Can African elephants survive and thrive in monostands of *Colophospermum mopane* woodlands?

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Abstract

Colophospermum mopane is an important food source for elephants during the dry season, being one of the few food plants still carrying leaves during this bottleneck period, and maintaining high feed value throughout the year. Several authors mention mopane as a bulk food for elephants, and one claims that elephants have been found feeding exclusively on mopane. Whether this is possible in terms of energy requirements is the focus of this literature review. Calculations have been made to see if elephants in different life stages can survive feeding on mopane during the different seasons, in terms of digestible energy requirements, intake and foraging time. The results indicate that elephants can indeed survive, in the scope of the criteria mentioned, on mopane solely, although time for ingestion and foraging has to be increased.

Additional key words: energy requirements, intake, foraging time, digestibility, food, modelling

Résumé

Les *Colophospermum mopane* sont une source de nourriture importante pour les éléphants en saison sèche, car c'est une des rares plantes qui portent encore des feuilles pendant cette période critique et elle garde une haute valeur nutritive toute l'année. Plusieurs auteurs mentionnent les *Mopane* comme étant la nourriture la plus consommée par les éléphants, et un dit même qu'on a vu des éléphants ne se nourrir que de *mopane.* L'objectif de cette revue de la littérature est de voir si ceci est possible en termes de besoins énergétiques. On a fait des calculs pour savoir si les éléphants à différentes étapes de leur vie peuvent survivre en se nourrissant de *mopane* au cours des différentes saisons, en termes de besoins énergétiques alimentaires, de temps d'absorption et de recherche de nourriture. Les résultats indiquent que les éléphants peuvent en effet survivre, pour ce qui est des critères mentionnés, avec uniquement des *mopane*, mais qu'il faut augmenter la durée d'ingestion et de quête de nourriture.

Mots clé supplémentaires : besoins énergétiques, temps d'absorption, recherche de nourriture, absorption, food, modelling

Introduction

Colophospermum mopane (Leguminosae: Caesalpinioideae) is a deciduous tree widely distributed across an area of 550,000 km^2 throughout southern Africa and occurring over a wide range of ecological conditions (Walker 1980; Timberlake 1995; Mapaure and Mhlanga 2000). Mopane is an important browse species for African elephants (*Loxodonta africana*), especially in the dry season as regrowth of leaves and the long leaf-carriage period continuing in the dry season are crucial to sustain elephants through this resource-deficient time of year (Walker 1980; Villier et al. 1991; Brophy et al. 1992; Dekker and Smit 1996; Rooke 1998; Smallie and O'Connor 2000; Ben-Shahar and Macdonald 2002). Mopane is known for its phenolic compounds, which have a negative effect on intake, protein and cell wall digestibility, and metabolism (Owen-Smith 1993; Rooke 1998; Aganga et al. 2000). In addition, in the northern Namib Desert mopane is one of the most important tree species elephants use as bulk forage (Viljoen 1989; Timberlake 1995). Ben-Shahar (1996) found that elephants in northern Botswana feed on mopane

exclusively, although according to Lewis (1986) they are not dependent on mopane solely. Nevertheless, elephant densities are higher within mopane areas than outside them (de Boer 2003). This implies that mopane is an important food source for elephants.

The aim of this research is to establish whether elephants can feed exclusively on mopane. Foraging time and amount of intake are constraining factors. Elephants tend to forage for 60% to 75% of the day (Owen-Smith 1988) to ingest their mean daily intake, which is around 4% (fresh weight) of the live body weight (Laws et al. 1970 in Williamson 1975). In addition, elephants have a short mean retention time, of 12–50 hours, and low digestive capacity (Owen-Smith 1988).

Literature collated focused on energy requirements of African elephants. Calculations on their energy requirements were made with regard to intake and foraging time. The data obtained in in vitro digestibility trials were used to assess the digestibility of mopane.

The study gives insight as to how the energy requirements of African elephants in *Colophospermum mopane* woodlands can be met, and it indicates how mopane woodlands may be managed to help conserve elephants in these areas.

Materials and methods

The study was carried out as a literature analysis with a modelling approach. The chemical composition of mopane leaves, as found in literature, as well as mopane leaves from Kruger National Park, South Africa, were analysed for nutrients.

Mature green and senescing mopane leaf samples were chemically analysed for digestibility. The samples were gathered during May 2002 (early dry season) in Kruger National Park, South Africa. The in vitro digestibility of the mopane leaves was determined following Tilly and Terry (1963).

The different seasons mentioned in this study are defined as follows:

- Late dry season: August, September, October; no rainfall, low temperatures
- Early wet season: November, December; medium rainfall, high temperatures
- Late wet season: January, February, March, April; main rainy season, high temperatures
- Early dry season: May, June, July; no rainfall, low temperatures

The energy requirements and foraging time for elephants of different sex and age categories feeding on three mopane sources including mature green leaves (MGL), senescing leaves (SL) and twig bark (TB) were calculated using the metabolizable energy (ME) requirements in table 1 provided by Meissner (1982). The energy contents for the three different mopane plant parts used were derived from Styles and Skinner (1997, 2000) and are listed in table 2. To calculate the daily intake (kg) the ME was converted to dry-matter intake incorporating digestibility, methane and urinary losses. Digestibility levels were obtained from Foose (1982) and from the in vitro digestibility analysis. Methane and urine losses were estimated at 14.13 kJ kg d^{-1} when the elephants were feeding on MGL, 12.24 kJ kg d^{-1} on SL, and 12.24 kJ kg d^{-1} on TB (Meissner et al. 1990). Foraging time was calculated using 2.4 trunkloads of 180 g of wet mass per minute as found by Guy (1975, in Owen-Smith 1988).

Table 1. Average metabolizable energy intake of African elephants for various age and sex classes

Elephant	Mass (kg)	Metabolizable energy (MJ/d)
Calf, 5 years	850	84.8
Cow, dry, 15 years	1850	285
Cow, dry, 50 years	3300	291
Cow, with calf, 15 years	1850	362
Cow, with calf, 50 years	3300	375
Bull, 15 years	2200	303
Bull, 50 years	3700	310

Source: Meissner 1982

Table 2. Gross energy contents (kJ/g plant material) in three *Colophospermum mopane* sources in Northern Tuli Game Reserve, Botswana, during four seasons

Season	Mature green leaves	Senescing leaves	Twig bark
Late dry	20.43 ± 2.31	17.65 ± 0.41	18.5 ± 1.0
Early wet	19.12 ± 0.40	18.48 ± 0.22	17.7 ± 0.1
Late wet	18.55 ± 0.33	16.75 ± 0.39	17.6 ± 0.2
Early dry	19.45 ± 0.32	16.97 ± 0.18	17.3 ± 0.3

Source: Styles and Skinner 1997, 2000

Results

Figure 1 shows the late dry season intake and foraging time for a bull elephant and a cow with a calf feeding on mature green mopane leaves. The energy content of mature green mopane leaves during the late dry season is 20.43 kJ g^{-1} plant material. The 50-year-old bull weighs 3700 kg and has a ME requirement of 310 MJ d^{-1}. Correcting for digestibility (29.2%), methane and urine losses, we determine that for the bull to fulfil its energy requirements, its late dry season intake needs to be 151.83 kg wet mass (WM) per day. The foraging time needed to ingest this amount of forage would be approximately 14 hours. The 50-year-old cow with a calf weighs 3300 kg and has an ME requirement of 375 MJ d^{-1}. Following the same procedure, we determine that its late dry season intake needs to be 176.70 kg WM d^{-1}, with a foraging time of approximately 16 hours.

The digestibility of senescing leaves for elephants is 24.1% and of twig bark 25%. Equation 1.1 expresses the diet necessary for a 50-year-old bull (3700 kg) to acquire the minimum energy requirements when feeding on three different mopane sources during the late dry season and equation 1.2 for a 50-year-old cow (3300 kg) with a calf.

$$\text{Eq. 1.1} \quad \frac{TB}{192}+\frac{MGL}{152}+\frac{SL}{209}=1,$$

$$\text{Eq. 1.2} \quad \frac{TB}{225}+\frac{MGL}{177}+\frac{SL}{244}=1,$$

where *TB* = twig bark, *MGL* = mature green leaves and *SL* = senescing leaves. If the sum is > 1 the diet is sufficient, if it is < 1 it is deficient.

For instance, if a bull elephant feeds on 134 kg of twig bark and 15 kg of green leaves, it must ingest another approximately 42 kg of senescing leaves to fulfil its daily energy requirements.

Intake and foraging time of elephants in different life stages and during all seasons feeding on the three sources of mopane are presented in figure 2 and table 3. Minimum intake as calculated in this study can vary between 40.57 and 257.27 kg/d, with foraging times varying between 3 h 45 min and 23 h 49 min per day, depending on the life stage, part of mopane ingested and season.

Figure 2 visualizes that the calculated intake from this study is always above the mean daily intake of 4% of the live bodyweight (see table 3). Table 3 presents the exact numbers and also how much the calculated intake is above the mean daily food in

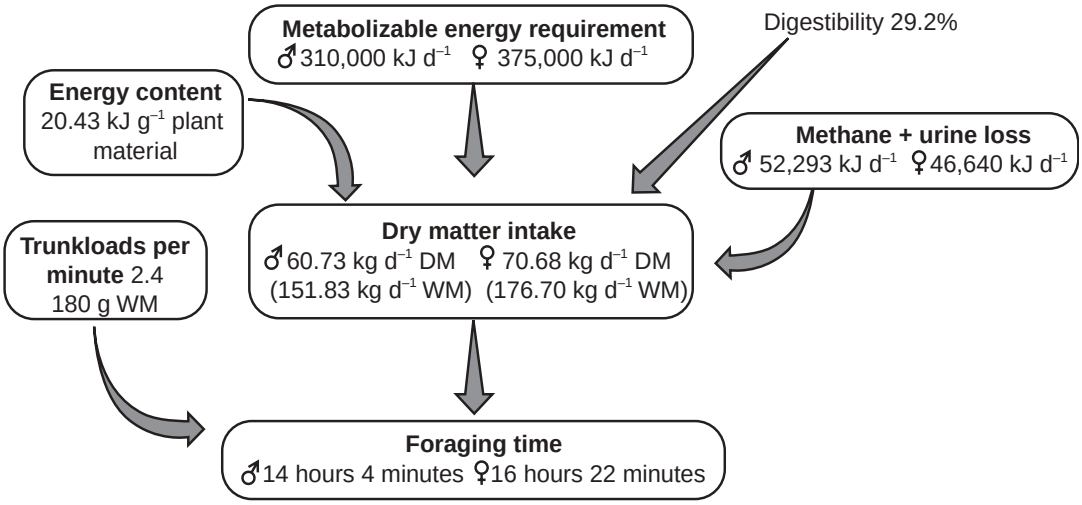

Figure 1. Late dry season intake and foraging time for a bull elephant (♂ : 50 yr; 3700 kg) and cow with a calf (♀ : 50 yr; 3300 kg), feeding on mature green *Colophospermum mopane* leaves (DM: dry mass, WM: wet mass).

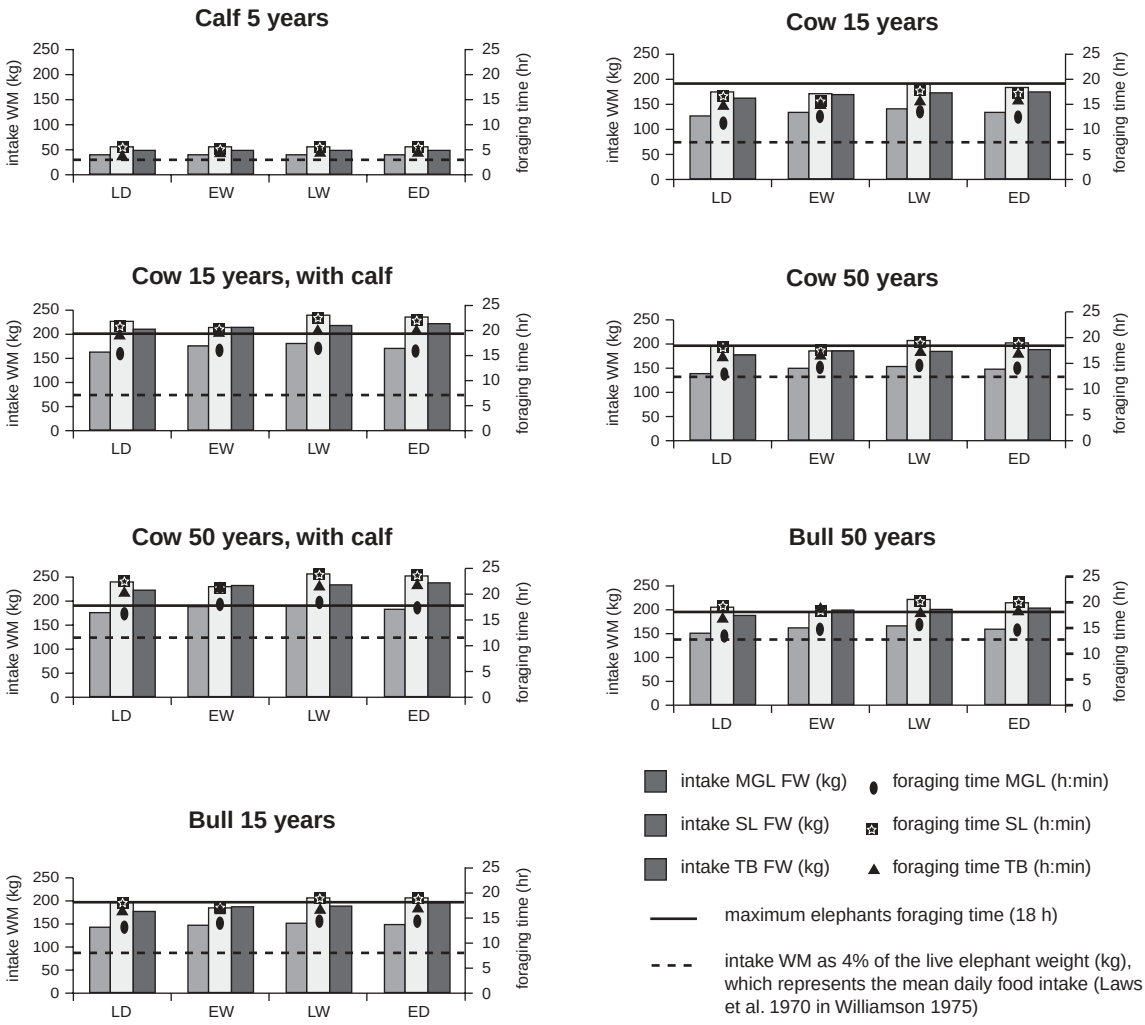

Figure 2. Simulated seasonal intake and foraging time for different sex and age categories when feeding on three mopane sources (excluding all other potential forage sources). Maximum foraging times for calves are unknown and therefore not included. FW – fresh weight, MGL – mature green leaves, SL – senescing leaves, TB – twig bark, WM – wet mass.

take, calculated from 4% live weight. This varies between 3% (bull 50 years old feeding on MGL during the late dry season) to 222% (cow 15 years old with calf, feeding on SL during summer) above the mean daily food intake, although the exact daily intake rates of lactating females and calves remain unknown.

Intake from mature green leaves always remains under the foraging time constraint for all life stages.

Foraging times when feeding on senescing leaves or twig bark are under the maximum foraging times for elephants, except for lactating cows (both 15 and 50 years of age feeding on SL and TB), 50-year-old cow (SL in the early and late dry and late wet seasons), 15-year-old bull (SL in late wet and early dry seasons) and 50-year-old bull (SL all seasons and TB in early and late wet and early dry seasons).

Discussion

The mean daily food intake (kg WM) was estimated at 4% of the live weight for all classes except lactating females, according to Laws et al. (1970 in Williamson 1975). In the case of the bull elephant, in figure 1, this would account for an intake of 148 kg WM, which is

Table 3. Simulated seasonal intake in wet mass (WM) kilograms and foraging time for different sex and age categories, when feeding on three mopane sources, including percentages of increase or decrease relative to mean daily intake and mean foraging time (FT) (max. 18 h)

				Mature green leaves				Senescing leaves				Twig bark			
Animal and weight (kg)	WM intake[a] (kg)	ME (kJ/d)	Season[b]	Intake (kg WM)	%[c]	FT (h:min)	%[d]	Intake (kg WM)	%[c]	FT (h:min)	%[d]	Intake (kg WM)	%[c]	FT (h:min)	%[d]
Calf 5 yr, 850	~ 34	84,800	LD	40.57	19	3:45	–79	55.96	65	5:11	–71	51.46	51	4:46	–74
			EW	43.35	28	4:01	–78	53.44	57	4:57	–73	53.79	58	4:59	–72
			LW	44.68	31	4:08	–77	58.96	73	5:28	–70	54.10	59	5:01	–72
			ED	42.62	25	3:57	–78	58.20	71	5:23	–70	55.03	62	5:06	–72
Cow 15 yr, 1850	74	285,000	LD	130.39	76	12:04	–33	180.82	144	16:45	–7	166.30	125	15:24	–14
			EW	139.33	88	12:54	–28	172.70	133	15:59	–11	173.81	135	16:06	–11
			LW	143.61	94	13:18	–26	190.53	157	17:38	–2	174.80	136	16:11	–10
			ED	136.96	85	12:41	–30	188.06	154	17:25	–3	177.84	140	16:28	–9
Cow 15 yr, w/calf 1850	~ 74	362,000	LD	162.66	120	15:04	–16	226.07	206	20:56	16	207.92	181	19:15	7
			EW	173.81	135	16:06	–11	215.92	192	20:00	11	217.32	194	20:07	12
			LW	179.15	142	16:35	–8	238.22	222	22:03	23	218.55	195	20:14	12
			ED	170.86	131	15:49	–12	235.13	218	21:46	21	222.34	200	20:35	14
Cow 50 yr, 3300	132	291,000	LD	141.50	7	13:06	–27	194.78	48	18:02	0	179.14	36	16:35	–8
			EW	151.32	15	14:01	–22	186.03	41	17:14	–4	187.24	42	17:20	–4
			LW	155.84	18	14:26	–20	205.24	55	19:00	6	188.30	43	17:26	–3
			ED	148.62	13	13:46	–24	202.58	53	18:45	4	191.56	45	17:44	–1
Cow 50 yr, w/calf 3300	~132	375,000	LD	176.70	34	16:22	–9	244.15	85	22:37	26	224.54	70	20:47	16
			EW	188.80	43	17:29	–3	233.19	77	21:35	20	234.69	78	21:44	21
			LW	194.61	47	18:01	0	257.27	95	23:49	32	236.03	79	21:51	21
			ED	185.60	41	17:11	–5	253.93	92	23:31	31	240.12	82	22:14	24
Bull 15 yr, 2200	88	303,000	LD	140.01	59	12:58	–28	193.91	120	17:57	0	178.35	103	16:31	–8
			EW	149.60	70	13:51	–23	185.21	110	17:09	–5	186.41	112	17:16	–4
			LW	154.20	75	14:17	–21	204.34	132	18:55	5	187.47	113	17:22	–4
			ED	147.06	67	13:37	–24	201.68	129	18:40	4	190.72	117	17:40	–2
Bull 50 yr, 3700	148	310,000	LD	151.83	3	14:04	–22	208.82	41	19:20	7	192.06	30	17:47	–1
			EW	162.23	10	15:01	–17	199.44	35	18:28	3	200.74	36	18:35	3
			LW	167.21	13	15:29	–14	220.04	49	20:22	13	201.88	36	18:42	4
			ED	159.48	8	14:46	–18	217.19	47	20:07	12	205.38	39	19:01	6

ME – metabolizable energy; [a] Mean daily intake, 4% of live weight; [b] LD – late dry, EW – early wet, LW – late wet, ED – early dry, [c] percentage relative to mean daily intake; [d] percentage relative to mean foraging time

3.8 kg less than the intake as calculated in this study, when feeding on mature green mopane leaves solely.

Elephants tend to forage 12–18 hours a day (Owen-Smith 1988). When feeding on mature green mopane leaves only, this bull elephant has to feed for at least 14 hours to achieve its digestible energy requirements, which is within the 12–18 hour range.

What is evident in figure 2 is that the total daily intake is not the highest during the late dry season, which would normally be expected because of the lower amount of energy in woody forage. However, the energy contents of mopane, as derived from Styles and Skinner (1997, 2000), give higher gross energy amounts in the late dry season for mature green leaves and twig bark than in the late wet season.

From our calculations it appears that an adult elephant bull can survive entirely on mature green mopane leaves during the late dry season only in terms of energy requirements, minimum daily intake and available foraging time.

The results in figure 2 and table 3 suggest that not all elephant age and sex classes can survive on mopane parts in terms of intake, as intake is usually more than the daily mean intake (4% of the live weight).

Some comments must be made:

- Metabolizable energy requirements are probably season dependent.
- The conversion rate used here to calculate forage dry matter to wet mass was 2.5 (40%). This value may fluctuate across seasons.
- The maximum intake rate calculated from the number of trunkloads per minute may vary across life stage and sex.
- In these calculations urinary and methane energy loss of 14.13 kJ kg^{-1} d^{-1} and 12.24 kJ kg^{-1} d^{-1} are used. These values are derived from Meissner et al. (1990), who calculated these amounts based on digestibility of 25% and 30%. However, the digestibility calculated in the article by Meissner et al. (1990) is calculated using the lignin index, meaning that digestibility might be overestimated. If this is true, the values for urinary and methane energy losses may be too high.
- Digestibility is probably not stable throughout the year.
- Intake might differ over the seasons.

The effect of secondary compounds on ingestion remains unknown. Mopane trees are known for their high amount of tannins, which could have a negative influence on intake, digestibility and metabolism. Therefore, tannins might influence the quality of mopane as a feed, because they may reduce the availability of nutrients. However, the negative effect of the mopane secondary compounds has not been included in this study, although it could affect the maximum admissible amount of mopane that an elephant can ingest, even when studies have shown that they can feed exclusively on mopane. Mopane makes up a considerable part of the diet for elephants in the northern Namib Desert (Viljoen 1989). In addition Ben-Shahar (1996) claimed that elephants in northern Botswana fed on mopane exclusively. The results of the minimum energy requirement calculations suggest that elephants can indeed survive by feeding on mopane only, although several assumptions incorporated in the calculations make it impossible to draw a hard conclusion as to whether this is so. However, we have shown that elephants seem to be able to survive on mopane entirely, as the energy contents are sufficient for elephants feeding solely on mopane parts during all seasons.

Conclusion

Colophospermum mopane is an important food source in the diet of elephants, especially during the dry season, as it makes up a considerable part of the diet. The nutritive quality of mopane throughout the year is high, and its energy content is sufficient for elephants feeding solely on mopane parts during all seasons to survive, although ingestion and daily foraging time need to be increased to obtain sufficient energy.

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