

**Review Paper**

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

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**ABSTRACT**

This is a review of the nutritional value of *Colophospermum mopane* leaves, twigs, pods and seeds and its chemical defence against browsers. This paper showed that *C. mopane* is nutritious and contain crude protein (CP), phosphorus (P), calcium (Ca), crude fibre (CF), energy, fatty acids and essential oil, which are necessary in the diet of herbivores. Despite the nutritional value of *C. mopane*, browsing is mainly during the dry season, when secondary metabolites such as total phenols (TP), condensed tannins (CT) and protein-precipitating tannins (PPT) are relatively low. This paper further showed that the nutritional value and secondary metabolites are high during leaf flush, but declined during the dry season as the leaves matured and aged. The ability of *C. mopane* to produce secondary metabolites is a critical adaptation mechanism in order to defend itself against browsers, especially during the growing season.

**Keywords:** crude protein, leaf quality, nutrition, phenols, tannins, mopani woodland.

**INTRODUCTION**

*Colophospermum mopane* (Benth.) J. Léonard, commonly known as mopane, is a leguminous tree or shrub belonging to the sub-family Caesalpinioideae of the family Fabaceae (Léonard, 1949). Mopane is a dominant tree or shrub within mopane woodland (Henning, 1976; Timberlake, 1995) in the low-lying areas of southern Africa's savanna ecosystem (White, 1983), between latitudes 9°S and 25°S (Werger and Coetzee, 1978). The distribution of mopane 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 (Figure 1). It is estimated that the area under mopane-dominated vegetation covers 550,000 km<sup>2</sup> (Mapaure, 1994).

Mopane is a deciduous species (Henning, 1976), and its leaves are alternate (Ross, 1977) with a single pair of large triangular leaflets resembling a butterfly shape (Henning, 1976; Timberlake, 1995; Sebege, 1999). It flushes the leaves after the first summer rains (Wessels, 2002), usually during October/November (Madams, 1990; Dekker and Smit, 1996). Young mopane leaves are reddish brown and glossy (Timberlake, 1995), and become green when they mature (Werger and Coetzee, 1978). The leaves turn yellowish with the onset of the dry season (Timberlake, 1995), and reddish-brown before they are shed (Werger and Coetzee, 1978). The dry or dead mopane leaves remain on the tree or shrub until they are blown-off by wind, mainly from August to October (Henning, 1976; Guy *et al.*, 1979; Dekker and Smit, 1996). The pods are yellowish brown in colour 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 (Timberlake, 1995), which enables the seeds to be easily dispersed by browsers.

Mopane is highly browsed by the greater kudu (*Tragelaphus strepsiceros*) (Hooimeijer *et al.*, 2005; Curlew, 2014), elephants (*Loxodonta africana*) (Kos *et al.*, 2012), and domestic animals such as cattle (Timberlake, 1995) and goats (Macala *et al.*, 1992). The nutritional value in mopane makes it to be an important dry-season browse for herbivores (Mosimanyana and Kiflewahid, 1988; Macala *et al.*, 1992; Timberlake, 1995; 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 nutritious and provide essential dry season browse (Mosimanyana and Kiflewahid, 1988; Macala *et al.*, 1992; Timberlake, 1995). The minimum value of crude protein in mopane leaves, twigs and pods during September is 8.4%, 4.2% and 8.6%, respectively (Table 1); while grasses contain less than 6% in that month (Timberlake, 1995). This implies that the nutritional value of mopane is generally higher than the grasses (Codron *et al.*, 2007), which makes mopane leaves, twigs, seeds and pods to be highly accepted by browsers in the mopane woodland, especially during the dry season (Timberlake, 1995; Hooimeijer *et al.*, 2005). Browse nutritional value of mopane therefore explain why most of the rangelands, game reserves, and national parks in the southern Africa's savanna are found in the mopani woodland. Most browsers utilise mopane during the dry season, but less favoured during the wet

season, due to the high levels of secondary metabolites such as phenols and tannins (Hooimeijer *et al.*, 2005; Wessels *et al.*, 2007).

Despite the value of mopane in providing nutritional browse to animals in mopane woodland, especially during the dry season (Macala *et al.*, 1992; Hooimeijer *et al.*, 2005), and drought years (Mosimanyana and Kiflewahid, 1988, 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; Voorthuizen, 1976; DHV, 1979; Mosimanyana and 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 and 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 mopani woodland and the browsers it support. As a result, there is a need to extensively review and integrate the available scanty information on mopane quality. Such information is crucial in order to better understand the browsers-plant relationship in the mopani woodland.

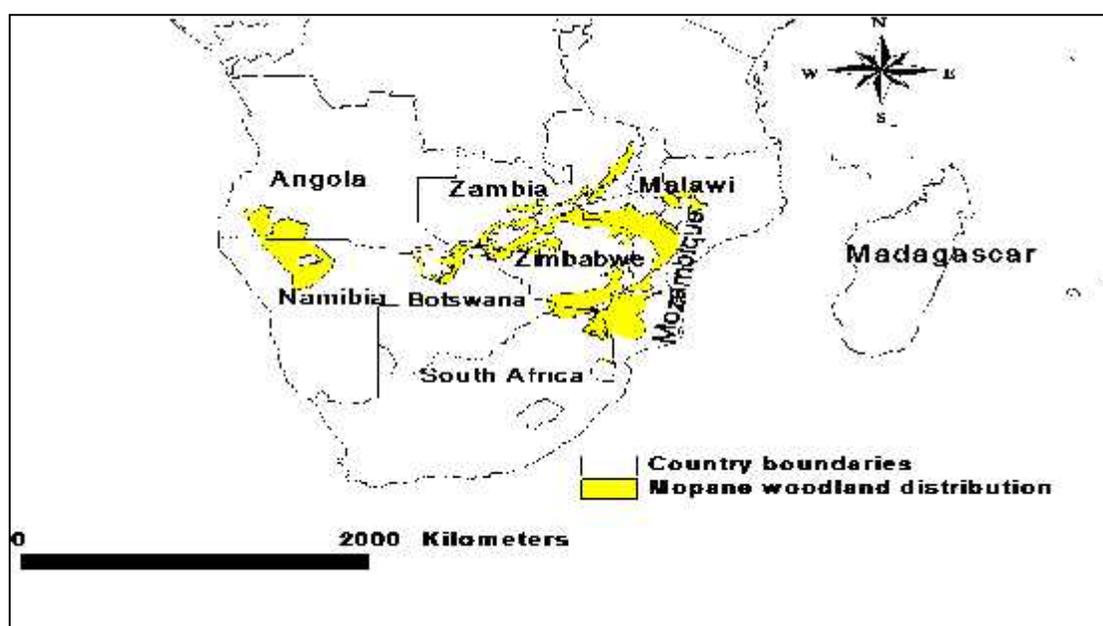


Figure 1: The distribution of mopane woodlands in southern Africa. Source: Makhado *et al.* (2014).

## METHODOLOGY

This paper provides a review of the existing and accessible literature from journal articles, books, conference proceedings and reports that deals with the nutritional value of mopane and its chemical defence against browsers in the low-lying areas of southern Africa's mopane woodland. Secondary data and information on the nutritional value of mopane and its chemical compounds were obtained from studies conducted in Zimbabwe, South Africa and Botswana. Such datasets were consolidated in Tables 1 and 3. The consolidated datasets were analysed further using descriptive statistics. In addition, the effect of rainfall and temperature in triggering the concentration of nutrients and secondary metabolites in mopane was determined using the Pearson Correlation Coefficient Analysis.

**Attractance to browsers – nutritional value:** Mopane is rich in vital nutrients such as crude protein, calcium, phosphorus (Bonsma, 1942; Hooimeijer *et al.*, 2005), and essential fatty acids (Lawton, 1968). The leaves also contain high concentration of energy, which is essential to the diet of browsers (Styles and 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 1), which suggest that the nutrient are relatively constant regardless of the season. However, these nutrients, excluding phosphorus, increased slightly from September and reached 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 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 is also triggered by rainfall (Table 2).

**Table 1.** Annual and seasonal nutritional values of *Colophospermum mopane*. The CP, P, Ca, CF concentration shows no significant variation over the year

Part	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Reference
<b>Leaves</b>													
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	
STDEV	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	0.12	*	*	*	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
<b>Seeds</b>													
CP (%)	*	*	*	19.5	*	*	*	*	*	*	*	*	b
P (%)	*	*	*	0.43	*	*	*	*	*	*	*	*	b
Ca (%)	*	*	*	0.35	*	*	*	*	*	*	*	*	b
<b>Pods</b>													
CP (%)	*	*	*	8.6-15.9	*	*	*	*	*	*	*	*	b, i
P (%)	*	*	*	0.16	*	*	*	*	*	*	*	*	b
Ca (%)	*	*	*	0.82	*	*	*	*	*	*	*	*	b
<b>Twigs</b>													
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 (°C)	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 and Skinner, 1997; g=Voorthuizen, 1976; h=World Bank Climate Data for South Africa and Botswana, 1960-1990; i=Myre and Coutinho, 1962; j=Walker, 1980. **Symbols:** CP=Crude Protein, P=Phosphorus, Ca=Calcium, EN=Energy, MO=Moisture, CF=Crude fibre; AverR=Average Monthly Rainfall; AverT=Average Monthly Temperature; \* =no data.

**Crude protein:** Protein synthesise 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 1), which is vital nutrient in the diet

of the browsers. The average crude protein values in mopane leaves ranged from a minimum of  $9.2\% \pm 2.8\%$  in October to  $13.9\% \pm 2.0\%$  in January. 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 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 implies 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 decline during the winter season. Crude protein values start to decline from its highest level in February until it reached its lowest level in October. High value of crude protein in mopane leaves were observed in November, December and January at  $13.0\pm 5.1\%$ ,  $12.0\pm 0.7\%$  and  $13.9\pm 2.0\%$  on average, respectively (Table

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 (Table 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 2). Table 2 shows a positive correlation between leaf quality and climatic variables, especially rainfall, which suggest that rainfall is the main variable that triggers the variation in the amount of nutrients and secondary metabolites in mopane leaf.

**Table 2: Pearson Correlation Coefficient Analysis between *Colophospermum mopane* leaf quality and climatic variability. Data used to test the correlation is at Tables 1 and 3**

	Correlation ( <i>r</i> )			
	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

**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 (Table 1), which suggests no pattern, except perhaps in the age of leaf after flushing. The concentration of phosphorus in mopane leaves range from a minimum of 0.12% from September to a maximum of 0.23% in November (Table 1).

On the contrary, the concentration of calcium in mopane leaves range 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 1), which does not fit 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 the month of 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 1).

**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. Table 1 shows that the concentration of energy in mopane leaves is lowest in January (18.55%), and

reached its maximum in July (20.43%). The amount of energy in mopane leaves showed insignificant variation throughout the seasons, which suggest that seasonal changes has insignificant 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 hindered 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 change throughout the year, but seems to be at its greatest during the summer season, and then declined during the winter season (Table 1). Though there is little 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 Cooper and Owen-Smith (1985) notion that fibre influences the digestibility as well as acceptability of the leaves by browsers, it is therefore suggested in this paper 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.

**Essential fatty acids and oil:** Mopane leaves also contain essential fatty acids (Lawton, 1968), which make browsers to be healthy (Timberlake, 1995). However, there is no data available on the amount of fatty acids in mopane leaves. This means that future studies on mopane leaf quality should also quantify the amount of essential fatty acids found in mopane leaves in order to close the current knowledge gap.

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

**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 assist them to co-exist in the same ecosystem (Scholes and Walker, 1993). Mopane for instance produces secondary metabolites such as tannins and phenols in order to reduce browsing pressure during the growing season (Wessels *et al.*, 2007). However, the level of secondary metabolites in mopane varies per season (Table 3). The concentration of total phenols, condensed tannins and protein-precipitating tannins in mopane foliage ranged from a minimum of 48.4 mg g<sup>-1</sup>, 53.1 mg g<sup>-1</sup> and 58.8 mg g<sup>-1</sup> in August to a maximum of 96.7 mg g<sup>-1</sup>, 112.4 mg g<sup>-1</sup> and 142.0 mg g<sup>-1</sup> in December, respectively (Table 3).

The concentration of tannins and phenols start to increase from September with the start of the rains, and reached maximum levels in December to January (Table 3). As also indicated by Coley (1988) and Wessels *et al.* (2006), green mopane leaves contain high amounts of tannins and phenols, as opposed to reddish-brown aged leaves. This confirms a pattern observed in this review (Table 3), which shows that phenols and tannins start to decline from February and reached its lowest level in July and August, when the leaves had reached final growth 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), plus a natural adaptation mechanism to inhibit herbivore from browsing the leaves during the growing season (Wessels *et al.*, 2007). In addition, the variation in the amount of secondary metabolites seems also to be triggered mainly by rainfall (Table 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 will mainly be experienced during winter as opposed to summer.

**Table 3. Concentration of secondary metabolites in *Colophospermum mopane* leaves. There is significant variation on the amount of TP, CT and PPT throughout the year, which follows leaf growth**

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Reference
TP (mg g <sup>-1</sup> )	*	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 <sup>-1</sup> )	*	98.0	*	83.9	*	62.4	*	53.1	*	101.0	*	112.4	a
CT (mg g <sup>-1</sup> )	*	63.19	*	70.87	*	*	74.29	*	*	80.05	*	*	c
PPT (mg g <sup>-1</sup> )	*	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 (°C)	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.

#### Mopane leaf quality and its implication to browsers:

Despite the nutritional value in mopane leaves, twigs, seeds and pods (Table 1), mopane is browsed mainly during the dry season (Macala *et al.*, 1992; Timberlake, 1995; Hooimeijer *et al.*, 2005; Makhado *et al.*, 2016), when the chemical deterrents such as tannins and phenols are at lower concentrations (Wessels *et al.*, 2007; Table 2). Feeding on green mopane leaves is limited because of high concentration of secondary metabolites (Table 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 (Cooper and Owen-Smith, 1985) reduces the crude protein digestibility of browse (Mosimanyana and Kiflewahid, 1988; Provenza *et al.*, 2003; Cooper and Owen-Smith, 1985; Macala *et al.*, 1992; Hooimeijer *et al.*, 2005; Wessels *et al.*, 2007). In addition, green mopane leaves have 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 and 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 (Bailey, 1978; Van Hoven, 1991). In addition, phenolic compounds make the leaves to be less palatable to herbivores (Cooper and 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 (Bailey, 1978; Tanner, 1988). High amount of tannin can also cause direct toxic effects on the gut (Kreber and Einhellig, 1977). According to Woodward and Reed (1989), the diet containing high tannins concentration can reduce the growth rate of animals, which happen 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 and Walker, 1993). Regardless of high secondary metabolites during summer and the risk associated with browsing such chemical compounds, Styles and Skinner (1997) and 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 high level. This implies that browsers such as the greater kudu can slightly tolerate secondary metabolites during summer season possibly by diversifyin gits diet (Hooimeijer *et al.*, 2005), which assist 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 prohibit them from causing a negative effect on the herbivores (Havenga, 2014). The proline-rich glycoprotein therefore plays a critical role in 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 elephants, which utilise mopane during the summer season, although at low quantity compared to winter season, might be having 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; Makhado *et al.*, 2016), enables it to marginally tolerate secondary metabolites in the mopane leaf, especially during the summer season.

**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 concentrations of secondary metabolites varies significantly throughout the year. The digestibility of mopane by browsers is high during the dry season, but declined during the summer season, which is influenced by high amount 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 in this review that the variation in mopane leaf quality is mainly related to the growth and age of the leaf, as determined by rainfall, which defines the growing seasons.

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