. Dynamics of savanna ecosystems. *Journal of Vegetation Science* 3: 293–300.

Skidmore, A.D., Ferwerda, J.G., Mutanga, O., Van Wieren, S.E., Peel, M., Grant, R.C., Prins, H.H.T., Balcika, F.B. & Venusa, V. 2010. Forage quality of savanna − Simultaneously mapping foliar protein and polyphenols for trees and grass using hyperspectral imagery. *Remote Sensing of Environment* 114: 64–72.

Skinner, J.D. & Chimimba, C.T. 2005. *The Mammals of the Southern African Sub-Region*. Cambridge University Press, Cambridge.

Smallie, J.J. & O’Connor, T.G. 2000. Elephant utilization of *Colophospermum mopane*: Possible benefits of hedging. *African Journal of Ecology* 38: 352–359.

Smit, G.N. 2014. BECVOL 3: An expansion of the aboveground biomass quantification model for trees and shrubs to include the wood component. *African Journal of Range & Forage Science* 31: 179–186.

Smit, G.N. 1994. The influence of intensity of tree thinning on mopani veld. PhD Thesis. University of Pretoria, Pretoria.

Smit, G.N. 2001. The influence of tree thinning on the vegetative growth and browse production of *Colophospermum mopane*. *South African Journal of Wildlife Research* 31: 99–114.

Smit, G.N. & Rethman, N.F.G. 1998. Root biomass, depth distribution and relationships with leaf biomass of *Colophospermum mopane*. *South African Journal of Botany* 64: 38–46.

Soetan, K.O., Olaiya, C.O. & Oyewole, O.E. 2010. The importance of mineral elements for humans, domestic animals and plants: A review. *African Journal of Food Science* 4: 200–222.

Stevens, N., Archibald, S.A., Nickless, A., Swemmer, A. & Scholes, R.J. 2016. Evidence for facultative deciduousness in *Colophospermum mopane* in semi-arid African savannas. *Austral Ecology* 41: 87–96.

Stevens, N., Swemmer, A.M., Ezzy, L. & Erasmus, B.F.N. 2014. Investigating potential determinants of the distribution limits of a savanna woody plant: *Colophospermum mopane*. *Journal of Vegetation Science* 25: 363–373.

Stock, W.D., Le Roux, D. & Van Der Heyden, F. 1993. Regrowth and tannin production in woody and succulent Karoo shrubs in response to simulated browsing. *Oecologia* 96: 562–568.

Styles, C.V. 1993. Relationship between herbivores and *Colophospermum mopane* of the Northern Tuli Game Reserve, Botswana. MSc Dissertation. University of Pretoria, Pretoria.

Styles, C.V. 1996. The biological ecology of *Imbrasia belina* (Sturniinae, Saturniidae) with reference to its behaviours, physiology, distribution, population dynamics, impact within mopane veld and utilization within South Africa. In: Gashe, B.A., Leggette, K. & Mpuchane, S.F. (Eds). Proceedings of the 1st Multidisciplinary Symposium on Plane. 18 June 1996. University of Botswana and the Kalahari Conservation Society, Gaborone. pp. 9–13.

Styles, C.V. & Skinner, J.D. 1997. Seasonal variation in the quality of mopane leaves as a source of browse for mammalian herbivores. *African Journal of Ecology* 35: 254–265.

Styles, C.V. & Skinner, J.D. 2000. The influence of large mammalian herbivores on growth form and utilization of mopane trees, *Colophospermum mopane* in Botswana’s Northern Tuli Game Reserve. *African Journal of Ecology* 38: 95–101.

Suttle, N. 2010. Mineral Nutrition of Livestock. 4th Edition. CABI publishing, United Kingdom.

Tanner, J.C. 1988. *Acacia* fruit supplementation of maize stover diets fed to sheep. MSc Dissertation, University of Reading, Reading.

Taylor, A., Lindsey, P. & Davies-Mostert, H. 2016. An assessment of the economic, social and conservation value of the wildlife ranching industry and its potential to support the green economy in South Africa. The Endangered Wildlife Trust, Johannesburg.

Thompson, J.G. 1960. A description of the growth habitats of mopani in relation to soil and climatic conditions. Proceedings of the First Federal Science Congress, 18–22 May. Rhodesia Scientific Association, Salisbury. pp. 181–186.

Tietema, T. 1989. The possibility of management of mopane woodland. SADCC Forestry Sector. Report of the Workshop on Management and Development of Indigenous Forests in the SADCC Region, Lilongwe, Malawi. pp. 263–282.

Tietema, T., Ditlhogo, M., Tibone, C. & Mathalaza, N. 1991. Characteristics of eight firewood species of Botswana. *Biomass and Bioenergy* 1: 41–46.

Tietema, T., Kgathi, D.L. & Merkesdal, E. 1988. Wood production and consumption in Dukwe: A feasibility study for a woodland management and plantation scheme. National Institution for Development Research and Documentation, Gaborone.

Timberlake, J.R. 1995. *Colophospermum mopane.* Annotated bibliography and review. The Zimbabwe Bulletin of Forestry Research No. 11. Forestry Commission of Zimbabwe, Bulawayo.

Timberlake, J.R. & Calvert, G.M. 1993. Preliminary root atlas for Zimbabwe and Zambia. Forest Research Bulletin 10. Zimbabwe Forestry Commission, Harare.

Timberlake, J., Chidumayo, E. & Sawadogo, L. 2010. Distribution and characteristics of African dry forests and woodlands. In: Chidumyo, E.N. & Gumbo, D.J. (Eds). *The Dry Forest and Woodlands of Africa: Managing for Products and Services*. Earthscan, London. pp. 11–42.

Timberlake, J.R., Nobanda, N. & Mapaure, I. 1993. Vegetation surveys of the communal lands - north and west Zimbabwe. *Kirkia* 14: 171–270.

Tolsma, D.J., Ernst, W.H.O., Verweij, R.A. & Vooijs, R. 1987. Seasonal variation of nutrient concentrations in a semi-arid savanna ecosystem in Botswana. *Journal of Ecology* 75: 755–770.

Toms, R. & Thagwana, M. 2005. On the trail of missing mopane worms. *Science in Africa*. January 2005. http://www.scienceinafrica.co.za/2005/january/mopane.htm [Accessed: 22 August 2016].

Van Der Waal, C. 2010. Nutrients in an African Savanna: The consequences of supply heterogeneity for plants and animals. PhD Thesis. Graduate School of Production Ecology and Resource Conservation. Wageningen University, Wageningen.

Van Hoven, W. 1991. Mortalities in kudu (*Tragelaphus strepsiceros*) populations related to chemical defence of trees. *Journal of African Zoology* 105: 141–145.

Van Reenen, D.D., Roering, C., Ashwal, L.D. & De Witt, M.J. 1992. Regional geological setting of the Limpopo Belt. *Precambrian Research* 55: 1–5.

Van Rooyen, J. 2009. Habitat and seasonal effects on the nutrient status of selected roan (*Hippotragus equinus*) and sable antelope (*Hippotragus niger*) populations in South Africa. MSc Dissertation. University of Pretoria, Pretoria.

Van Soest, P.J. 1987. *The Nutritional Ecology of the Ruminant*. Cornell University Press, New York.

Van Soest, P.J. 1994. *Nutritional Ecology of the Ruminant*. 2nd Edition. Cornell University Press, Ithaca, New York.

Van Voorthuizen, E.G. 1976. The mopane tree. *Botswana Notes and Records* 8: 223–230.

Venter, F. & Venter J.A. 1996. *Making the most of Indigenous Trees*. Briza Publications, Pretoria.

Villalba, J.J. & Provenza, F.D. 1999. Nutrient-specific preferences by lambs conditioned with intraruminal infusions of starch, casein and water. *Journal of Animal Sciences* 77: 378–387.

Walker, B.H. 1980. A review of browse and its role in the livestock production in southern Africa. In: Le Houérou, H.N. (Ed.). *Browse in Africa: The current state of knowledge.* International Livestock Centre for Africa, Addis Ababa, Ethiopia. pp. 7–24.

Walker, B.H., Emslie, R.H., Owen-Smith, R.N. & Scholes, R.J. 1987. To cull or not to cull: lessons from a southern African drought. *Journal of Applied Ecology* 24: 381–401.

Warlaw, G.M. & Smith, A.S. 2011. Contemporary nutrition. 8th Edition. McGraw-Hill, New York.

Webb, E.C., Hornsveld, M., Van Niekerk, W.A. & Van Ryssen, J.B.J. 2016. Nutrition of wild ruminants in intensive breeding systems. University of Pretoria, Pretoria.

Werger, M.J.A. & Coetzee, B.J. 1978. The Sudano-Zambezian region. In: Werger, M.J.A. (Ed.). *Biogeography and Ecology of Southern Africa*. W. Junk Publishers, The Hague. pp. 301–453.

Wessels, D. 2002. Management of mopani veld. University of the North, Mankweng. http://r4d.dfid.gov.uk/PDF/Outputs/Forestry/R7822_-_Q2_-_Management_mopane_veld.pdf [Accessed: 28 April 2015].

Wessels, D., Mushongohande, M. & Potgieter, M. 2006. Mopane tree ecology and management. In: Ghazoul, J. (Ed.). Mopane Woodlands and the Mopane Worm: Enhancing Rural Livelihoods and Resource Sustainability. Final Technical Report, DFID Project Reference Number R 7822. pp. 7–17. https://assets.publishing.service.gov.uk/media/57a08c42e5274a31e00010da/R7822-FTR.pdf [Accessed: 22 August 2016].

Wessels, D.C.J., Van der Waal, C. & De Boer, W.F. 2007. Induced chemical defences in *Colophospermum mopane* trees. *African Journal of Range & Forage Science* 24: 141–147.

Wessels, K., Steenkamp, K., Von Maltitz, G. & Archibald, S. 2011. Remotely sensed vegetation phenology for describing and predicting the biomes of South Africa. *Applied Vegetation Science* 14: 49–66.

Westoby, M. 1978. What are the biological bases of varied diets? *American Naturalist* 112: 627–631.

White, F. 1983. *The Vegetation of Africa*. United Nations Educational, Scientific and Cultural Organization, Paris.

White, M.A., Thomton, P.E. & Running, S.W. 1997. A continental phenology model for monitoring vegetation responses to interannual climatic variability. *Global Biogeochemical Cycles* 11: 217–234.

Whitecross, M.A., Witkowski, E.T.F. & Archibald, S. & 2012. Savanna tree-grass interactions: A phenological investigation of green-up in relation to water availability over three seasons. *South African Journal of Botany* 108: 29–40.

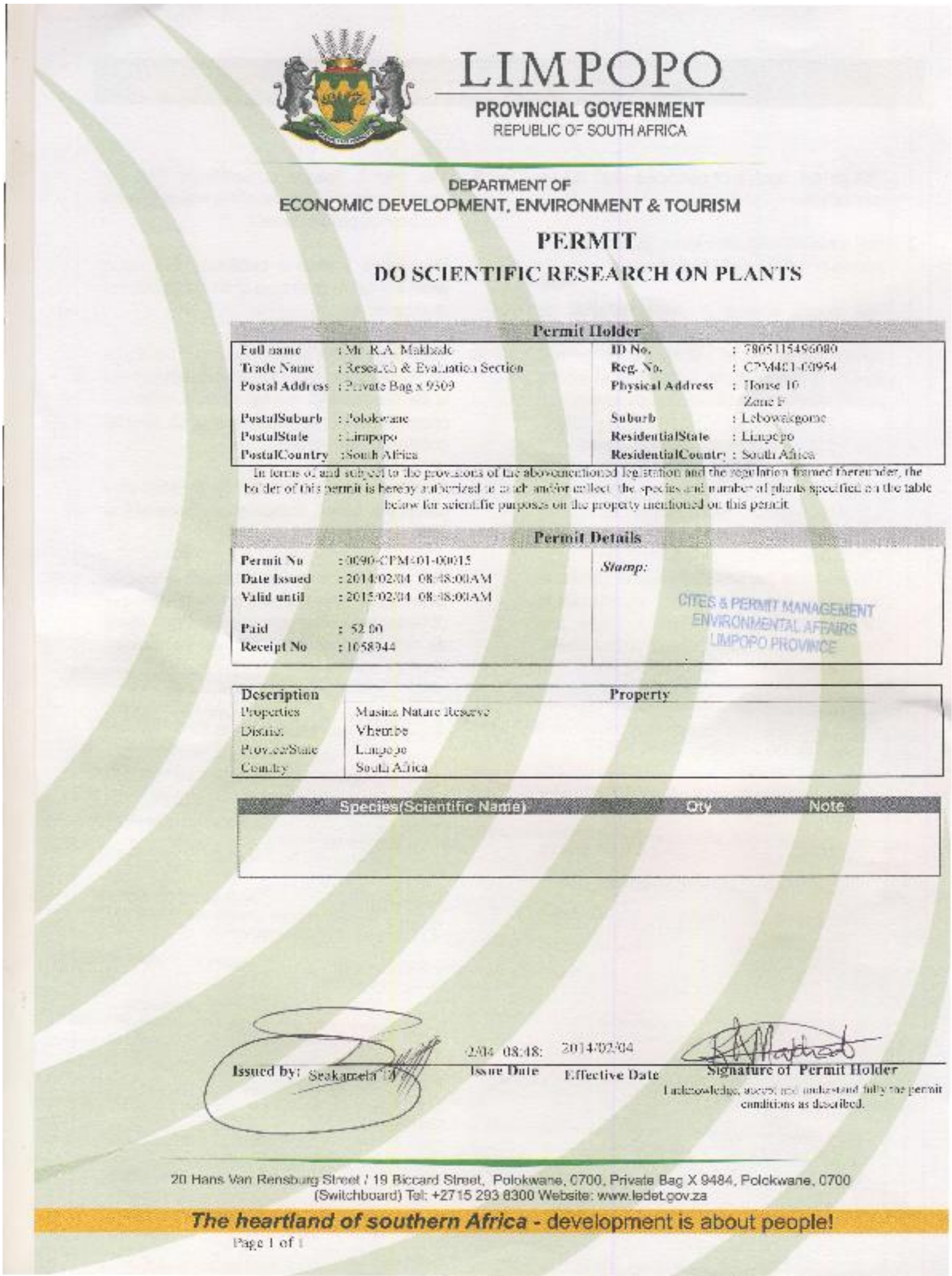
Whitecross, M.A., Archibald, S. & Witkowski, E.T.F. 2012. Do freeze events create a demographic bottleneck for *Colophospermum mopane*? *South African Journal of Botany* 83: 9–18.

Williams, R.J., Myers, B.A., Eamus, D. & Duff, G.A. 1999. Reproductive phenology of woody species in a North Australian tropical savanna. *Biotropica* 31: 626–636.

Woodward, A. & Reed, J.D. 1989. The influence of polyphenolics on the nutritive value of browse. *ILCA Bulletin* 13: 2–11.

World Bank Climate Data for South Africa and Botswana. 1960-1990. Rainfall and Temperature Data for South Africa and Botswana. Climate Change Knowledge Portal. http://data.worldbank.org/country [Accessed: 30 June 2015].

APPENDIX 1: Permit to conduct research at Musina Nature Reserve



LIMPOPO
PROVINCIAL GOVERNMENT
REPUBLIC OF SOUTH AFRICA

DEPARTMENT OF
ECONOMIC DEVELOPMENT, ENVIRONMENT & TOURISM

PERMIT
DO SCIENTIFIC RESEARCH ON PLANTS

Permit Holder

Full name	: Mr R.A. Makhado	**ID No.**	: 7805115496080
Trade Name	: Research & Evaluation Section	**Reg. No.**	: CPM401-00954
Postal Address	: Private Bag x 9309	**Physical Address**	: House 10 Zone F
PostalSuburb	: Polokwane	**Suburb**	: Lebowakgomo
PostalState	: Limpopo	**ResidentialState**	: Limpopo
PostalCountry	: South Africa	**ResidentialCountry**	: South Africa

In terms of and subject to the provisions of the abovementioned legislation and the regulation framed thereunder, the holder of this permit is hereby authorized to catch and/or collect the species and number of plants specified on the table below for scientific purposes on the property mentioned on this permit.

Permit Details

Permit No	: 0090-CPM401-00015	***Stamp:***
Date Issued	: 2014/02/04 08:48:00AM	CITES & PERMIT MANAGEMENT ENVIRONMENTAL AFFAIRS LIMPOPO PROVINCE
Valid until	: 2015/02/04 08:48:00AM	
Paid	: 52.00	
Receipt No	: 1058944	

Description	**Property**
Properties	Musina Nature Reserve
District	Vhembe
Province/State	Limpopo
Country	South Africa

Species(Scientific Name)	Qty	Note

Issued by: Seakamela

2/04 08:48: **Issue Date**

2014/02/04 **Effective Date**

Signature of Permit Holder
I acknowledge, accept and understand fully the permit conditions as described.

20 Hans Van Rensburg Street / 19 Biccard Street, Polokwane, 0700, Private Bag X 9484, Polokwane, 0700
(Switchboard) Tel: +2715 293 8300 Website: www.ledet.gov.za

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