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RELATIONSHIPS BETWEEN HERBIVORES AND *COLOPHOSPERMUM MOPANE* OF THE NORTHERN TULI GAME RESERVE, BOTSWANA

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RELATIONSHIPS BETWEEN HERBIVORES AND *COLOPHOSPERMUM MOPANE* OF THE NORTHERN TULI GAME RESERVE, BOTSWANA

by

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Man has lost the capacity

to foresee and to forestall.

He will end by

destroying the earth.

ALBERT SCHWEITZER

THIS THESIS IS DEDICATED TO MY PARENTS

TOM AND LORNA STYLES

FOR THE EDUCATION THEY HAVE GIVEN ME

Blessed is he who has found his work;

let him ask no other blessedness.

Thomas Carlyle

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by

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Abstract

This study elicits the resilience of *Colophospermum mopane* as a tree. Elephant impact is extremely important in creating and maintaining niche requirements of other organisms, especially insects, associated with mopane trees. The value of mopane as a browse is documented seasonally, this resource proving to have been previously underrated. Plant apparency results from mopane trees having different insect associations. These insect associations are of great ecological importance, and their relationships with elephants, previously overlooked, are documented. Mopane moth caterpillars, absent from within the confines of the NTGR for almost twenty years, are often encountered just outside the NTGR. Factors hypothesized to be responsible for their local extinction include ant predation, edaphic factors and browse quality differences, between mopane trees in the NTGR and those in adjoining areas. This study concludes that large mammals, especially elephants, are managing the resources of the NTGR.

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STUDY SITE

STUDY AREA

FIGURE 1: LOCATION OF THE NORTHERN TULI GAME RESERVE.

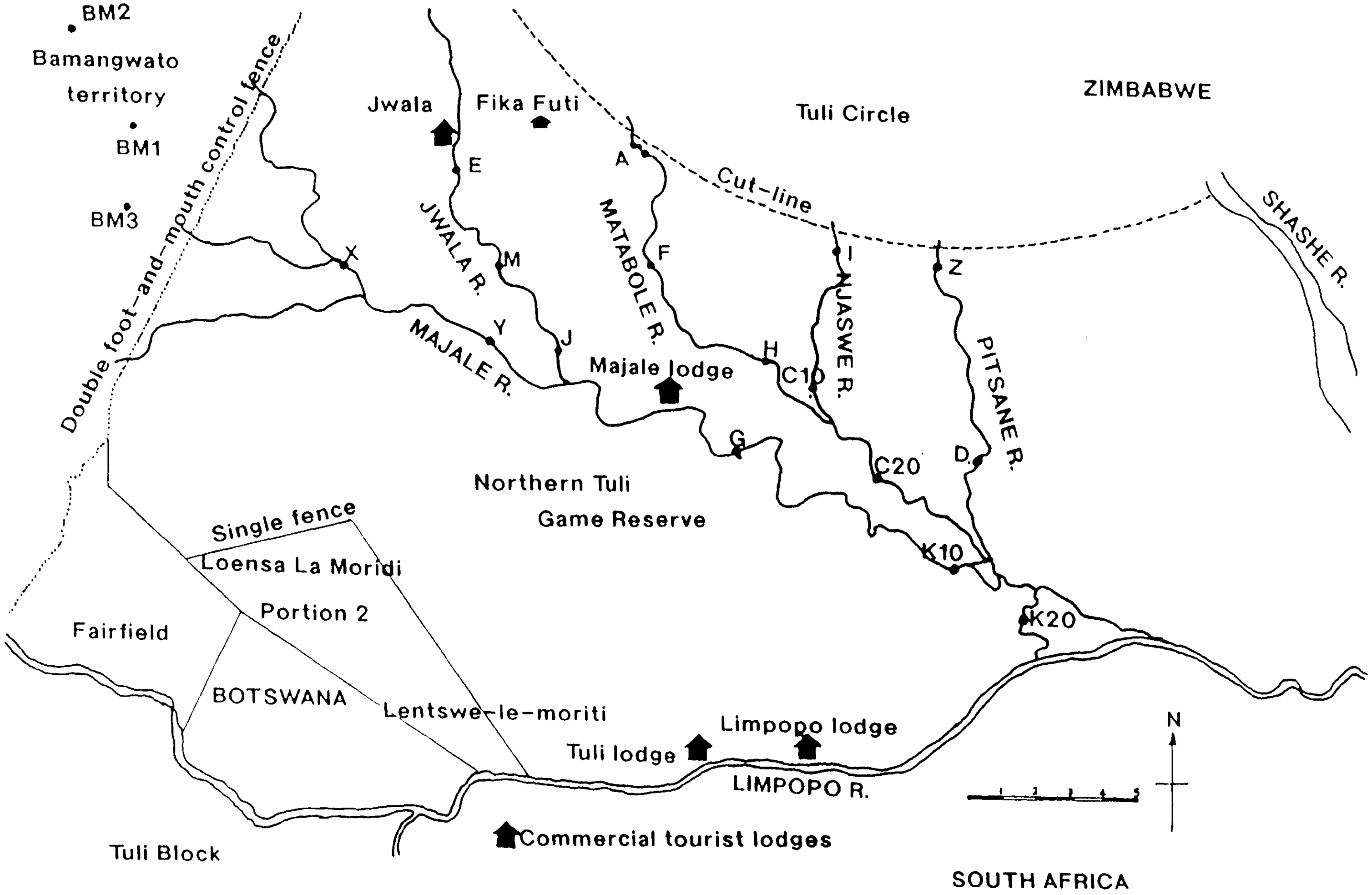

FIGURE 2: THE NORTHERN TULI GAME RESERVE.

LOCATION

The Northern Tuli Game Reserve (NTGR) lies in the eastern corner of Botswana, between 21°55'S and 22°15'S and between 28°55'E and 29°15'E, where Botswana, South Africa and Zimbabwe converge (Fig. 1). The NTGR constitutes the north-eastern extremity of a 350km long strip of land known as the Tuli Block. The NTGR is bounded in the north by the Tuli Circle, in the south by the Limpopo and Motloutse Rivers, in the east by the Shashe River, and in the west by the Tuli Block backline (a double foot-and-mouth disease control fence).

The NTGR is constituted of nine original farms, some of which have been divided up into several portions. With the exception of the fences shown in Fig. 2, the farms are unfenced. Areas in the NTGR which are utilized for purposes other than conservation include Fairfield, which is used for livestock farming, and Portion 2 of Loensa-la-Moriti, which is used for crop and pastoral production. The remainder of the NTGR is maintained as a private game reserve, comprising an area of approximately 65 000ha. Together with the adjacent Tuli Circle Conservation Area in Zimbabwe, the total conserved area comprises approximately 100 000ha (McKenzie 1990).

CLIMATE

The climate of the region incorporating the NTGR is semi-arid tropical, with a low and unpredictable rainfall (Harrison 1984). The long-term average rainfall is 369,5mm (1965 - 1989), with peak rainfall years receiving up to 660mm (1976) and low rainfall years receiving as little as 180mm (1989). Rain falls mainly between November and February, usually in the form of thunderstorms. Summer maximum temperatures exceed 42°C, whereas winter temperatures may be as low as -5°C (McKenzie 1990). The rainfall for the study period is presented in the form of a histogram (Fig. 3).

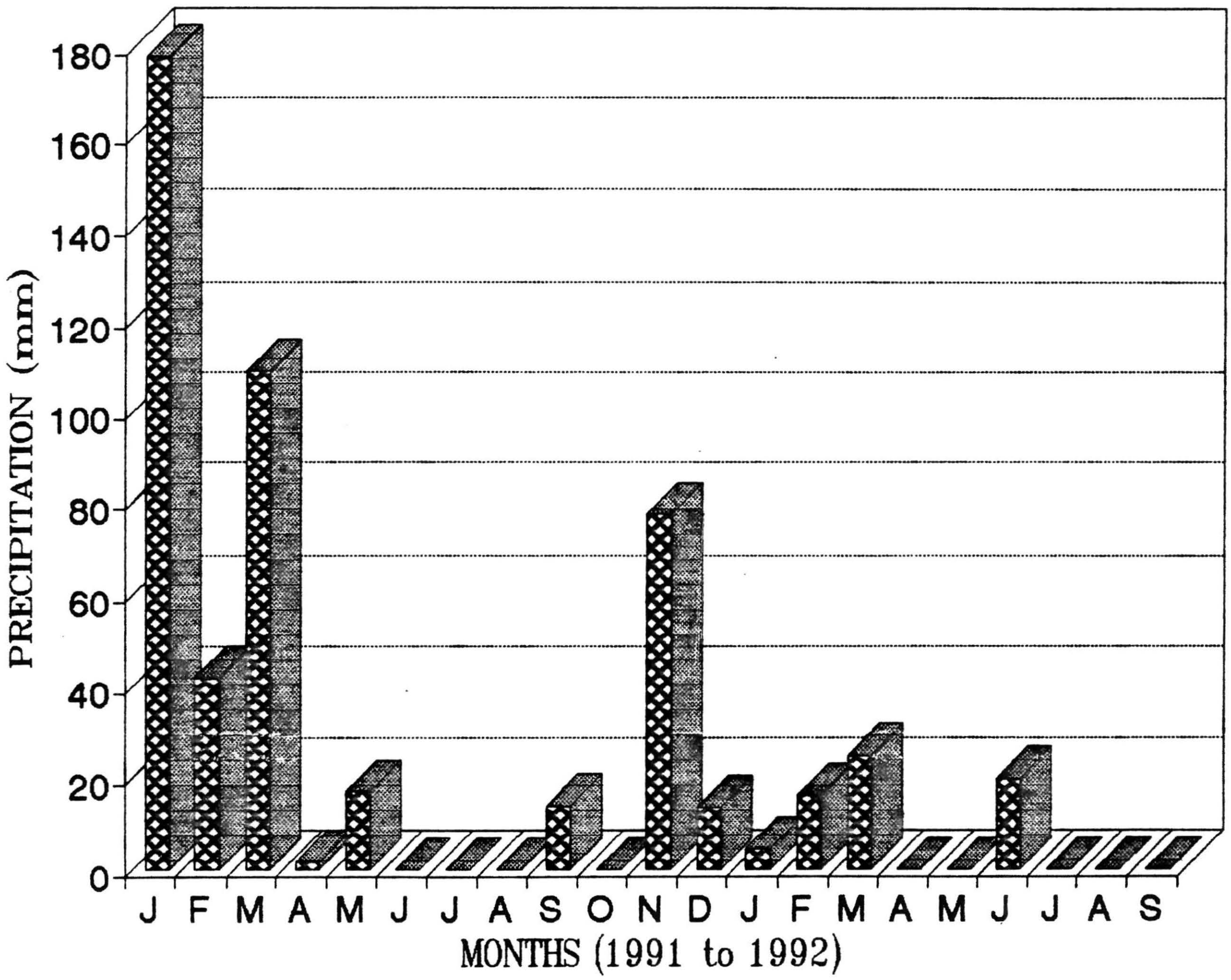

FIGURE 3: HISTOGRAM OF MONTHLY PRECIPITATION RECORDED AT PONTDRIFT FOR THE PERIOD OF THE PRESENT STUDY

GEOLOGY AND SOILS

The description given here is derived from Joubert (1984) as described in McKenzie (1990). The geological substratum of the NTGR is composed of deep Clarens Sandstone formation overlain by Letaba and Sabi River basalt formations. Numerous east-west dolerite dykes intrude these strata. The sandstone is only exposed along the southern extremities of the NTGR along the Limpopo and Motloutse Rivers. The rest of the NTGR is dominated by the basalt formations. Extensive alluvial plains occur along all the major rivers, including the lower reaches of the Majale River (McKenzie 1990).

TOPOGRAPHY AND DRAINAGE

The description given here is derived from McKenzie (1990). The NTGR is extensively dissected by incisive drainage lines. Most of the NTGR is drained by the Majale River which terminates in the south-central portion of the NTGR where it enters the Limpopo River. Other minor rivers flow directly into the Motloutse and Shashe Rivers. All these rivers flow sporadically in summer and are dry, excepting a few isolated pools, during winter. The incisive topography of the basalt regions is abruptly replaced by the undulating older flood-plains along all the major rivers. The flood-plain is interrupted by sandstone formations in the south and west, and by the dolerite dykes in the other parts (McKenzie 1990).

VEGETATION

The vegetation of the NTGR falls within the broad classification of Mopane Veld (Acocks 1975). The vegetation comprises three major landscapes, the Floodplains on Alluvium, the *Colophospermum mopane/Terminalia prunioides* veld on Basalt, and the Karoo Sandstone landscape (McKenzie 1990). The riverine areas are characterized by:

SPECIES	COMMON NAME	FAMILY
Acacia albida	Ana tree	Leguminosae
Xanthocercis zambesiaca	Mashatu tree	Leguminosae
Schotia brachypetala	Weeping boer bean	Leguminosae
Acacia nigrescens	Knob thorn	Leguminosae
Acacia tortilis	Umbrella thorn	Leguminosae
Combretum hereroense	Russet bushwillow	Combretaceae
Combretum imberbe	Leadwood	Combretaceae
Lonchocarpus capassa	Apple leaf	Leguminosae
Colophospermum mopane	Mopane	Leguminosae
Boscia albitrunca	Shepherd's tree	Capparaceae
Croton megalobotrys	Lowveld fever berry	Euphorbiaceae
Ziziphus mucronata	Buffalo thorn	Rhamnaceae
Combretum apiculatum	Red bushwillow	Combretaceae
Terminalia prunioides	Lowveld cluster leaf	Combretaceae
Salvadora angustifolia	Mustard bush	Salvadoraceae
Boscia foetida	Smelly boscia	Capparaceae
Ficus sycamorus	Sycamore fig	Moraceae
Berchemia discolor	Brown ivory	Rhamnaceae
Albizia brevifolia	Mountain albizia	Leguminosae
Hyphaene natalensis	Mlala palm	Arecaceae
Peltophorum africanum	Weeping wattle	Leguminosae
Sclerocarya birrea	Marula	Anacardiaceae
Cassia abbreviata	Sjambok pod	Leguminosae
Sterculia rogersii	Common star chestnut	Sterculiaceae
Pappea capensis	Jacket plum	Sapindaceae

Lannea stuhlmannii	False marula	Anacardiaceae
Spirostachys africana	Tamboti	Euphorbiaceae
Commiphora pyracanthoides	Common commiphora	Burseraceae
Commiphora merkeri	Zebra bark corkwood	Burseraceae
Kirkia acuminata	White seringa	Simaroubaceae
Markhamia acuminata	Bean tree	Bignoniaceae
Acacia galpinii	Monkey thorn	Leguminosae
Acacia xanthophloea	Fever tree	Leguminosae

Other tree species encountered within the confines of the NTGR are:

SPECIES	**COMMON NAME**	**FAMILY**
Adansonia digitata	Baobab	Bombacaceae
Sesamothamnus lugardii	Transvaal sesame bush	Pedaliaceae
Acacia senegal	Three-thorned acacia	Leguminosae
Acacia nebrownii	Water acacia	Leguminosae
Steganotaenia araliacea	Carrot tree	Leguminosae

Prominent shrubs are *Diospyros lycioides* (bladdernut), *Acacia schweinfurthii* (scrambling river acacia) and *Rhigozum brevispinosum.* On the steep undercut rocky walls of the major river courses the sandpaper bush, *Ehretia amoena*, is commonly encountered. *Enneapogon cenchroides* is the most commonly encountered grass species, with varying associations with *Setaria verticillata, Cenchrus ciliaris, Urochloa mosambicensis, Cynodon dactylon, Panicum coloratum, Eragrostis spp., Aristida spp.* and *Digitaria spp.*. A homogenous stand of the very tall *Sporobilis consimilis* or elephant grass, is encountered in the south-central region of Mashatu, where it forms a large marshy area (McKenzie 1990).

FAUNA:

ORDER: CARNIVORA

SPECIES	COMMON NAME
Acinonyx jubatus	Cheetah
Canis mesomelas	Black-backed jackal
Civettictis civetta	African civet
Crocuta crocuta	Spotted hyaena
Felis caracal	Caracal
Felis lybica	African wild cat
Genetta genetta	Small-spotted genet
Genetta tigrina	Large spotted genet
Ichneumia albicaudata	White-tailed mongoose
Mellivora capensis	Ratel
Mungos mungo	Banded mongoose
Panthera leo	Lion
Panthera pardus	Leopard
Proteles cristatus	Aardwolf

ORDER: ARTIODACTYLA

SPECIES	COMMON NAME
Aepyceros melampus	Impala
Connochaetes taurinus	Blue wildebeest
Giraffa camelopardalis	Giraffe
Kobus ellipsiprymnus	Waterbuck
Phacochoerus aethiopicus	Warthog

Potomachoerus porcus	Bushpig
Raphicerus campestris	Steenbok
Sylvicapra grimmia	Common/Grey duiker
Taurotragus oryx	Eland
Tragelaphus scriptus	Bushbuck
Tragelaphus strepsiceros	Greater kudu
Rhapicerus sharpei	Sharpe's grysbok
Oreotragus oreotragus	Klipspringer

ORDER: PERISSODACTYLA

SPECIES	**COMMON NAME**
Equus burchelli	Burchell's zebra

OTHERS:

SPECIES	**COMMON NAME**	**ORDER**
Cercopithecus aethiopicus	Vervet monkey	Primates
Hystrix africae-australis	Cape porcupine	Rodentia
Lepus saxatilis	Scrub hare	Lagomorpha
Pedetes capensis	Spring hare	Rodentia
Loxodonta africana	African elephant	Proboscidea
Orycteropus afer	Aardvark	Pholidota
Papio ursinus	Chacma baboon	Primates
Paraxerus cepapi	Tree squirrel	Rodentia
Galago moholi	Lesser bushbaby	Primates

CHAPTER

TWO

CHAPTER

TWO

INTRODUCTION

INTRODUCTION

Colophospermum mopane (Caesalpinioideae; Leguminosae), an endomycorrhizal tree species, forms extensive, almost monospecific stands (Lüdemann 1960; Thompson 1960; Cole 1963; von Breitenbach 1965; de Winter *et al.* 1966; Hogberg & Piearce 1986), usually dominating the vegetation structure in an area (Bonsma 1942; van Wyk & Fairall 1969; Hall-Martin 1974a; Acocks 1975; Kelly & Walker 1976; le Roux 1980; Scholes 1983; Ernst & Sekhwela 1987; Nott & Stander 1991). Sometimes the mopane tree is the sole woody species present (Hall-Martin 1974b; le Roux *et al.* 1988). The distribution of this tree species is known to include Mocambique, Zimbabwe, Zambia, Angola, Botswana, Namibia, South Africa and the southern-most part of Malawi (Obermeijer 1933; Ellis 1950; Coates-Palgrave 1988). Werger & Coetzee (1978) make mention of mopane occurring in the valleys of some of southern Africa's largest rivers, namely the Zambesi, Luangwa, Shire, Save, Limpopo, Okavango and Cunene. Mopane trees are usually encountered on alluvial soils in hot low-lying areas (300 to 600m above sea level) of south tropical Africa (de Winter *et al.* 1966; Coates-Palgrave 1988). Frost seems largely responsible for limiting the geographical distribution of mopane (von Breitenbach 1965; Gertenbach 1987). Henning & White (1974) have found that the mopane, although very resistant to drought, is not resistant to fire damage, burning even when green due to the high turpentine level in the plant (van Wyk & Fairall 1969; Bonsma 1976; Gertenbach & Potgieter 1979). Rainfall over the mopane veld of southern Africa averages 300-400mm, with the humidity generally being high (Bonsma 1976). In the Kruger National Park the 500mm isotherm serves as the southernmost boundary of the mopane veld (Gertenbach 1987). Evidence exists that mopane trees do not favour alkaline soils *per se* and that they will grow better on fertile, slightly acid permeable soil (Gertenbach 1987). However, these trees are most often excluded from these soils by deep-rooting *Acacia* species (Cole 1967), and consequently usually occurs on soils with a high ph (Cole 1963). In the Kruger National Park, mopane occurs on soil whose ph ranges from 6,0 to 8,8 (van Rooyen *et al.* 1981). Mopane seems to thrive where the exchange calcium in the B horizon of the soil is high, and where the B horizon is shallow (Gertenbach 1987). According to Gertenbach (1987) factors which are known to largely influence the occurrence of mopane are:

1: [Ca] in the A horizon
2: [PO_4] in the B horizon
3: ph of the A horizon
4: Depth of the B horizon
5: High [Na]
6: High [Mg]

Mature leaflets of the tree demonstrate a tripartite nature. The two basal papilionaceous leaflets, being mirror images of each other, together resemble the wings of a butterfly. The cluster is capped by a terminal vestigial leaflet which atrophies when 3 to 5mm in length (Stein 1978; van Wyk 1984; Coates-Palgrave 1988). The embryonic mopane leaf has a large tip leaflet endowed with a well developed vascular system (Stein 1978). Early in its development the terminal leaflet reveals the presence of resin cavities (Stein 1978). Oates (1972) speculates that the aromatic resin in the leaves could possibly be the reason why mopane is not readily taken by browsing animals. In hot, dry weather, or at midday, the leaflets fold up together so that the only shade they throw is the shadow of their thin edges (Palmer & Pitman 1972).

The pod is flat and kidney-shaped, and the single seed within is yellowish, wrinkled, and covered with resinous dots. The resin makes the seed sticky, reportedly causing it to cling to the hooves of passing animals, and as a consequence, being dispersed (Palmer & Pitman

1972; Coates-Palgrave 1977,1988). Such seed dispersal by adhesion is termed epizoochory (Sorenson 1986). Both mopane leaves and seeds have a very strong turpentine smell, yet when eaten by cattle this does not taint their meat or milk (von Breitenbach 1965; Bonsma 1976).

According to Oates (1972), mopane is virtually evergreen, losing its leaves for only a very short period before the rainy season. In the NTGR mopane appears semi-deciduous, never completely losing its leaves (Lind 1974). While leaves do senesce through winter, old leaves are usually retained on the lower crown. It has been reported that mopane may be extremely important to the general ungulate spectrum as a potential source of browse during droughts (Oates 1972; Hall-Martin & Basson 1974; Lind 1974; Sauer *et al.* 1977).

The NTGR is internationally renowned for its large elephant *Loxodonta africana* herds, which are a major tourist attraction. Yet elephants, due to their destructive feeding habits, especially the removal of stem bark by tusking, generate cause for management concern. Strip barking of trees by elephants is not known to have an immediate ill-effect but, as Thompson (1975) indicates, the removal of strips of bark allows access to insects and fungi which can ultimately cause the death of the tree. In larger trees, especially *Acacia* species, damage to bark allows the introduction of borer beetles, which may weaken the tree and lead to its falling (Croze 1974b). Because of this, strip barking can be as harmful to the tree in the long run as complete ring barking (Guy *et al.* 1979). In the mopane, however, the removal of stem bark by elephants does not adversely affect the biology of the tree.

Mopane is a host plant for a few endemic species of invertebrates, two of the endemics being monophagous insects (Ernst & Sekhwela 1987). One of these is the mopane moth *Imbrasia* (*Gonimbrasia*) *belina*, a saturniid, whose caterpillars feed predominantly on the leaves of mopane trees (Pinhey 1975; Skaife 1979; Oberprieler 1986,1990). Caterpillars of the mopane moth have been absent from within the confines of the NTGR for the last two decades.

The mopane tree community of the NTGR has two very definite components or morphs. The one morph, loosely referred to as a "bonsai", is a very short (not usually taller than

3,5m), robust mopane tree occurring as extensive hedges in the open areas away from the watercourses. This morph results from the removal of branches by large mammalian herbivores, the hedges being kept in the suppressed-tier state. The other morph is a much taller (usually in excess of 6m), relatively undamaged mopane tree, individuals belonging to this component being encountered along the riverine fringes of most of the major watercourses in the NTGR. These mopane hedges have been regarded as being indicative of excessive browsing pressures by large mammals, especially elephants. The present study thus undertook to investigate the utilization of this tree by herbivores, the key objective being to collate the findings into a management policy for this the dominant tree type of the NTGR. The results provided as to the effects herbivores (**elephants especially**) are having on the ecology of this tree, could then be incorporated into the overall management policy of the NTGR.

In an attempt to realize the above goal, certain objectives were set, these being:

1: The seasonal variations in the chemical composition of mopane leaves as a source of browse needed to be investigated, emphasis being placed on the value of this available resource for mammalian herbivores, and on relating the seasonal browse quality of mopane to the probable browsing pressures the trees would be experiencing for that season.

2: As it was believed that mopane is not readily accepted as a browse due to the aromatic nature of the leaves, this needed investigating. The volatile components of both the young green and mature green leaves of *Colophospermum mopane* were to be analyzed using two different concentrating techniques and Gas Chromatography and Mass

Spectroscopy (GC-MS). The purpose behind this was to assist our understanding of the feeding preferences different herbivores within the veld type exhibited for different phenophases (leaf types eg. young; mature). The identified compounds would then be correlated with the known chemical profiles of the phenophases to ascertain whether or not a mammalian herbivore could perceive browse quality merely from the volatile substances that phenophase emits.

3: Agents responsible for the removal of mopane branches, the possible reasons why mopane twig bark is so sought after, and the ecological implications of such hedges for the NTGR's management policy, needed studying. The removal of marked branches from a stand of hedged trees was to be recorded seasonally, as was the occurrence of undigested twig material in the faeces of elephants. Moreover, it was necessary to analyze the seasonal chemical composition of mopane twig bark in an attempt to relate these results to the seasonal utilization of branches by large mammals.

4: The seasonal removal of stem bark from mature mopane trees whose bark was highly accessible, needed to be monitored in an effort to determine to what degree elephants were utilizing this resource. The chemical composition of mopane stem bark was also to be investigated to determine whether some chemical feature it possesses might explain the utilization of stem bark of this tree species by elephants. The amount of debarking a mopane tree can withstand was to be investigated using an experiment in which mopane trees were subjected to different amounts of stem bark removal, and the phenological changes the tree underwent, recorded.

5: Essential to the understanding of the autecology surrounding any plant species, is the mode(s) of seed dispersal. In the literature it is claimed that the dispersal of diaspores of *C. mopane* occurs by epizoochory due to the sticky nature of the diaspore. Field observations questioned this mode of dispersal, and it was thus deemed necessary to investigate the matter further, as epizoochory inferred an inextricable link between herbivores and the mopane tree.

6: Possible ungulate feeding preferences for different food parts of *C. mopane* were to be investigated using goats *Capra hircus* as study subjects. Goats were chosen as they are easy animals to handle and observe in captivity, and because they are selective intermediate feeders, choosing a mixed diet. Impala *Aepyceros melampus*, the most abundant ungulate species of the NTGR, is also a selective intermediate feeder. Thus the purpose of this investigation was to use goats as an indicator of the probable feeding preferences impala would show for mopane, this hopefully furthering our understanding of the relationship between impala and mopane trees in the NTGR. Moreover, this investigation would also allow for the testing of whether goats do indeed serve as direct indicators of browse quality, their preferences reportedly being for food items having little fibre and few condensed tannins.

7: Preliminary field observations revealed that elephant-damaged areas on mopane trees often served as a nesting site for certain insects such as mopane bees *Trigona* spp. and cocktail ants *Crematogaster* spp.. It was decided that the utilization of elephant damaged trees by some of the insects commonly encountered in the mopane veld type was to be studied. The destructive effect of elephants on habitats is well documented, but the possible advantages of their tree-damaging habits is not recorded. The records were to be seasonal, in the hope that should seasonal relationships between insects and mopane trees exist, that these could be related to the seasonal relationships between mammals and mopane trees.

8: Caterpillars of the mopane moth have been absent from within the confines of the NTGR for nearly the last two decades. It was thus necessary to determine why these caterpillars, one of the major herbivores of the mopane tree, have become locally extinct. Possible factors such as ant predation, edaphic factors and leaf chemistry were to be investigated in an attempt to explain their local absence.

CHAPTER

THREE

GENERAL METHODS

TECHNIQUES EMPLOYED TO INVESTIGATE THE SEASONAL CHEMICAL PROFILES OF THE MOPANE PLANT MATERIAL COLLECTED.

The seasonal differences between the chemical composition of mopane plant parts, was investigated by collecting independent samples on a seasonal basis. Samples were dried in an oven at 50°C for 96 h, and then ground in a Wiley mill (40-mesh). Percent crude protein content (CP) and percent nitrogen content (NI) were determined using a macrokjeldahl method. The amount of available energy (EN) in the samples, was determined using a CP 400 bomb calorimeter (Coalab supplies (Pty) Ltd., Johannesburg). The results are expressed in kJ/g plant material. The condensed tannin content (CT) of the samples was determined using a slight modification of the vanillin assay (Terrill *et al.* 1990). One hundred milligrams of the sample was weighed out and added to 5ml MeOH. After centrifugation for 10 min at 3000xG, two 1ml aliquots of the sample were removed, one representing the blank, the other the sample. These aliquots were redissolved in a 5ml MeOH solution (4ml HCl, 96 ml MeOH and 2g Vanillin reagent). The samples, covered in aluminium foil to prevent light oxidation from biasing results, were placed in a waterbath at 30°C for 10 min, after which the absorbance was measured on a spectrophotometer at 495nm. Commercially available catechin was used as standard. Results are expressed in mg Catechin/g plant material. The protein precipitation capacity (PP) was determined using the radial diffusion assay described in Hagerman (1987). Total phenolic content (TP) of the samples was determined by using a slight modification of the Prussian blue redox assay described in Price & Butler (1977). One hundred milligrams of dry material was added to 5ml MeOH and centrifuged for 10 min at

3000xG. Two 0,5ml aliquots of the sample were used, one representing the standard and the other the sample. The following reagents were added to the aliquots, 30ml H_2O, 3ml 0,005M $FeCl_3$ and 3ml 0,008M $K_3Fe(CN)_6$. After 10 minutes, the absorbance was measured on a spectrophotometer at 720nm. Commercially available catechin was used as standard. Results are expressed in mg Catechin/g plant material. The methods used to determine the percent Neutral Detergent Fibre (NDF), and percent Acid Detergent Fibre (ADF) content of the samples, are according to Robertson & van Soest (1981) and Goering & van Soest (1970). The moisture content (MO) of the samples was determined as follows: samples collected were placed into plastic packets and sealed. The samples were weighed in the packets, and the masses of the packets were then measured so as to give the true mass of the sample by subtraction. Samples were dried in an oven for 72 h and their dry masses determined. The percent moisture in the sample collected was calculated by dividing the mass lost during drying by its wet mass. All results for each parameter for each season were ranked and the differences between overall seasonal contents for each parameter investigated using the Kruskall-Wallis Analysis by Ranks Test. If a significant difference was obtained the seasonal differences were identified using the Mann-Whitney Test, each season being tested against every other season. For every parameter studied all seasons were ranked according to their mean value, and the ranks for the seasons combined to determine a palatability index based on the ranks assigned. Where seasons were not being compared the results obtained for the respective parameters of the respective plant parts were compared using the Mann-Whitney Test (Siegel 1956).

CHAPTER

FOUR

THE SEASONAL CHEMISTRY OF *COLOPHOSPERMUM MOPANE*

SEASONAL VARIATIONS IN THE QUALITY OF MOPANE LEAVES AS A SOURCE OF BROWSE FOR MAMMALIAN HERBIVORES

INTRODUCTION:

Studies have shown that the quality of leaves as food for herbivores involves a complex combination of characteristics which often change in the course of a season (Scriber & Fenny 1979; Schroeder & Malmer 1980; Cooper *et al.* 1988). In southern Africa, browse is more important to mixed-feeding herbivores in the dry season than is grass (Anderson & Walker 1974), the nutritional value of browse (dicotyledonous plants) generally being higher than that of grass, especially when grass lignifies (Bonsma 1942; Dietz 1965). The browse available on semi-deciduous tree species such as the mopane, is commonly regarded as the current season's growth of leaves and twigs (Blair 1971; Halls & Harlow 1971; Bobeck & Dzieciolowski 1972).

When herbivores exert sufficient selective pressure on their hosts, hosts do not respond passively to damage (Rhoades 1979; Baldwin & Schultz 1983; Teague 1989; Lundberg & Astrom 1990), but evolve defenses, termed inducible defenses (Hendrix 1988; Edelstein-Keshet & Rausher 1989), such as toxic chemicals, protective physical factors and nutrient deficiencies that tend to reduce or at least discourage attack (Bate-Smith 1971; Freeland & Janzen 1974; Arnold & Hill 1975; Coley 1986; Karban *et al.* 1989; Lundberg & Astrom 1990; Teague *et al.* 1990). Thus the value of a host plant's tissue for herbivores is a function of its nutrient and secondary compound contents (Rosenthal & Janzen 1979). It seems especially difficult for a plant to defend its young leaves through physical constraints, because a tough cuticle and a high content of dry matter, both resulting in unpalatability (Coley 1983), are not compatible with the rapid expansion and high metabolic activity of young leaves (Harper 1989). Moreover, any plant that invests in defenses will reduce its losses to herbivores (Coley *et al.* 1985), as the palatability of browse is determined largely by its chemical and mechanical properties (Jachmann & Bell 1985) and secondary metabolite concentrations (Schoonhoven & Derksen-Koppers 1976). Furthermore, acceptability of a plant as food for a herbivore is determined by a combination of feeding incentives and deterrents (Buchsbaum *et al.* 1984).

Coley *et al.* (1985) suggest that both the quantity and the quality of the plant defense is determined mainly by the resource availability of the environment in which the plant occurs. Highly predictable plants such as long-lived climax species are thought to be unable to escape their enemies in either space or time, therefore favouring the evolution of quantitative rather than qualitative defenses (Jing & Coley 1990). Carbon-based defenses seem to be associated with habitats of low resource availability (Rhoades & Cates 1976; Coley et al. 1985). Toxic secondary compounds are more likely to be found in vulnerable plant parts (McKey 1979) such as leaves, than in woody plant parts (Barnes 1982). The accumulation of tannins, or other allelochemical substances, represents a significant caloric cost to the plant (Barbour *et al.* 1987). Janzen (1974) hypothesizes that the caloric energy invested in defense should be proportional to the metabolic cost of replacing browsed tissue. Thus it is expected that a tissue rich in digestible carbohydrates and inorganic nutrients would also be relatively rich in palatability-reducing defense compounds (Barbour *et al.* 1987), a most important group of secondary plant metabolites being tannins (Haslam 1979; Martin & Martin 1982; Tempel 1982; van Hoven 1984; Bernays *et al.* 1989).

The role tannins play at the ecological level is certainly varied, involving a defense mechanism against herbivory through their adverse effects on protein digestion and enzyme activity (Goldstein & Swain 1965; Swain 1965,1979a,b; McLeod 1974; Feeny 1968,1976;

Rhoades & Cates 1976; Cates & Rhoades 1977; Cameron & Lapoint 1977; Mould & Robbins 1982; Coley 1983; Zucker 1983; Cooper & Owen-Smith 1985; Goldstein & Spencer 1985; Robbins *et al.* 1987a,b; Happe *et al.* 1990).

The purpose of the present investigation was to determine the seasonal chemical profiles of mopane as a browse, and to attempt to ascertain whether the mopane undergoes seasonal changes in leaf chemistry, and whether or not these changes would meet the yearly requirements of browsing mammals.

MATERIALS AND METHODS:

Each season, independent samples of green and senescing (yellow colour) mopane leaves were collected. Four leaf classes (phenophases) were identified over the spring leaf flush period (October). Independent samples were collected for each of the four leaf classes. The four classes are:

Class 1: The newly emerged leaf primordia having a definite red colour.

Class 2: Very new green leaves.

Class 3: The mature mopane leaflet possessing a dark green colour.

Class 4: Senescing leaves retained on the canopy.

A sample comprised leaves collected all around the canopy at a height of 2m above ground level, so taking into consideration the effect aspect could have on the chemical composition of the leaves. The methods used to analyze the samples' chemical composition are described under general methods.

The number of leaflets (**developing ones**) a mopane branch possesses over the period from leaf flush to first signs of leaf senescence was determined. This was done by marking 500 branches around a waterhole, an area which experienced heavy mammal utilization by both grazing and browsing ungulates. This site was chosen as it should provide a good representation of how the number of leaflets on a branch vary with seasonality, and what the rate of removal of mopane leaf material by browsers could be. Branches were marked using numbered plastic botanical tags, secured to the base of the branch where it emerged from the main stem zone, so making them unobtrusive. Five branches all occurring between 0,5m and 2,0m above ground level were marked on each tree, so rendering their leaves highly accessible to browsing ungulates. The trees chosen were all adjacent to the main animal approach paths to water, but were never closer than 30m from the water because, at this distance, the animals lost interest in feeding and moved rapidly to drink. The first leaflet count was done in spring and thereafter counts of the number of leaflet pairs on the marked branches were repeated during the summer and autumn sampling periods.

The phenological differences the two dominant mopane morphs of the NTGR display are so extreme, that it was deemed necessary to investigate the period of spring leaf flush, one of the most important periods in the NTGR (P. le Roux *pers. comm.*)[1], comparing the phenologies of the two morphs. The present study was conducted during the last week of October 1992, the period when the mopane trees of the NTGR were well into their initial stages of spring leaf flush. Six sites were chosen, three along the Jwala riverine fringe where the dominant mopane morph is a tall relatively undamaged one, and three sites on the open plains where the dominant morph is the "bonsai" morph. At each site one hundred trees were sampled. The various stages of leaf flush that a mopane tree undergoes were classified as follows:

STAGE 1: The new emerging leaf primordia possessing a definite red colour.

STAGE 2: The "red buds" as described above, but now green.

STAGE 3: The new leaflet having emerged, but no unfurling as yet.

STAGE 4: The young green leaflet is now completely unfurled, and the new flush of greenery on the tree is easily visible from at least 25m.

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RESULTS:

TABLE 1: THE MEAN SEASONAL CHEMICAL CONTENT OF MATURE GREEN MOPANE LEAVES

						SIGNIFICANCE			
SN	PAR	N	$\bar{X}$±S.D.	RANK	K-W	WI	SP	SU	AU
WI	CP	20	9,31±0,27	4	***	-	***	***	***
SP		20	9,74±0,25	3		-	-	***	***
SU		20	15,92±0,12	1		-	-	-	***
AU		20	12,90±0,50	2		-	-	-	-
WI	NI	20	1,49±0,04	4	***	-	***	***	***
SP		20	1,56±0,04	3		-	-	***	***
SU		20	2,55±0,02	1		-	-	-	***
AU		20	2,06±0,08	2		-	-	-	-
WI	EN	20	20,43±2,31	1	***	-	***	***	*
SP		20	19,12±0,40	2		-	-	***	***
SU		20	18,55±0,33	4		-	-	-	***
AU		20	19,45±0,32	3		-	-	-	-
WI	MO	15	32,73±2,16	4	***	-	***	***	***
SP		15	45,81±1,91	1		-	-	N/S	***
SU		15	43,05±4,20	2		-	-	-	N/S
AU		15	41,13±3,25	3		-	-	-	-
WI	CT	10	74,29±0,91	3	***	-	***	***	***
SP		10	80,05±1,90	4		-	-	***	***
SU		10	63,19±2,89	1		-	-	-	***
AU		10	70,87±0,99	2		-	-	-	-
WI	TP	10	206,5±5,45	4	***	-	***	***	*
SP		10	176,3±2,70	1		-	-	***	***
SU		10	183,9±3,05	2		-	-	-	*
AU		10	194,3±6,85	3		-	-	-	-
WI	PP	10	38,50±3,23	1	***	-	***	***	***
SP		10	69,83±5,68	4		-	-	***	***
SU		10	41,05±4,06	2		-	-	-	N/S
AU		10	48,43±5,15	3		-	-	-	-
WI	NDF	4	35,45	1					
SP		4	39,26	4					
SU		4	38,02	3					
AU		4	37,25	2					
WI	ADF	4	27,76	1					
SP		4	32,24	4					
SU		4	31,40	3					
AU		4	29,65	2					

KEY: WI- WINTER; SP- SPRING; SU- SUMMER; AU- AUTUMN; CP- CRUDE PROTEIN; NI- NITROGEN; EN- ENERGY; MO- MOISTURE; CT- CONDENSED TANNIN; TP- TOTAL PHENOLIC; PP- PROTEIN PRECIPITATION; NDF- NEUTRAL DETERGENT FIBRE; ADF- ACID DETERGENT FIBRE.

(**Significance values:** ***, <0,001; **, <0,01; *, <0,05; N/S, non-significant)

For mature green mopane leaves, according to the Kruskall-Wallis results, highly significant differences (p<0,001) exist between all parameters for all seasons. Summer is the season whose green leaf component has both significantly (p<0,001; Mann-Whitney Tests) more nitrogen and crude protein. Autumn green leaves have significantly (p<0,05) more energy than do the other seasons. Spring green leaves have the highest moisture content seasonally, this being significantly different (p<0,001) from those of both autumn and winter. Summer's green leaves have the fewest condensed tannins (p<0,001), while green leaves have the fewest total phenolics (p<0,05). Note that winter's green leaf component has the lowest protein precipitation capacity (p<0,001) and the lowest fibre content (NDF and ADF).

TABLE 2: SEASONAL PALATABILITY AS DETERMINED BY THE RANK VALUES ASSIGNED IN TABLE 1

SEASON	RANK VALUES	$\bar{X}$ VALUE	FINAL PALATABILITY RANK
WINTER	4 4 1 4 3 4 1 1 1	2,56	3
SPRING	3 3 2 1 4 1 4 4 4	2,89	4
SUMMER	1 1 4 2 1 2 2 3 3	2,11	1
AUTUMN	2 2 3 3 2 3 3 2 2	2,44	2

TABLE 3: THE MEAN SEASONAL CHEMICAL CONTENT OF SENESCING MOPANE LEAVES

SN	PAR	N	$\bar{X}$±S.D.	RANK	K-W	SIGNIFICANCE			
						WI	SP	SU	AU
WI	CP	20	3,41±0,17	2	***	-	***	***	***
SP		20	3,59±0,18	1		-	-	***	***
SU		20	3,05±0,13	4		-	-	-	***
AU		20	3,23±0,11	3		-	-	-	-
WI	NI	20	0,54±0,03	2	***	-	***	***	*
SP		20	0,58±0,03	1		-	-	***	***
SU		20	0,49±0,02	4		-	-	-	***
AU		20	0,52±0,02	3		-	-	-	-
WI	EN	20	17,65±0,41	2	***	-	***	***	***
SP		20	18,48±0,22	1		-	-	***	***
SU		20	16,75±0,39	4		-	-	-	*
AU		20	16,97±0,18	3		-	-	-	-
WI	CT	10	71,17±1,18	4	**	-	***	N/S	N/S
SP		10	68,35±0,97	1		-	-	N/S	***
SU		10	69,79±1,92	2		-	-	-	N/S
AU		10	70,99±1,10	3		-	-	-	-
WI	TP	10	309,5±7,87	4	***	-	***	***	***
SP		10	279,5±8,05	2		-	-	N/S	*
SU		10	286,8±19,3	3		-	-	-	N/S
AU		10	271,4±4,74	1		-	-	-	-
WI	PP	10	73,23±6,29	3	N/S				
SP		10	74,93±5,80	4					
SU		10	68,53±5,68	2					
AU		10	68,43±10,6	1					

According to the Kruskall-Wallis results, highly significant differences ($p<0,01$) exist between all parameters except protein precipitation, for all seasons. The highly significant (p<0,001) differences between the condensed tannin contents between winter and spring and spring and summer samples, result from the spring samples having the lowest average condensed tannin content. Winter samples have the highest average total phenolic content, hence the significant differences (p<0,001) between the winter samples and all the other seasons' samples. A significant difference (p<0,05) exists between the total phenolic content in the spring and autumn senesced leaf samples.

TABLE 4: SEASONAL PALATABILITY AS DETERMINED BY THE RANK VALUES ASSIGNED IN TABLE 3

SEASON	RANK VALUES	$\bar{X}$ VALUE	FINAL PALATABILITY RANK
WINTER	2 2 2 4 4 3	2,83	3
SPRING	1 1 1 1 2 4	1,67	1
SUMMER	4 4 4 2 3 2	3,12	4
AUTUMN	3 3 3 3 1 1	2,33	2

TABLE 5: THE MEAN CHEMICAL CONTENT OF FOUR CLASSES OF SPRING LEAVES

						SIGNIFICANCE			
SN	PAR	N	$\bar{X}$±S.D.	RANK	K-W	VY	YN	GL	SL
VY	CP	20	13,33±0,21	2	***	-	***	***	***
YN		20	17,57±0,44	1		-	-	***	***
GL		20	9,74±0,25	3		-	-	-	***
SL		20	3,59±0,18	4		-	-	-	-
VY	NI	20	2,13±0,03	2	***	-	***	***	***
YN		20	2,81±0,07	1		-	-	***	***
GL		20	1,56±0,04	3		-	-	-	***
SL		20	0,58±0,03	4		-	-	-	-
VY	EN	20	20,96±0,15	1	***	-	***	***	***
YN		20	20,02±0,12	2		-	-	***	***
GL		20	19,12±0,40	3		-	-	-	***
SL		20	18,48±0,22	4		-	-	-	-
VY	MO	15	40,87±2,50	2	***	-	N/S	***	
YN		15	39,93±2,94	3		-	-	***	
GL		15	45,81±1,91	1		-	-	-	
VY	CT	10	70,63±1,68	3	***	-	***	***	**
YN		10	61,73±2,42	1		-	-	***	***
GL		10	80,05±1,90	4		-	-	-	***
SL		10	68,35±0,97	2		-	-	-	-
VY	TP	10	192,1±7,60	3	***	-	***	**	***
YN		10	147,7±4,22	1		-	-	***	***
GL		10	176,3±2,70	2		-	-	-	***
SL		10	249,5±8,05	4		-	-	-	-
VY	PP	10	106,5±13,1	4	***	-	***	***	***
YN		10	58,58±3,74	1		-	-	***	***
GL		10	69,83±5,68	2		-	-	-	N/S
SL		10	74,93±5,80	3		-	-	-	-
VY	NDF	4	20,92	1					
YN		4	35,50	2					
GL		4	39,26	4					
SL		4	35,53	3					
VY	ADF	4	22,64	1					
YN		4	30,98	3					
GL		4	32,24	4					
SL		4	30,24	2					

KEY: VY- VERY YOUNG LEAVES; YN- YOUNG GREEN LEAVES; GL- GREEN MOPANE LEAVES; SL- SENESCING LEAVES

According to the Kruskall-Wallis results, highly significant differences ($p<0,001$) exist between all parameters investigated for the above phenophases. Young green mopane leaves, have significantly more ($p<0,001$; Mann-Whitney Test) crude protein and nitrogen than do any of the other leaf types studied. They also have a significantly lower (p<0,001) condensed tannin content, and the lowest mean protein precipitation capacity value. In addition, they also possess the second highest amount of available energy. Although the young mopane leaves have significantly less (p<0,001) moisture than do the fully developed green leaves, the above parameters definitely identify them as the most palatable, and thus valuable, mopane phenophase for herbivores. This phenophase also has less fibre (NDF and ADF values) than do the mature green mopane leaves.

Mature green leaves have approximately half the crude protein and nitrogen content of young leaves, and significantly less (p<0,001) available energy. However, they do have significantly more (p<0,001) moisture. Nevertheless, this phenophase has a significantly greater (p<0,001) condensed tannin and total phenolic content than any of the other leaf types, and a higher protein precipitation capacity. Of the green leaf types studied over the spring flush, this leaf type would rank second to young leaves in palatability to mammalian herbivores, very young mopane leaves ranking third.

TABLE 6: SEASONAL PALATABILITY AS DETERMINED BY THE RANK VALUES ASSIGNED IN TABLE 5

LEAF TYPE	RANK VALUES	$\bar{X}$ VALUE	FINAL PALATABILITY RANK
VERY YOUNG	2 2 1 2 3 3 4 1 1	2,11	2
YOUNG	1 1 2 3 1 1 1 2 3	1,67	1
GREEN	3 3 3 3 4 2 2 4 4	3,11	4
SENESCING	4 4 4 1 2 4 3 3 2	3,00	3

TABLE 7: COMPARATIVE RESULTS SHOWING THE PHENOLOGICAL DIFFERENCES IN THE TIMING OF LEAF FLUSH BY THE TWO DOMINANT MOPANE MORPHS

DATE	SITE	N	No. IN FLUSH	No. IN STAGE1	No. IN STAGE2	No. IN STAGE3	No. IN STAGE4
08\10\91							
	OPEN A	100	31	17	14	00	00
	OPEN B	100	41	25	14	02	00
	OPEN C	100	36	21	10	05	00
$\bar{X}$			**36**	**21**	**13**	**02**	**00**
	RIVER A	100	16	15	01	00	00
	RIVER B	100	22	16	06	00	00
	RIVER C	100	11	11	09	02	00
$\bar{X}$			**16**	**13**	**03**	**00**	**00**
24\10\91							
	OPEN A	100	57	23	21	10	03
	OPEN B	100	71	27	22	19	03
	OPEN C	100	79	14	23	17	25
$\bar{X}$			**69**	**21**	**22**	**15**	**11**
	RIVER A	100	48	29	15	04	00
	RIVER B	100	47	36	11	00	00
	RIVER C	100	31	25	05	01	00
$\bar{X}$			**42**	**30**	**10**	**02**	**00**

The comparative phenological results show very interesting differences between the bonsai mopane trees of the open plains and the much taller, less-damaged mopane trees of the riverine fringe. Resplendent in the early October sample (08\10\91) is that many more mopane trees in the open (36%) are beginning their spring leaf flush than are mopane trees along the rivers (16%).

This trend is even more evident in the later sample (24\10\91), 69% of the bonsai mopane trees being in leaf as opposed to 42% of the riverine mopane trees. Furthermore, note the vast differences between the number of bonsai's in an advanced state of leaf flush (S3: 15% ; S4: 11%), as opposed to the riverine mopane's (S3: 2% ; S4: 0%). Thus, the heavily browsed bonsai mopane trees come into leaf flush earlier, and are thus in an advanced state of leafiness earlier than their taller, less-browsed riverine counterparts.

TABLE 8: DIFFERENCES BETWEEN THE NUMBER OF DEVELOPING LEAFLETS ON BRANCHES FROM LEAF FLUSH (SPRING) TO LEAF SENESCENCE (AUTUMN)

SEASON	N	$\bar{X}$ No. LEAFLETS	SIGNIFICANCE (t-test) SP	 SU	 AU
emerging					
SPRING	500	22,05±14,15	-	***	(N/S)
SUMMER	500	30,51±26,82	-	-	***
AUTUMN	500	21,11±20,40	-	-	-
senescing					

The counts performed for the three seasons associated with the period from leaf flush to beginnings of leaf senescence, show that highly significant differences exist between the spring and summer (p<0,001) and summer and autumn leaf counts (p<0,001). No difference exists between the spring and autumn leaf counts (p>0,05). The differences that exist between the spring and summer, and autumn and summer samples, arise from the increase in the mean number of leaflets per branch from summer through to autumn, hence the non-significant result for the spring-autumn comparison.

DISCUSSION:

It has been stated that mammalian herbivores seek out mopane leaves as a form of browse when environmental conditions are poor and the veld is desolate, this having led to the perception of mopane as being a less-palatable browse, which is utilized only under adverse conditions (Lind 1974).

The severe drought during the 1991-1992 study period, resulted in the veld being probably at its most desolate (A. McKenzie *pers. comm.*)[2]. Leaves were absent from most of the woody tree species present in the NTGR by the end of November, as most new young leaves atrophied in the face of the moisture shortage. The fact that mopane trees underwent leaf flush independent of rainfall, and maintained leaf development and production under such adverse conditions, confirms that these trees indeed act as an emergency food supply for mammalian herbivores.

As a form of browse available to mammalian herbivores, the mature green leaves of *Colophospermum mopane* are most palatable over the summer and autumn seasons, seasonal palatability in descending order of preference as evident from chemical studies done, being first summer and autumn, then winter and finally spring. Over the summer-autumn period animals utilized these trees extensively due to the leafless condition of the other woody species present in association with mopane trees. Palatability appears to decrease with the onset of winter, largely due to an increase in the condensed tannin and total phenolic contents. However, the protein precipitation capacity of this season's leaf material is concomitantly at its lowest, and this may well offset the previous two parameters, rendering the overall seasonal change in palatability from autumn to winter, hardly significant. The seasonal

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palatability of the mopane tree as browse, does undergo significant seasonal changes, but such are the fluctuations in the chemical composition of the browse, that mopane trees always act as a utilizable emergency resource for mammalian herbivores should adverse conditions, especially dry conditions prevail, resulting in a food shortage.

In spring the mature green mopane leaf is least palatable. This condition coincides with the mopane spring leaf flush beginning in early October, when the NTGR was at its most desolate. Very few woody species had any leaves except for some of the large riverine trees whose leaves were well beyond the reach of browsing mammals other than elephants and giraffes *Giraffa camelopardalis.* The emergence of the new green foliage triggers its utilization by impala, kudu *Tragelaphus strepsiceros*, steenbok *Rhapicerus campestris*, grey duiker *Sylvicapra grimmia*, eland *Taurotragus oryx*, giraffes, elephants and occasionally even wildebeest *Connochaetes taurinus* and zebra *Equus burchelli.* Most of these animal species were hardly ever seen feeding off the mature leaves, irrespective of season. The nutritional quality of semi-deciduous leaves decreases with maturity largely because mature leaves generally contain fewer nutrients (Mattson 1980; Schroeder 1986) than immature leaves (Schultz *et al.* 1982; Schroeder 1986).

The beginning of a growing season often heralds the reduction in chemical defenses and an increase in shoot nutrients, which results in an increase in the palatability of a woody species (Bryant *et al.* 1983; Cooper & Owen-Smith 1985; Dannell & Huss-Dannell 1985; Cooper *et al.* 1988; du Toit 1988; Bernays *et al.* 1989), and consequently it is common for plants to demonstrate striking seasonal differences in the intensity of defoliation (van der Meijden *et al.* 1988). A consequence of this is discrete browsing *i.e.* the habit of using the most nutritious parts of the plant (Stenseth 1981; Astrom *et al.* 1990). Mopane was never thought to rank high in the diet of impala, kudu, steenbok or grey duiker, yet these ungulate species fed almost exclusively on young mopane leaves, while they were slowly approaching a waterhole from which these observations were made. Virtually no herbivore consumes all parts of a plant (except in the cases of small seed predators) and observations of herbivores eating this or that species of plant are of limited value (Janzen 1981), as prevailing environmental conditions often dictate which plant parts are selected.

The new leaf flush, which are higher in nitrogen, young leaves typically having more nitrogen than mature leaves (Coley & Aide 1991), is of great value to the herbivores of the NTGR. Moreover, utilization is positively correlated with nitrogen content (Jachmann & Bell 1985; Kursar & Coley 1991).

Though woody plants frequently experience severe browsing (Bryant *et al.* 1983), their responses to browsing or defoliation are still poorly understood (Caldwell *et al.* 1981; Welker *et al.* 1985; Welker *et al.* 1987). Mature woody plants respond to browsing by producing juvenile shoots with well developed chemical defenses (Bryant *et al.* 1983). However, du Toit *et al.* (1990) state that shoot regrowth in heavily browsed trees is exceptionally rapid, young leaves generally having low levels of condensed tannins and high levels of total nitrogen.

Leaves of the very palatable acacia species, *Acacia tortilis*, were found to have a 3% nitrogen content in their leaves (du Toit *et al.* 1991). Young mopane leaves have a mean nitrogen content of 2,8%, a value very nearly equalling that of *A. tortilis*. In a semi-arid area of Kenya, the highly palatable legume *Leucaena leucocephala* being considered to be the best browse available, was found to have a 4,4% nitrogen content, and a relatively low fibre content of 28,6% and 19,6% for NDF and ADF respectively (Wandera *et al.* 1991). Young mopane leaves have a fibre content of 35,5% and 30,9% for NDF and ADF respectively. *Eulalia villosa* (Gramineae) is generally regarded as a palatable grass species (Tainton *et al.* 1985). Analysis of this grass found the condensed tannin content and protein precipitation capacity to be 76,1 mg Catechin/g dry material (mg C./g) and 61,1 respectively (du Toit, Wolfson & Ellis 1991). In comparison, young mopane leaves have a condensed tannin content of 61,7mg C./g dry material and a protein precipitation capacity of 58,6. In both cases the values for the browse is lower, and so it can be confidently said that young leaves of *C. mopane* are of better nutritive value for herbivores than is the palatable grass *E. villosa*. In addition, young leaves have a mean total phenolic content of 147,7 mg C./g dry material, this being significantly lower than that of *Acacia nilotica* (373,3 mg C./g), a palatable woody species (du Toit *et al.* 1990). *Acacia tortilis* was recorded as having a total phenolic content in its leaves of 90,9 mg C./g (du Toit *et al.* 1990).

High levels of inducible defenses can regulate herbivore populations under a wide variety of conditions and may suppress herbivore populations (Edelstein-Keshet & Rausher 1989). It is thus crucial for the carrying capacity of the NTGR to have a massive mopane leaf flush available at a critical time when leaves have a very low secondary compound content, to carry the herbivores through this needy period.

On the other hand, synchronous production of young leaves by mopane trees during times of low herbivore density may permit them to avoid most herbivores and satiate those that are present (Aide 1988; Aide 1991), herbivore feeding on hosts generally being limited to harvesting less than 10% of a host's energy resources (Pimentel 1988). du Toit *et al.* (1990) found the tannin content in leaves on *Acacia nigrescens* trees experiencing frequent browsing, to be far lower than in trees of the same species which did not experience browsing. This is a direct indication that severe browsing can increase palatability (Ernst *et al.* 1991), and so mammalian herbivores must be capable, to some degree, of managing their resources (Gordon & Lindsay 1990). Nevertheless, according to du Toit *et al.* (1991) the benefits of concentrated browsing (high productivity) appear to be relatively short lived, preliminary evidence indicating that the browsed species are being replaced by less palatable and productive species. This may indeed be the case in less robust woody species eg. mimosoid legumes such as acacias, but due to the resilience of *C. mopane*, this can be disregarded.

The very palatable nature of the young leaf is attributed to the heavy browsing pressure mopane trees within the NTGR experience. The young leaf material analyzed was collected from trees heavily browsed by elephants and eland, such trees being kept in a suppressed state resulting in the formation of extensive hedges. The end of the dry season in the NTGR, a period occurring concomitantly with the spring leaf flush, is usually a period of severe food shortage. The young green mopane leaves emerging independently of rain, have a crude protein content of 17,5%, a value far exceeding the requirements of kudu (Owen-Smith & Cooper 1989). The crude protein content of the diet of kudu, a very selective feeder, in a savanna biome was found to vary between 12-14% during the late wet season, declining to about 9% at the end of the dry season (Owen-Smith & Cooper 1989). They also found newly emerged leaves of certain unpalatable savanna tree species whose browse was generally regarded as being unpalatable, to be highly palatable. Mature mopane leaves have a crude protein content varying from 9,3% in winter to 15,9% in summer.

Guy *et al.* (1979) conducted a study on the phenology of some Zimbabwean trees. He found that in most species the flower buds were seen at about the same time as the emergence of the new leaves. *Colophospermum mopane* was an exception, the formation of flower buds being delayed until after the leaf flush. The flowers of *C. mopane* are insignificant, being small and greenish in colour, the flowering season being erratic, varying from October to March, trees sometimes not flowering for several years (Guy *et al.* 1979; Coates-Palgrave 1988). My results together with the afore-mentioned phenological observations again emphasize the importance of the spring leaf flush of *C. mopane*. It is however, very interesting to consider the possible ecological reasons for this temporal separation of flower emergence and leaf emergence. Young leaves, due to their being highly palatable, should experience quite severe herbivory, both by megaherbivores such as elephants, and mammalian ungulate browsers. Should flowers also be present at this time, the chances of their being devoured by the herbivores who are relying on mopane over this needy period, is great. This would prove to be a very disadvantageous condition as flowering is a process of mass energy expenditure by a plant to reproduce.

Martin (1974) reports that if young and newly matured leaves of *C. mopane* were removed soon after the flush, regrowth over the remainder of the growing season was negligible. My results are not in agreement, three trees defoliated completely in early spring for experimental purposes, all showed signs of new leaf emergence only three weeks after the mass defoliation occurred. It is hypothesized that the first spring flush of *C. mopane* in the NTGR is a highly palatable one, with massive amounts of nutrients being mobilized from sinks within the plant to the sources (new young leaves). Upon defoliation occurring a new growth spurt occurs and new young leaves again emerge. When the herbivore pressure on the mopane trees of the NTGR is alleviated, usually through rain, and browsing levels have decreased due the emergence of leaves on other woody species, flowering will occur, the chances of the flowers being eaten now being negligible.

The results obtained for the leaf counts show an increase in the average number of developing leaflets on twigs from spring to summer followed by a decrease to autumn. This substantiates the utilization of mopane by mammals over this very dry period from summer through to early autumn due to the exceedingly poor rainfall (45mm Sep '91 to Sep '92; Pontdrift Records). Furthermore, this result correlates well with the documented seasonal palatability changes the green leaves undergo.

Senescing mopane leaves are an important source of food for the general ungulate spectrum of the NTGR, their value also being documented by Kelly & Walker (1976), impala being known to feed readily on these leaves. The riverine mopane trees retain far more dry leaf material than does the bonsai of the open plains, and thus the importance of the riverine mopane can be related back to making food available to ungulates over the dry season in the form of dry leaf material. These highly palatable senescing leaves in spring alleviate the necessity for a herbivore to browse the newly emerging mopane leaf buds.

Classical theory predicts that inconspicuous plants or tissues have such a low risk of consumption that defenses are not adaptive (Feeny 1976; Rhoades & Cates 1976). Only when escape cannot be achieved, as would be the case in monospecific stands, should defenses evolve (Henderson 1990). Mechanisms by which leaves defend themselves against damage or death might be expected to be concentrated at the time when leaves are most valuable to the plant (Harper 1989). Senescing leaves are most unpalatable in summer when the mature green mopane leaves are at their most palatable. Palatability of senescing leaves increases substantially into autumn, decreasing again slightly at the onset of winter. The very high levels of total phenolics may well be to reduce the rate of decay of leaves once they have fallen, so maintaining the emergency food supply for animals.

Senescing mopane leaves are at their most palatable in spring, this coinciding with the leaf flush, mopane buds being highly unpalatable. In spring senescing mopane leaves contain very little crude protein and nitrogen, but do possess a relatively high amount of available energy. Their condensed tannin content only differs significantly from that of green leaves. Furthermore, this phenophase has a high total phenolic content, the value being greater than that for any of the other leaf types, but they do not have a protein precipitation capacity different from that of young or green mopane leaves. In addition, senescing leaves have a relatively low fibre content, their NDF and ADF values respectively being very similar to those for young green mopane leaves.

Very young mopane leaves have significantly less crude protein and nitrogen than do the young leaves, nevertheless the concentration of both these parameters in this phenophase is relatively high. This together with the high available energy and moisture content, definitely place very young mopane leaves in a category that should attract browser attention. However, chemical defenses in the form of condensed tannins and total phenolics are very prevalent in this leaf type. Very young mopane leaves have a significantly greater condensed tannin and total phenolic content than do any of the other leaf types studied. The very high protein precipitation capacity of very young leaves and the abundance of the distasteful compounds, are mechanisms which deter herbivores from feeding off this leaf type of the mopane tree. This result supports the findings of Jachmann (1988) that newly sprouted woody vegetation in a *Combretum/Terminalia* savanna had high levels of secondary compounds, decreasing to lower levels after 3-6 weeks of growth.

In conclusion, it is felt that mopane trees have been exceedingly maligned in their ecological importance for mammalian ungulates. This is substantiated by the subtle changes the leaf classes of this tree species undergo in their chemical composition, each palatability change either for the better or worse, being complemented by changes in the other leaf classes so that an overall balance for the good of herbivores in general, is maintained.

AN ATTEMPT TO CORRELATE UNGULATE FEEDING PREFERENCE BEHAVIOUR WITH THE VOLATILE COMPOUNDS PRESENT IN YOUNG AND MATURE LEAVES OF *COLOPHOSPERMUM MOPANE* (CAESALPINIOIDEAE; LEGUMINOSAE)

INTRODUCTION:

Acceptability of a plant as food for a herbivore is determined by a combination of feeding incentives and deterrents (Buchsbaum *et al.* 1984). Selection processes whereby herbivores evaluate browse include not only looking at the plant, but also smelling and tasting it (Oh *et al.* 1968; Frost 1981). Several plants rejected by impala lambs in a feeding trial had a definite odour (Frost 1981). When forage plants contain volatile compounds which are known to inhibit rumen microbial activity, it is logical to expect that ruminants' feed intake or sensitivity would in turn be affected by those volatile compounds in both ways, olfactory and antirumen microbial action (Oh *et al.* 1967).

Early in its development the terminal leaflet reveals the presence of resin cavities (Stein 1978). Oates (1972) speculates that the aroma of the resin in mopane leaves could possibly be the reason why mopane is not readily taken by browsing animals. Both mopane leaves and seeds have a very strong turpentine smell (Bonsma 1976). Dunham (1980), using a tame impala, conducted an experiment on ten plant species to determine the mean bite rates and mean food rate intakes. Results revealed that for mopane the mean bite rate was the lowest, whilst the mean food rate intake was the highest, indicating the ease with which browsers could utilize mopane due to its relatively large leaves and absence of spinescence (van Wyk 1972).

Certain oils in woody plant foliage are known to both smell strongly and inhibit digestion in the rumen (Rutherford 1979). Natural resistance to herbivores occurs within plants (Radwan *et al.* 1982), and essential oils and their terpenoid components have been prominent among chemical factors postulated to influence the animals' feeding preferences (Radwan & Crouch 1974). Monoterpene hydrocarbons such as alpha pinene, beta pinene and limonene have been shown to either promote slightly or have no effect on the microbial activity in the rumen of deer *Cervus* spp., however, they did promote rumen activity in sheep *Ovis aries* (Oh *et al.* 1967). Ponderosa pine *Pinus ponderosa* twigs collected from trees used by tassel-eared squirrels *Sciurus aberti* contained smaller amounts of monoterpenes than did twigs from similar trees not used by the squirrels as a food source (Farentinos *et al.* 1981).

Radwan *et al.* (1982) analyzed the essential oils in the foliage, stems and roots of ponderosa pine seedlings in an attempt to elaborate on the differential preferences of gophers for ponderosa pine. Oils were found to be composed mostly of monoterpene hydrocarbons. Results showed that neither yield nor constituents of foliage oils were significantly correlated with gopher damage. Oxygenated monoterpenes such as alpha-terpineol, terpinen-4-ol, fenchyl alcohol, linalool and citronellol are known to inhibit rumen microbial activity (Oh *et al.* 1967). Monoterpene esters such as citronellyl acetate and bornyl acetate are known to moderately inhibit microbial activity (Oh *et al.* 1967). Insects have been found to prefer trees which contain low concentrations of the monoterpene hydrocarbon limonene (Sturgeon 1979).

"Pine oil" is a general term referring to a complex mixture of oleoresins and terpene hydrocarbons produced in a living tree (Richmond 1985). Turpentine is comprised primarily of monoterpene hydrocarbons, and alone is attractive; however, its presence, along with the presence of ethanol will markedly increase attraction (Phillips *et al.* 1988; Chenier & Philogenie 1989).

Most unpalatable species seem to become temporarily more acceptable when their new leaves emerge at the start of the growing season (Owen-Smith & Cooper 1987,1988; Cooper *et al.* 1988). The nutritional quality of deciduous leaves decreases with maturity largely because mature leaves are reported to contain fewer nutrients (Mattson 1980; Schroeder 1986) but more fibre and tannins (Schultz *et al.* 1982; Schroeder 1986) than immature leaves.

The purpose of the present study was to investigate the volatile compounds present in the young green and mature green leaves of *Colophospermum mopane*, and to attempt to correlate the compounds present with the known palatability of the leaf. These results may explain whether the volatile spectrum a herbivore perceives could serve as an indicator of browse quality.

MATERIALS AND METHODS:

Samples of the volatile organic compounds produced by the mopane leaves were collected by using standard carbon traps (NIOSH), a well documented technique which is often employed for sampling air. A set of samples was also taken using a new technique which employs a fused silica trap coated internally with an ultra-thick film of silicone rubber (Burger *et al.* 1990). This second technique was included in the study since the method of desorbing the samples from the trap does not require the use of solvents. This reduces interference and the possible formation of artifacts, which often results when using solvents. The concentrating mechanism in the thick film traps, furthermore, is one of dissolution into a liquid-like phase rather than adsorption onto an active surface. This increases the chance of releasing intact molecules of labile and polar compounds for final analyses.

The carbon traps (NIOSH) were extracted with pure carbon disulphide according to a standard method (NIOSH) and 3μl of each extract was analyzed by GC-MS. The samples on the thick film traps (Burger *et al.* 1990) were desorbed in the hot GC inlet and focused on a cold column, after which they were analyzed using GC/MS. The instrumental conditions used for the analysis of these samples can be found in Table 3. A number of compounds were detected in the samples and the mass spectra obtained from these substances were used to tentatively identify the compounds. A mass spectral database, the Wiley Library of Mass Spectral Data, containing about 140 000 mass spectra, was used to compare each mass spectrum obtained with the standard spectra in the database. Matches of better than 90% were taken up in a list of tentatively identified compounds. Samples were collected *in situ* by building a cloth enclosure around a portion of the tree, in an attempt to minimize wind effects and the chance of the leaf actually coming into contact with the collecting tube. One sample was collected for each of the two study leaf classes. Sampling was conducted around midday using a standard air sampler with a vacuum control facility, electricity being supplied from the battery of the Land Rover on which the cloth enclosure had been built.

To investigate the differences between the chemical composition of the young green and mature green leaves of the mopane, independent samples were collected for both leaf types, and the analysis done according to the methods described under general methods.

RESULTS:

TABLE 9: LIST OF VOLATILE COMPOUNDS IN THE YOUNG LEAVES AS IMPLICATED BY GC-MS AND THE CORRESPONDING PEAK AREAS AS NORMALIZED TO THE LARGEST PEAK

COMPOUND	CARBON	THICK FILM
alpha pinene	100%	49,6%
beta pinene	4,0%	2,6%
limonene	n/d	5,3%
hexanol acetate	5,4%	11,4%
linalool	Trace	4,1%
alpha cubebene	4,5%	54,4%
alpha copaene	n/d	47,4%
hexenyl methylbutanoate	n/d	1,3%
caryophyllene	14,4%	100%
alpha humelene	1,1%	30,3%
aromadendrene	0,4%	0,8%
beta cubebene	2,9%	30,7%
dimethyl tetrahydro naphthalene	7,1%	16,7%
delta cadinene	n/d	7,4%
dimethyl hexahydro naphthalene	5,9%	7,9%

TABLE 10: LIST OF VOLATILE COMPOUNDS IN THE MATURE GREEN LEAVES AS IMPLICATED BY GC-MS AND THE CORRESPONDING PEAK AREAS AS NORMALIZED TO THE LARGEST PEAK

COMPOUND	CARBON	THICK FILM
alpha pinene	100%	9,5%
benzoic acid	n/d	1,0%
isobenzofurandione	n/d	1,9%
alpha cubebene	4,8%	30,8%
alpha copaene	n/d	52,4%
caryophyllene	9,5%	100%
alpha humelene	0,9%	42,9%
beta cubebene	0,5%	18,7%
dimethyl tetrahydro naphthalene	0,3%	62,7%
delta cadinene	3,3%	17,4%

n/d: not done.

TABLE 11: TABLE OF INSTRUMENT CONDITIONS

Mass spectrometer : Hewlett Packard hp 5988 Quadrupole
Operation temperature : Full Scan, electron impact ionization.
Source temperature : 200°C
Interface temperature : 280°C
Gas Chromatograph : Hewlett Packard hp 5890
Column : Fused silica capillary column, 0,32mm ID x 25m, SE-30, 0,4μm.
Carrier Gas : Helium
Inlet Temperature : 230°C
Column Temp. Programme : 40°C for 2 min, then 5°C/min to 280°C.

TABLE 12: LIST OF THE VOLATILE COMPOUNDS, THE GROUPS TO WHICH THEY BELONG AND THEIR EFFECT (INHIBITORY/PROMOTORY from Oh *et al.* 1967) ON RUMEN MICROBIAL ACTIVITY

MONOTERPENE HYDROCARBONS/ SESQUITERPENES (Promoting Group)	**OXYGENATED MONOTERPENES/ ESTERS (Inhibiting Group)**
alpha pinene (MH)	linalool (OM)
beta pinene (MH)	hexanol acetate (E)
limonene (MH)	
alpha cubebene (S)	caryophyllene (S)
alpha copaene (S)	
hexenyl methylbutanoate (S)	
alpha humelene (S)	
aromadendrene (S)	
beta cubebene (S)	
delta cadinene (S)	

TABLE 13: PERCENT CONCENTRATIONS* USING THE THICK FILM RESULTS OF THE INDIVIDUAL VOLATILES RELATIVE TO THE SUM OF TOTAL VOLATILES FOR BOTH YOUNG GREEN (YN) AND MATURE GREEN (GL) LEAVES

LEAF CLASS	VOLATILE	P/I	CONC[1].	INDIV. %
YN	alpha pinene	P	0,50	20,49
	beta pinene	P	0,03	01,22
	limonene	P	0,05	02,04
	alpha cubebene	P	0,54	22,13
	alpha copaene	P	0,47	19,26
	hexenyl methylbutanoate	P	0,01	00,44
	alpha humelene	P	0,30	12,29
	aromadendrene	P	0,01	00,44
	beta cubebene	P	0,31	12,70
	delta cadinene	P	0,07	02,86
	linalool	I	0,04	01,63
	hexanol acetate	I	0,11	04,50
			$\sum$=2,44	100,0
GL	alpha pinene	P	0,10	05,81
	alpha cubebene	P	0,31	18,02
	alpha copaene	P	0,52	30,23
	alpha humelene	P	0,43	25,00
	beta cubebene	P	0,19	11,04
	delta cadinene	P	0,17	09,90
			$\sum$=1,72	100,0

*: Based on relative peak areas only.

1: Figures from Tables 1 and 2.

Caryophyllene being the major volatile peak in both leaf types relative to which the percentages of all the other volatiles were calculated, was excluded from the above list, its effect being assumed to be neither promotory nor inhibitory of rumen functions. Alpha pinene is far more prevalent as a peak in the young leaves when compared with the old leaves. The young green mopane leaf also has beta pinene and limonene present, both compounds along with alpha pinene being known to facilitate rumen microbial activity. In total, the young green leaf has ten volatile compounds identified whose effects should aid rumen microbial processes, with only two volatile compounds, both comprising very little of the overall volatile spectrum, inhibiting rumen activity. Mature green leaves have only six volatile compounds identified, all of which should aid rumen fermentation processes. The following compounds have not been included in the table due to their not being monoterpenes nor sesquiterpenes, and their effect not being known on the rumen: dimethyl tetrahydro naphthalene and dimethyl hexahydro naphthalene, both being polycyclic benzenoid hydrocarbons, benzoic acid and isobenzofurandione. These are all aromatic compounds in the true chemical sense. Linalool, an oxygenated monoterpene, and hexanol acetate, an ester, are both compounds which do inhibit rumen microbial activity. However, due to their low percent occurrence and the wide spectrum of compounds present in the young leaf whose effects aid rumen processes, the negative effects these compounds may have on the rumen are probably neutralised.

TABLE 14: THE MEAN SEASONAL CHEMICAL CONTENT OF TWO CLASSES OF LEAVES OVER THE SPRING LEAF FLUSH PERIOD (Table adapted from Tables 1 and 5 respectively for the purpose of this explanation)

SN	PAR	N	$\bar{X}$±S.D.	RANK	SIGNIFICANCE
YN	CP	20	17,57±0,44	1	***
GL		20	9,74±0,25	2	
YN	NI	20	2,81±0,07	1	***
GL		20	1,56±0,04	2	
YN	EN	20	20,02±0,12	1	***
GL		20	19,12±0,40	2	
YN	MO	15	39,93±2,94	2	***
GL		15	45,81±1,91	1	
YN	CT	10	61,73±2,42	1	***
GL		10	80,05±1,90	2	
YN	TP	10	147,7±4,22	1	***
GL		10	176,3±2,70	2	
YN	PP	10	58,58±5,68	1	***
GL		10	69,83±5,68	2	
YN	NDF	4	35,50	1	
GL		4	39,26	2	
YN	ADF	4	30,98	1	
GL		4	32,24	2	

(**Significance values:** ***, <0,001; **, <0,01; *, <0,05; N/S, non-significant)

Young green mopane leaves, have significantly more (p<0,001) crude protein and nitrogen than do the older mature green leaves. They also have a significantly lower (p<0,001) condensed tannin content, and the lowest mean protein precipitation capacity value. In addition, they possess a higher amount of available energy. Although the young mopane leaves have significantly less ($p<0,001$) moisture than do the fully developed green leaves, the above parameters definitely identify them as being more palatable, and thus more valuable for herbivores than are the mature green mopane leaves. Young green mopane leaves have a lower fibre content (NDF and ADF values) than do the mature green mopane leaves, this further substantiating their being more palatable.

TABLE 15: COMPARATIVE PALATABILITY OF THE TWO LEAF CLASSES AS DETERMINED BY RANKS ASSIGNED IN TABLE 14

LEAF TYPE	RANK VALUES	$\bar{X}$ VALUE	FINAL PALATABILITY RANK
YOUNG	1 1 1 2 1 1 1 1 1	1,11	1
MATURE	2 2 2 1 2 2 2 2 2	1,88	2

TABLE 16: LIST OF VOLATILE COMPOUNDS WHOSE SMELLS AS PERCEIVED BY HUMANS, HAVE BEEN DOCUMENTED (According to Hall *et al.* 1985)

NAME: **Alpha and Beta Pinene** $C_{10}H_{16}$
SOURCE: Terpene hydrocarbon
ODOUR: Very volatile; Harsh spicy odour with fresh undertones.
OTHER: Colourless liquid, occurring in very many essential oils.

NAME: **Hexanol acetate** (Leaf alcohol) $C_6H_{12}O$
SOURCE: Alcohol
ODOUR: Very powerful odour reminiscent of freshly cut grass.
OTHER: Colourless liquid, occurring naturally in many essential oils.

NAME: **Limonene** $C_{10}H_{16}$
SOURCE: Terpene hydrocarbon
ODOUR: Bright, fresh clean odour typical of citrus fruits, somewhat harsh and bitter.
OTHER: Colourless liquid.

NAME: **Linalool** $C_{10}H_{18}O$
SOURCE: Alcohol
ODOUR: Has a very attractive floral odour with spicy and lemony undertones.
OTHER: Colourless liquid.

NAME: **Caryophyllene** $C_{15}H_{24}$
SOURCE: Sesquiterpene hydrocarbon
ODOUR: Somewhat spicy, acidic woody aroma.
OTHER: Colourless liquid, found in numerous oils.

DISCUSSION:

Fifteen different volatile compounds were identified in the young green leaves, and ten in mature green leaves of *C. mopane* (thick film results). The greater part of the substances detected in the samples were terpenes. The mass spectra of these compounds are very similar and therefore it is difficult to identify these substances just by their mass spectra. It will be necessary to analyze pure individual compounds, under the same analytical conditions, to confirm the identity of the volatile substances obtained in the leaves, acquired by using both a gas chromatographic retention index and mass spectrometry. There appears to be a significant difference between the results obtained from the carbon and the thick-film traps. It would appear that the substances at low concentration levels are determined more easily using the thick-film concentrators. This is probably because no solvent extraction procedures are required to isolate the trapped material for analysis. Low concentration levels of substances such as linalool were detected with these traps (see Table 9), but were not observed in the extracts from the carbon traps. The carbon tubes appear to be more efficient in trapping the very volatile substances (see Tables 9 and 10). Because of the dilution that occurs when using a solvent to extract the substances from the carbon traps, compounds occurring at trace levels are sometimes difficult to detect.

Ruminants may select their food for chemical compounds such as protein, minerals, nonprotein nitrogenous compounds etc., or volatile flavour compounds which in turn directly affect the animal's taste, smell, touch, vision etc. (Oh *et al.* 1967). The results obtained do suggest that the wider spectrum of compounds in young leaves, recorded as aiding rumen microbial activity, could serve as an indicator to herbivores of the palatability of the young leaf. The results expressed in Table 13 clearly confirm this, the young leaf having far greater concentrations of nutritious compounds and lower concentrations of distasteful compounds than do the older mature green leaves.

Limonene is a toxin which when present in large quantities is known to deter feeding by insects (Sturgeon 1979). Limonene is present only in the young green leaves and not in the older mature green leaves. Although additional sampling is necessary to confirm the absence of limonene in mature mopane leaves, certain ecological deductions can be made. Mopane moths (*Imbrasia belina*; Saturniidae) lay their eggs on the underside of mature mopane leaves (R. Oberprieler *pers. comm.*)[3]. The eggs hatch and caterpillars often colloquially referred to as "mopane worms" emerge. The caterpillars have been seen to concentrate their feeding activities almost exclusively on the mature green leaves of the mopane. If limonene is indeed such an active deterrent to feeding, then this is possibly why the caterpillars do not feed on the young leaves of the tree. The present study has shown the young mopane leaf to actually be far more palatable for mammalian herbivores than is the older green leaf, having significantly greater amounts ($p<0,001$, $N=20$) of crude protein, nitrogen and available energy, but fewer amounts ($p<0,001$, $N=10$) of total phenolics and condensed tannins, and a lower protein precipitation capacity ($p<0,001$, $N=10$), as is reflected in Table 14.

Linalool, a monoterpene alcohol, has been documented as being an inhibitor of rumen microbial activity (Oh *et al.* 1967). Linalool was found only in young green leaves of *C. mopane*. Observations made in the field showed budding commences in early October. This

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CHAPTER

FIVE

young leaf material was very much sought after by mammalian ungulates of the NTGR, such as eland, kudu, impala, grey duiker, steenbok, and occasionally even grazing ruminants such as wildebeest were observed feeding on young leaves. As already noted, young mopane leaves possess literally every positive characteristic demanded by a good browse type. Linalool may slow the digestion rate of the young leaves, but whether or not it has adverse effects on the eventual nutrition made available to the ruminant through rumen fermentation processes needs testing and quantification.

In conclusion, although all ecological dynamics discussed are very hypothetical, being based on tentative identifications of compounds and spectra in different leaf types, the implications are that the spectrum of volatile compounds an ungulate is exposed to, do possibly serve as an indicator of browse quality. This study has concentrated on the relative amounts of the volatile compounds. A better statistical approach, using larger sample sizes, and calculating the absolute amounts of volatile compounds rather than the relative amounts, would contribute to furthering the understanding we have of an animal's ability to perceive browse quality, and may further our knowledge as to the differential use of mopane phenophases by ungulates.

CHAPTER

FIVE

ON THE ECOLOGY OF MOPANE HEDGES, A PHENOMENON INDUCED BY LARGE BROWSING MAMMALS

INTRODUCTION:

An empirical relationship is known to exist between large herbivore biomass, energy expenditure and production and mean annual precipitation, these results indicating the need for comprehensive studies of ecosystems and the large complement of mammalian herbivores they support (Coe *et al.* 1976).

The food choices and food-related habitat preferences of African elephants have been exhaustively documented in the literature (Buss 1961; Field 1971; Guy 1976; Short 1981; Barnes 1982a,1983a; Jachmann & Bell 1985; Lewis 1986; Smithers 1986; Pienaar *et al.* 1987; Viljoen 1989; Mwalyosi 1990; Jachmann & Croes 1991; Ruggiero 1992), yet little is known about the quality of their diet (Lewis 1986; Meissner *et al.* 1990). More needs to be known about their impact on tree communities, seasonal changes in the chemical content and composition of both the bark and foliage of browse species (Croze 1974a), and responses of woody plants to browsing (Caldwell *et al.* 1981; Walker *et al.* 1987). Currently, research is concentrating on these aspects (Skarpe & Bergstrom 1986; Tolsma *et al.* 1987a; Tolsma *et al.* 1987b; Skarpe 1990).

Elephants are known to eat the majority of woodland tree species, more or less in proportion to their occurrence, yet some species such as the mopane are definitely favoured as browse (van Wyk & Fairall 1969; Jarman 1971; Palmer & Pitman 1972; Caughley 1976; Guy 1976; Huntley 1982; van Wyk 1984; de Villiers & Kok 1988; Stuart & Stuart 1988; Viljoen 1989; Skinner & Smithers 1990), browse being important in the elephant diet as the major source of crude protein (Mwalyosi 1990).

THE RELATIONSHIPS BETWEEN *COLOPHOSPERMUM MOPANE* AND MAMMALS

The mopane trees of the NTGR exhibit two very definite components or morphs. The one morph, loosely referred to as a "bonsai", is a very short (not usually taller than 3,5m), robust mopane tree occurring in the open areas away from the watercourses where it forms extensive hedges. This morph results from the removal of branches by large mammalian herbivores, the hedges being kept in the suppressed-tier state. The other morph is a much taller (usually in excess of 6m), relatively undamaged mopane tree, individuals belonging to this component being encountered along the riverine fringes of most of the major watercourses in the NTGR.

The present study was conducted to investigate agents responsible for the seasonal removal of branches, the possible reasons why mopane twig bark is so sought after, and the ecological implications of such hedges for the NTGR's management policy.

MATERIALS AND METHODS:

Elephant faecal samples were collected seasonally in order that the amount of twig material in the diet could be assessed. Samples collected were placed in large paper bags and stored in a cool place. The sample was kept moist by sealing the paper bag, this facilitating the sifting procedure, the material never drying out, so preventing the material from breaking and disintegrating when sifting. All pieces of undigested mopane twig material were removed from the samples using forceps. Finally, the twig material removed, and what remained of the sample, were dried in an oven at 50°C for 72 h and then their respective masses determined. The percent dry twig mass of mopane in the faecal sample was determined by dividing the dry mass of the leaf or twig sample by the remaining mass of the dry faecal sample. Variation in the overall seasonal content of material was tested using a Kruskall-Wallis (K-W) Analysis by Ranks Test. Differences between the seasonal content of undigested twig material in samples was tested using the Mann-Whitney Test.

The investigation of the seasonal removal of mopane branches required a site situated in an area of already hedged mopane trees, this serving as an indicator of the occurrence of regular branch browsing. The chosen site lay on Mashatu Reserve in Elephant Valley, an area where the hedged bonsai mopane morph predominates. Five hundred branches (ten on each of fifty tagged trees) were marked using a mocca-coloured non-volatile paint. The bases of the branches were painted where they emerged from the main stem. It was recorded whether the branch was new or old growth. The site was visited on a seasonal basis and the tagged trees checked for the presence/absence of marked branches. Seasonal variation in the intensity of removal of both the young and old branches was tested using the Mann-Whitney Test.

The impact large herbivores are having, being very obvious in the hedged areas, resulted in a comparative study of the phenology of bonsai mopane trees with that of their much taller, less-damaged riverine counterparts. The present study was conducted towards the end of October 1992. Six sites were chosen, three along the Jwala riverine fringe where the dominant mopane morph is tall and relatively undamaged, and three sites on the open plains where the dominant morph is the bonsai. At each site one hundred trees were sampled. Records were made of the following:

i) Were pods to be found on the tree, and if so, were they abundant or few? Few pods was defined as the tree bearing pods, but, their presence not being easily visible from 50m and their occurrence over the canopy being scattered. The abundant pod condition was defined as the pods being easily visible from 50m due to their being very numerous and thus relatively evenly distributed over the canopy.

ii) Were old leaves present on the tree, and if so were they abundant or few? The conditions described above for distinguishing between abundant and few apply to these records.

The seasonal chemical composition of mopane twig bark was investigated in an attempt to correlate these factors with the branch browsing effect on a seasonal basis. Twig bark was collected from independent samples on a seasonal basis. The bark was removed with the aid of a scalpel. Analysis was done according to the methods described under the general methods section.

RESULTS:

TABLE 17: THE NUMBER OF ELEPHANTS AND ELAND IN THE NORTHERN TULI GAME RESERVE AS ESTIMATED FROM AERIAL SURVEYS (le Roux 1991)

SPECIES	YEAR	NUMBER	No./km^2
ELEPHANTS	1984	567	0,57
	1986	576	0,58
	1987	258	0,26
	1988	617	0,62
	1989	406	0,41
	1991	627	0,63
$\bar{X}$			0,51±0,15
ELAND	1984	438	0,44
	1986	573	0,57
	1987	296	0,30
	1988	293	0,29
	1989	99	0,09
	1991	343	0,34
$\bar{X}$			0,34±0,16

TABLE 18: VALUES SHOWING THE SEASONAL CONTENT (%) OF UNDIGESTED MOPANE TWIGS IN ELEPHANT FAECAL SAMPLES

				SIGNIFICANCE			
SEASON	N	$\bar{X}$±S.D.	K-W TEST	WI	SP	SU	AU
WINTER	15	9,71±2,0	***	-	N/S	**	N/S
SPRING	06	9,22±1,3		-	-	*	N/S
SUMMER	15	12,0±2,0		-	-	-	*
AUTUMN	15	10,1±1,9		-	-	-	-

(**Significance values**: ***, <0,001; **, <0,01; *, <0,05; N/S, non-significant)

Statistical tests show that highly significant differences (p<0,01, Kruskall-Wallis Test) exist between the overall seasonal content of undigested mopane leaf and twig material in the collected elephant faecal samples. No seasonal differences (p>0,05; Mann-Whitney Test) exist between the undigested mopane leaf content in faecal samples collected over the winter and autumn and spring and autumn periods. This results from the mean values of leaf material in the samples collected for these seasons being so similar. However, highly significant differences (p<0,001) do exist between the winter and summer, spring and summer and summer and autumn periods, the differences resulting from the content of leaf material in the summer samples being higher. A significant difference (p<0,05) exists between the winter and spring sampling periods, the difference arising largely from the small sample size for spring. No seasonal differences (p>0,05) exist between the content of undigested mopane twig material in the elephant faecal samples collected over the winter and spring, winter and autumn and summer and autumn periods. Significant differences (p<0,05) do exist between the spring and summer and summer and autumn periods due to the low twig content in the summer samples. A highly significant difference (p<0,01) exists between the winter and summer periods, the winter samples having the greatest percentage of undigested mopane twigs, whilst the summer samples had the lowest percentage of undigested mopane twigs.

TABLE 19: TABLE OF VALUES SHOWING THE SEASONAL REMOVAL OF NEW AND OLD MOPANE BRANCHES FROM MARKED TREES IN A HEDGED AREA ON MASHATU

SN	REV.	TTL.	REM.	No NEW	%	No OLD	%	SIGNIFICANCE WI	SP	SU	AU
WI	00	500	00	00	00	00	00	-	-	-	-
SP	33	467	33	31	94	02	06	-	-	***	***
SU	106	361	139	75	71	31	29	-	-	-	***
AU	49	312	188	36	73	13	27	-	-	-	-

KEY: REV: No. removed that season; TTL: Total no. branches remaining; REM: Total no. branches removed to date.

TABLE 20: RESULTS SHOWING THE SEASONAL REMOVAL OF MARKED YOUNG AND OLD MOPANE BRANCHES

	YOUNG BRANCHES				OLD BRANCHES			
SEASON	WI	SP	SU	AU	WI	SP	SU	AU
WI	-	-	-	-	-	-	-	-
SP	-	-	***	***	-	-	N/S	*
SU	-	-	-	N/S	-	-	-	N/S
AU	-	-	-	-	-	-	-	-

The seasonal results obtained show that over a ten month period, 188 (37,6%) branches from a total of 500 marked branches were removed. The removal of the first 33 (spring record) branches is directly attributable to eland, elephants being absent from the mopane dominated areas of the NTGR over that period. The removal of an additional 106 branches between the spring-summer period, heralds the return after rain of elephants to the mopane dominated areas of the NTGR. Notice how simultaneously the percent of old growth removed increases from 6% (spring) to 29% (summer) due to elephants not being as selective as are eland, eland definitely concentrating their attentions on the younger branches whose bark peels off more easily due to its being less dissected, a phenomenon associated with ageing.

The highly significant differences ($p<0,001$) between the number of young branches removed in the spring and summer and spring and autumn records is directly attributable to the percent new growth removed for spring being much higher than for the other two seasons. A significant difference ($p<0,05$) exists between the number of old mopane branches removed in the spring and autumn records, attributable to the low percent removal of old growth in spring due to the absence of elephants from the site prior to the record.

TABLE 21: THE MEAN SEASONAL CHEMICAL COMPOSITION OF MOPANE TWIG BARK

						SIGNIFICANCE			
SN	PAR	N	$\bar{X}$±S.D.	K-W	RANK	WI	SP	SU	AU
WI	CP	20	5,31±0,16	***	4	-	**	***	***
SP		20	5,43±0,10		3	-	-	***	***
SU		20	5,67±0,09		2	-	-	-	***
AU		20	5,84±0,18		1	-	-	-	-
WI	NI	20	0,93±0,03	***	4	-	*	***	***
SP		20	0,87±0,02		3	-	-	***	***
SU		20	0,91±0,01		2	-	-	-	***
AU		20	0,85±0,03		1	-	-	-	-
WI	EN	20	18,47±2,95	***	1	-	N/S	*	***
SP		20	17,70±0,11		2	-	-	**	***
SU		20	17,58±0,19		3	-	-	-	**
AU		20	17,32±0,25		4	-	-	-	-
WI	MO	15	33,66±2,77	***	4	-	***	***	***
SP		15	40,97±4,97		1	-	-	N/S	N/S
SU		15	38,34±2,83		3	-	-	-	N/S
AU		15	38,42±3,05		2	-	-	-	-
WI	CT	10	64,99±0,90	***	1	-	**	***	***
SP		10	66,55±0,89		2	-	-	*	N/S
SU		10	68,47±1,73		4	-	-	-	N/S
AU		10	67,63±1,70		3	-	-	-	-
WI	TP	10	425,1±3,46	***	1	-	***	***	***
SP		10	447,8±6,12		3	-	-	***	***
SU		10	482,2±3,59		4	-	-	-	***
AU		10	436,6±2,90		2	-	-	-	-
WI	PP	10	44,15±10,2	***	2	-	N/S	N/S	N/S
SP		10	61,20±9,91		3	-	-	*	N/S
SU		10	30,40±4,49		1	-	-	-	N/S
AU		10	44,15±10,2		2	-	-	-	-
WI	NDF	4	48,53		2				
SP		4	53,18		3				
SU		4	47,12		1				
AU		4	53,30		4				
WI	ADF	4	38,26		1				
SP		4	45,22		4				
SU		4	39,09		2				
AU		4	42,29		3				

The seasonal differences for mopane twig bark samples are highly significant ($p<0,001$, Kruskall-Wallis Test) for all the parameters for all seasons. A non-significant difference ($p>0,05$) exists between the amount of energy available in the winter and spring samples, while significant differences ($p<0,05$) exist between all of the other seasons. The highly significant differences ($p<0,001$) between the moisture content in the collected twig bark samples results from the winter samples having much less moisture than did any of the other seasons' samples. Highly significant differences ($p<0,01$) exist between the condensed tannin content of the winter samples when compared with other seasons' samples, due to the condensed tannin content of mopane twig bark being lowest during winter. The summer months reveal mopane twig bark as having the lowest protein precipitation capacity, even when it had the highest seasonal content of both total phenolics and condensed tannins. The significant decrease ($p<0,05$) in the protein precipitation capacity of twig bark from spring to summer, spring having the highest protein precipitation value, implies an increase in the food value of twig bark from spring to summer, this correlating well with the highly significant ($p<0,001$) increase from spring to summer, of both the mopane twig bark crude protein and nitrogen content. Lucerne was used as a standard against which to test the samples, the NDF and ADF values obtained for this highly palatable fodder being 50,9 and 40,5 respectively ($N=4$). The NDF content of mopane twig bark varies from between 47% (summer) to 53% in spring. Twig bark NDF content increases by 5% from winter to spring, followed by a 6% decrease to summer and then again a 4% increase into autumn. Similarly, the above trend is paralleled for the ADF content of mopane twig bark.

TABLE 22: SEASONAL PALATABILITY OF MOPANE TWIG BARK AS DETERMINED BY THE RANKS ASSIGNED IN TABLE 21

SEASON	RANK VALUES	$\bar{X}$ VALUE	FINAL PALATABILITY RANK
WINTER	4 4 1 4 1 1 2 2 1	2,22	1
SPRING	3 3 2 1 2 3 3 3 4	2,67	3
SUMMER	2 2 3 3 4 4 1 1 2	2,44	2
AUTUMN	1 1 4 2 3 2 2 4 3	2,44	2

TABLE 23: COMPARATIVE ECOLOGICAL DIFFERENCES REVEALED BY THE TWO DOMINANT MOPANE MORPHS

			PODS			OLD LEAVES	
SITE	N	No.WITH PODS	No. ABUN	No. FEW	No.WITH OLD LVS	No. ABUN	No. FEW
BONSAI							
A	100	36	11	25	98	19	79
B	100	46	30	16	85	5	80
C	100	39	15	24	88	27	61
$\bar{X}$		**40,3**	**18,7**	**21,7**	**90,3**	**17**	**73,3**
RIVERINE							
A	100	36	19	17	99	32	67
B	100	57	38	19	100	85	15
C	100	51	29	22	97	48	49
$\bar{X}$		**48**	**28,7**	**19,3**	**98,7**	**55**	**43,7**

The heavy browsing pressure large mammals in the area impose upon the bonsai morph does not however, prevent this morph from setting seed. Results show that 40,3% of 300 bonsai mopane trees sampled had set seed, 46,4% having an abundant number of seeds, and 53,6% having few seeds. Of the 300 riverine mopane trees sampled, 59,8% had an abundant number of pods, and 40,2% had few seeds. The riverine trees do not, however, lose as much of their leaf material as do the bonsai mopane trees of the open areas, the percent values for riverine and bonsai trees having old leaves present being 98,7% and 90,3% respectively. A difference occurs in the number of trees still having a lot of leaf material on them at this point of the dry season, far more riverine trees (55,8%) having many leaves on them than do the bonsai trees of the open areas (18,8%).

TABLE 24: ANNUAL PRECIPITATION FIGURES FROM 1980 TO 1992 (JAN-SEP) ACCORDING TO THE PONTDRIFT BORDER POST ON THE EDGE OF THE NTGR

YEAR	PRECIPITATION(mm)
1980	423,2
1981	438,8
1982	223,5
1983	237,5
1984	313,5
1985	571,0
1986	279,5
1987	298,5
1988	272,5
1989	180,0
1990	263,0
1991	452,5
1992	47,5

DISCUSSION:

Elephant browsing is regarded as a prime factor in the suppression of woody vegetation (Laws 1969; Harrington & Ross 1974; Weyerhauser 1985; de Villiers & Kok 1988; Jachmann & Croes 1991; Nott & Stander 1991), and can prevent tree regeneration if primary production is adversely affected by browsing during the previous season, eventually reducing species richness (Smart *et al.* 1985). Consequently management of this megaherbivore gives cause for concern (Anderson & Walker 1974; Pienaar 1983; Smart *et al.* 1985; Viljoen & Bothma 1990; Jachmann & Croes 1991; Lewis 1991; Novellie *et al.* 1991; Hall-Martin 1992; Jachmann 1992), and an elephant density of between 0,3-0,6 animals/km^2 is suggested to keep short term vegetation changes to a minimum (Hall-Martin 1984; Jachmann & Croes 1991).

Elephant damage to mopane woodland usually takes the form of broken stems and branches and large areas exist where mopane trees have been reduced to an average height of 1-2m (Anderson & Walker 1974; Guy 1981; O'Connor & Campbell 1986), yet because few mopane trees die, the biomass remains relatively unaltered (Guy 1981). Those parts of a tree known to be utilized by elephants vary considerably during the year (de Villiers & Kok 1988). In the wet season elephants eat leaves and twigs, which begin to form the bulk of their diet in the early dry season (Jarman 1971). During the dry season elephants generally take only branches when browsing on mopane trees (Jarman 1971; Lewis 1987), since leaves have either senesced or are avoided (Lewis 1987). According to Guy (1976) more than 90% of the bark utilized by elephants comes from branches with a diameter of between 0,1cm and 0,2cm.

Figures from the last game count (1991) using an aerial survey technique, show the number of eland and elephants for the entire conservation area to be 0,34 animals/km^2 and

0,63 animals/km^2 respectively. Herds of more than 200 eland are not an uncommon sight in the hedges over the dry period before spring rains. Whilst doing game counts, eland are most often encountered in the areas of short hedged mopane trees, rarely being encountered outside these, and if so, usually on the fringes.

The palatability of mopane twig bark does not seem to have any effect on the utilization of branches by large browsing mammals. Eland, and not elephants, are responsible for the removal of the marked branches over the winter-spring period, this being the transition period during which the palatability of the twig bark changes from its most palatable (winter) to its least palatable (spring). This decrease in palatability may be directly attributable to the sap rising in the trees over this period, so increasing the moisture content of the bark (see Table 21). This rising of sap in the plant is associated with increases in both the condensed tannin, total phenolic and protein precipitation capacity of the twig bark.

Eland concentrate their attention on new young growth (see Table 19) whose bark can be peeled off more easily than the bark on older growth, whose nature is very dissected, making it difficult to be removed in strips. Elephants are usually absent from the mopane tree community of the NTGR over this period, especially if conditions are dry, concentrating on the Shashe-Limpopo riverine fringes of the NTGR, where they feed on Mlala palms *Hyphaene natalensis*, the browse available on the big riverine trees, and on the grass sward on the floodplains of these major watercourses. The absence of elephants in spring from the mopane dominated communities was apparent from the few fresh faecal droppings encountered. The crude protein content of food resources selected by elephants is known to range from 6,69% in the dry season to 10,7% in the wet season (Meissner *et al.* 1990). During the dry season (late autumn to early spring) the crude protein content of both the branches and leaves of the mopane tree is low, and could serve as a further explanation for the movement of elephants away from the areas where mopane trees predominate.

Elephant sightings in a mopane woodland in the Luangwa Valley, Zambia had decreased dramatically until the emergence of fresh mopane foliage brought them back (Lewis 1987). Analyzing the chemical composition of leaf material being utilized by elephants in the *Brachystegia* woodland of the Kasungu National Park, showed a significant correlation between utilization and protein content (Jachmann & Bell 1985). *Markhamia obtusifolia*, one of the species heavily browsed upon in the above study had a nitrogen content of 1,26%. Young mopane leaves have a high nitrogen content of 2,81% (N=20), even exceeding that recorded for palatable acacias eg. *Acacia galpinii*: 1,57% ; *Acacia sieberana*: 1,23% (Jachmann & Bell 1985). Young, protein-rich mopane leaves are sought after by elephants, so much so, that elephants will return *en masse* to the mopane dominated areas of the NTGR when the new leaves are emerging.

The change from spring to summer and an increase in twig bark palatability, also sees a vast increase in the number of branches removed (106 as opposed to 33). This increase results from the return of elephants to the hedged areas which are now in leaf, which is further substantiated by the increased content of undigested twig bark in the faecal samples ($p<0,05$, Mann-Whitney Test; Table 18) in summer. Lewis (1986) found branch browsing on mopane by elephants to be greatest in September and October (Lewis 1986), this coinciding with the period when mopane have fewest leaves available to browsers (Hall-Martin 1974a). The sharp decrease in the number of branches removed from summer to autumn results from elephants moving out of the area dominated by mopane trees, back to the Shashe-Limpopo riverine community in search of water (see Table 24). However, the fairly high percentage of old growth removed indicates that elephants were present, a few small herds still being encountered at that time.

Eland feed readily on mopane year round irrespective of the palatability (especially polyphenolics) of the phenophases, and are thus commonly encountered in the mopane-dominated areas of the NTGR. Recently it has also been shown that mammalian herbivores may possess defensive mechanisms against polyphenolics such as tannins, through the secretion of proline-rich salivary proteins which render substances like tannins inactive to a degree, so reducing their effects (Mole *et al.* 1990). Their large body size and foregut fermentation confers upon them the capacity to process and survive on even poor quality forages with low fermentation rates, since metabolic needs scale with weight and gut contents scale isometrically with weight (Demment & van Soest 1985). This longer retention by large-bodied ruminants increases digestive efficiency relative to that of smaller animals (Illius & Gordon 1992), implying habitat selection to be less important for the large animal. Eland may well be utilizing the twig bark over the early spring period before the emergence of the highly palatable young green mopane leaves, to obtain sufficient moisture at a time when moisture is usually very scarce, especially in the absence of rain during the present study.

Taylor & Walker (1978) found that in a mopane savanna, the percentage mopane utilized by browsing animals on a seasonal basis varied from 4 to 12%. Lewis (1987) states that a mopane branch is typically not browsed more than once during the same season. The present study found mopane branches to have been browsed on up to three times a season (winter), but then this is the season when mopane twig bark is at its most palatable (see Table 22).

According to Caughley (1976) abundant regeneration is a necessary condition for the continued health of the mopane association. Mopane seedlings establish with little interference from elephants, and obtain a height of about 1m before being browsed. Above this height, the rate of browsing increases to such an extent that growth may be precluded beyond 2m (Caughley 1976), the main feeding level of elephants being below 3m (Guy 1976). Preferred species, such as the mopane, are constantly browsed and kept at the preferred feeding level (Jachmann & Bell 1985). This results in a suppressed tier of scrub mopane with few seedlings ever breaking away to form tall mature trees. Caughley (1976) claims that seeding of mopane is a function of the tree height rather than of age or girth, so eliminating the upper tier of mopane also eliminates the source of mopane seed. The heavy browsing pressure that the bonsai morph is exposed to, is however, not that excessive that this morph is no longer capable of seed production, a necessary condition for the perpetuation of any plant species in a community. Paige & Whitham (1987) showed that browsed plants of *Ipomopsis aggregata* had greater seed production than unbrowsed plants. The present study provides the first unequivocal support for the prediction proposed by Owen & Weigert (1976), that consumers can increase plant fitness (Owen 1990). In contrast, seed production by *C. mopane* is recorded as only beginning at a height of 5m in specimens in Zambia's Luangwa Valley (Lewis 1991). The bonsai morph of the NTGR does set seed in the areas studied, and though fewer bonsai trees had seeds on them when compared with the taller riverine trees, more bonsai's had an abundant number of seeds. Thus the large mammals utilizing this bonsai morph of *C. mopane* are not eliminating seed production.

Senescing mopane leaves, the old leaf material mostly present on the riverine trees, are an important source of food for the general ungulate spectrum of the NTGR, impala being known to feed readily on fallen mopane leaves. The riverine mopane trees retain far more dry leaf material than does the bonsai of the open plains. The importance of the riverine mopane can be related to providing food for ungulates over the dry season in the form of dry leaf material, due to their good seed set which assists in maintaining this woody plant species.

The importance of the mopane spring leaf flush is noted by Bonsma (1942), who states that the flush of new growth of woody vegetation begins up to a month and a half before the onset of the rains. This availability of fresh green leaves comes at a time when the herbaceous layer consist of dry, dead or dormant grasses, and is regarded as an important factor in the nutrition of herbivores (Kelly & Walker 1976).

The heavily browsed bonsai trees of the NTGR begin their spring leaf flush well before their much taller, less-damaged riverine counterparts. This contradicts the results of Lewis (1987) who revealed that mopane trees with a low past use by elephants showed a positive correlation between simulated browse damage and subsequent regrowth. Trees with a high past use showed no correlation (Astle 1971; Lewis 1987). Elephant browsing has been recorded as reducing primary stem production in mopane trees by up to 100% (Lewis 1986).

Studies have shown that plants with the shoot apex removed produce greater yields than do those plants whose apices were left intact (Clifford 1979; Argall & Stewart 1984; Sheldon 1986; Benner 1988). This is further substantiated by the findings of (Jachmann & Bell 1985) which state that the amount of browse available on small coppiced trees far exceeds that on tall mature trees. Regular browsing it appears, stimulates trees to continually produce new leaf material. This is resplendent in the heavily browsed bonsai trees of the NTGR being in an advanced state of leaf flush while the leaf primordia on the less-browsed riverine mopane trees are only emerging. The bonsai mopane trees do compensate for the low shoot growth early in the season by increasing the amount of leaf per unit shoot later in the season, a phenomenon already documented for woody plants species (Teague & Walker 1988). However, the continued overuse of coppiced trees often results in large-scale die-offs of that tree class through the reduction of its ability to survive stressful climatic conditions (Lewis 1987). This high mortality through over-use does not seem to apply to the mopane trees of the NTGR. Moreover, mopane trees that were heavily utilized by elephants in the Luangwa Valley showed very low rates of mortality (Lewis 1991).

These vast areas of hedged mopane trees within the NTGR have been regarded as areas of ecological disorder, resulting from excessively heavy browsing pressures on mopane trees by elephants, a situation demanding that eventually a decision on the culling of elephants be taken. The results from the present study question the supposed impact elephants are having, hedging being a phenomenon largely resulting from browsing by eland. As Riney (1982) states, certain shapes can be created by more than one species. He goes on to say that mopane about 1,5 - 3,0m high can be modified by both eland and elephants to a hedge shape, and using this evidence alone it is difficult to distinguish hedged forms created by these two species on this particular height class of mopane. According to Lewis (1986) the dependence of elephants on mopane appears to have been largely overemphasized, but he probably did not taken into account the fact that most of southern Africa's conserved elephant populations are now supported by mopane trees (N. Owen-Smith *pers. comm.*)[1].

The impact elephants and eland are having on the area may not be aesthetically pleasing, but their activities are responsible for a mopane morph which is robust, comes into leaf early, keeps on producing new leaves even in the presence of heavy utilization, and which proves to be an available, palatable resource in the NTGR for mammalian ungulates when food is scarce.

The present study supports the notion proposed by Cody (1991), that selection favours local morphological diversification of species into distinct growth forms under particular circumstances, such natural niche axes being a fundamental aspect of resource partitioning in plant communities. Finally, it is hoped that this scientific study will assist in the conservation and management of Botswana's animal species, as requested by Mundell (1992), especially elephants, a species central to many recent debates and discussions.

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THE CHEMICAL COMPOSITION OF MOPANE STEM BARK, ITS SEASONAL UTILIZATION BY ELEPHANTS AND THE RESILIENCE OF THE TREE TO DEBARKING

INTRODUCTION:

Nearly twenty years ago the need to be know more about tree succession and seasonal changes in the chemical content and composition of trees' bark was identified (Croze 1974a). The crude protein content of food resources selected by elephants ranges from 6,69% in the dry season to 10,7% in the wet season (Meissner *et al.* 1990). During 1972 an attempt was made to isolate factors responsible for elephants' preference for mopane's bark. Bark is a nontechnical term used to describe the tissues external to the vascular cambium and wood (xylem) (Stafford *et al.* 1989). Bark samples were collected in September and October. Each sample consisted of portions of bark from 30 - 50 different trees and samples were collected from different areas where the tree species were widespread in the NTGR. Detailed chemical analyses for nitrogen, phosphorus, potassium, sulphur, calcium, magnesium, iron, sodium, manganese, boron, copper, zinc, nickel, crude protein and ether extract content, failed to indicate any significant differences between those tree species elephants preferred and those species which showed no signs of damage (Thompson 1975).

Those parts of a tree known to be utilized by elephants vary considerably during the year. In mid-winter elephants have been reported as beginning to eat branches and strip bark from mopane (Jarman 1971). It has been suggested that elephants obtain calcium by debarking trees (Bax & Sheldrick 1963; Dougall & Sheldrick 1964). Anderson and Walker (1974) found that the majority of mopane trees whose bark had been removed by elephants had a trunk diameter in excess of 0,2m. Strip barking of trees by elephants is not known to have an immediate ill-effect, but as Thompson (1975) points out, the removal of strips of bark allows access to insects and fungi which can ultimately cause the death of the tree.

In the present study the seasonal chemical composition of mopane stem bark was investigated in an attempt to isolate possible factors that could explain its utilization by elephants, as well as examining the degree of debarking this tree species can withstand.

MATERIALS AND METHODS:

The amount of stem bark removed on a seasonal basis from large mopane trees was determined using four sites, three along the riverine fringe of the Jwala river, and one along the riverine fringe of the Majale river. Trees chosen at each site had tall single stems, no coppice growth whatsoever, and all were highly accessible from any side of approach. These parameters were decided upon as such a mopane tree yields itself to the removal of its stem bark by elephants due to the easy accessibility of the bark. Records were made for all trees of the diameter at breast height (DBH divided by two gives radius, r), and the height (h) of the trunk above the ground to the first fork. This allowed for the calculation of the total amount of stem bark available on the entire trunk using the following equation:

$$\textbf{Amount of available stem bark} = 2\pi r.h$$

This equation assumes that the trunk of a mopane tree is cylindrical and not conical.

All areas of damage on a tree's trunk were recorded, measurements of their lengths and breadths being made to calculate the area (lxb) of the bark. The amount of bark removed was expressed as a percentage of the total amount of stem bark available. Trees were checked seasonally for the presence of any new damage.

Each season stem bark samples were collected for analysis. Independent samples were removed with an axe, tissues external to the red cambial region being collected. The samples were then analyzed according to the methods described in Chapter 3.

RESULTS:

TABLE 25: THE PERCENT MOPANE STEM BARK REMOVED FROM TREES AT FOUR SITES, AND THE SEASONAL UTILIZATION BY ELEPHANTS

No	SITE	N	% DAM	$\bar{X}$ B.DIAM	$\bar{X}$ AMOUNT BARK/TREE(cm^2)	$\bar{X}$ % BARK REMOVED	NEW DAMAGE
1	JWALA1	50	42	20,15±8,97	12734,2±9138,2	5,18±9,37	NONE
2	JWALA2	50	30	26,46±8,93	19455,7±9818,7	1,28±4,12	NONE
3	JWALA3	100	41	30,94±9,92	25068,3±13607,2	4,15±9,67	NONE
4	MAJALE	50	54	25,14±7,61	18863,6±9180,2	2,84±4,07	NONE

The above results show that for the 250 large single-stemmed mopane trees chosen in order to record the seasonal removal of bark, not one tree had any bark removed from its trunk from July 1991 to April 1992. Furthermore, the mean percent of stem bark removed from the trees at the four sites was in all cases but for Jwala1, less than 5%. The lowest number of undamaged trees was recorded at Jwala3, where 41 % of the trees randomly selected for sampling records, were damaged in some way.

TABLE 26: THE MEAN SEASONAL CHEMICAL COMPOSITION OF THE STEM BARK OF MOPANE

						SIGNIFICANCE			
SN	PAR	N	$\bar{X}$±S.D.	K-W	RANK	WI	SP	SU	AU
WI	CP	20	3,60±0,18	***	3	-	***	***	***
SP		20	4,00±0,25		1	-	-	N/S	***
SU		20	3,99±0,08		2	-	-	-	***
AU		20	3,60±0,18		3	-	-	-	-
WI	NI	20	0,75±0,02	***	1	-	***	***	***
SP		20	0,64±0,04		2	-	-	N/S	***
SU		20	0,64±0,01		2	-	-	-	***
AU		20	0,58±0,03		3	-	-	-	-
WI	EN	20	17,61±1,5	***	1	-	***	***	***
SP		20	15,00±0,23		4	-	-	***	***
SU		20	15,26±0,49		3	-	-	-	*
AU		20	15,55±0,33		2	-	-	-	-
WI	MO	15	3,74±1,07	***	4	-	***	***	***
SP		15	6,01±0,31		3	-	-	***	N/S
SU		15	7,79±0,36		1	-	-	-	***
AU		15	6,32±0,45		2	-	-	-	-
WI	CT	10	57,79±1,21	***	1	-	***	N/S	**
SP		10	61,51±1,19		4	-	-	***	***
SU		10	58,69±1,15		2	-	-	-	N/S
AU		10	59,35±0,68		3	-	-	-	-
WI	TP	10	141,4±5,29	***	4	-	***	***	***
SP		10	102,2±7,21		1	-	-	***	***
SU		10	114,9±4,77		2	-	-	-	***
AU		10	128,4±2,26		3	-	-	-	-
WI	PP	10	38,50±3,23	***	1	-	*	N/S	***
SP		10	45,15±7,28		3	-	-	N/S	N/S
SU		10	39,13±3,29		2	-	-	-	***
AU		10	49,83±5,19		4	-	-	- -	

(**Significance values:** ***, <0,001; **, <0,01; *, <0,05; N/S, non-significant).

According to the results obtained from the Kruskall-Wallis tests, highly significant differences exist between all parameters for every season. Highly significant differences (p<0,001, Mann-Whitney Tests) exist between the crude protein and nitrogen content of all seasons, but for spring and summer. From spring to summer there is virtually no change in the crude protein and nitrogen content of mopane stem bark. Differences between the amount of available energy in mopane stem bark are significant for all seasons, the highest average amount of available energy being present in the winter samples collected. The high energy content of mopane stem bark in winter, is offset by the significantly low ($p<0,001$) moisture content, when compared to the moisture contents of samples for the other seasons. Summer stem bark samples have the highest moisture content, the increase in percent moisture from spring being highly significant ($p<0,001$). This is followed by a significant decrease ($p<0,001$) in the moisture content from summer to autumn. The condensed tannin content of mopane stem bark increases significantly ($p<0,001$) from winter to spring, where it peaks seasonally, the spring condensed tannin content being significantly higher than that for the summer and autumn samples. In winter, mopane stem bark has the most total phenolics present, and in spring the fewest. However, winter stem bark samples have the lowest protein precipitation capacity, autumn being the season when mopane stem bark has its greatest protein precipitation capacity.

TABLE 27: SEASONAL PALATABILITY AS DETERMINED BY RANKS ASSIGNED IN TABLE 26

SEASON	RANK VALUES	$\bar{X}$ VALUE	FINAL PALATABILITY RANK
WINTER	3 1 1 4 1 4 1	2,14	1
SPRING	1 2 4 3 4 1 3	2,57	3
SUMMER	2 2 3 1 2 2 2	2,28	2
AUTUMN	4 3 2 2 3 3 4	2,86	4

TABLE 28: TABLE DESCRIBING MOPANE TREE CONDITION AFTER INFLICTING DIFFERENTIAL DEGREES OF DAMAGE TO SELECTED MOPANE TREES

PERCENT REMOVED	LEAF COLOUR CHANGES	SIGNS OF SENESCENCE	GROWTH TIP DIE-BACK	PODS PRESENT	TREE DEAD
25	NONE	NONE	NONE	YES	NO
50	NONE	NONE	NONE	YES	NO
75	NONE	NONE	NONE	YES	NO
95	NONE	NONE	NONE	YES	NO
100	YES	YES	YES	NONE	YES

DISCUSSION:

From the data collected on the seasonal removal of stem bark on marked mopane trees by elephants, it is apparent that no tree experienced any stem bark removal during the study period (June 1991 - April 1992), even though elephant herds were often encountered in the vicinity of the sites. The mean amount of stem bark removed at each site is low (less than 6%), three of the four sites having fewer than 50% of the chosen trees showing any signs of stem bark removal.

Mopane stem bark is at its most palatable in winter, followed by summer, spring and finally autumn. In winter, stem bark has a crude protein content of 3,6% a nitrogen content of 0,75%, 17,6kJ of available energy per gram material, and a moisture content of 3,7%. The condensed tannin content and total phenolic content were 57,8 and 141,4 mg Catechin/g sample respectively. Elephants being monogastric animals are unlikely to have their digestion affected by tannins and phenolics (Milton 1979; Calvert 1985). Crude protein is very important in an elephant's dietary selection (Mwalyosi 1990). Seasonally, the crude protein content of mopane stem bark varies from 3,6% to 4,0%. This is a relatively low crude protein content, and so it is hypothesized that elephants will only utilize the stem bark of mopane trees over periods when the amount of crude protein the animal is taking in is low (eg. in winter), this being an available resource from which the crude protein dietary intake can be supplemented.

The resilience of the mopane tree to debarking is evident from the results expressed in Table 28. Six months after the trees had been debarked, the specimen with 95% of its stem bark removed showed no die back of growth tips, no visible signs of mass leaf senescence and even new pod development. It thus appears that a mopane tree can withstand up to 95% of its stem bark being removed without showing visible signs of stress and the symptoms one usually associates with a dying tree (branch die-back, twig bark sloughing-off, no seed set *etc*.).

When the trunk of a mopane tree is damaged, the area of bark removed soon becomes sticky. Within a few days, thick golden resinous strands are apparent over most of the length of the wound. This weeping continues for up to four weeks, soon after which the now multi-layered resinous wound covering, having sealed most of the debarked area, turns an opaque white colour and hardens. It is under this protective covering that new bark is generated. Small green nodules, the newly synthesized bark, appear under the resinous covering about three months after the debarking occurred. This process appears to be a very definite wound regeneration response by the mopane.

Whilst the resin is still sticky, numerous insects are found both in and on the strands. Mopane bees, small stingless bees characteristic of mopane veld, appear to harvest the resinous exudate in some form or another, concentrating their activities around the very fluid areas of the exudates. These resinous compounds may well be what these bees use to build and maintain the waxy tubular entrance to their nest, the entrance so often seen protruding from an elephant-damaged area on the stem. Numerous bees and other insects, however, get trapped in the resinous exudates and these then serve as a source of food for birds. Red-billed woodhoopoes *Phoeniculus purpureus* were often seen pecking at the insects trapped in the resin strands, such birds being very adept at moving along a vertical trunk due to their zygodactyl toe organisation.

In conclusion, it is felt that in the past far too much emphasis has been placed on the impact elephant bark-stripping is having on mopane trees. The mopane tree is a very resilient tree type and is capable of tolerating incredible punishment imposed upon it by large mammals. The removal of a portion of the stem bark from a tree does not imply that the mopane tree will die, the experiment conducted indicating just how much bark must be removed before the tree dies. The resilient nature of the mopane tree is hypothesized as resulting from the possibility that elephants may have to fall back on these trees in times of need, and the resultant heavy utilization could result in mass destruction and die-offs should this resilience factor not exist.

ON EPIZOOCHORY AS THE MODE OF DISPERSAL OF DIASPORES OF *COLOPHOSPERMUM MOPANE* (CAESALPINIOIDEAE; LEGUMINOSAE)

INTRODUCTION:

The generic name, *Colophospermum*, is derived from the Greek words meaning "seed inhabiting the light" and this possibly refers to the fact the seed, which is not released from the pod, always remains above ground *i.e.* in the light and does not germinate in the soil (de Winter *et al.* 1966). The pod of *Colophospermum mopane* is flat and kidney shaped, the single seed within being yellowish and wrinkled, and covered with resinous dots which make it sticky to the touch, reportedly allowing it to cling to the hooves of passing ungulates, so being dispersed (von Breitenbach 1965; Palmer & Pitman 1972; Coates-Palgrave 1977,1988; van Wyk 1984). According to Sorenson (1986), such a means of dispersal is termed epizoochory, epizoochory falling within a broader category often referred to as exozoochory.

A seed is a multifunctional structure derived from multiple tissues of diverse origin and ploidy, each of which is influenced by the other, and each of which has a somewhat different genetic framework from which to diversify (van Staden *et al.* 1989). Therefore the structure of a seed is determined by superimposing contemporary selective influences onto a framework determined historically and which may be adapted more or less readily (van Staden *et al.* 1989).

Being a caesalpinioid legume, implies that the seeds of *C. mopane* are probably derived from anatropous ovules (Kopooshian & Isely 1966), and the seed being enclosed in a hard pod, probably implies that this woody species' seeds have a physical dormancy, imposed by the pod not the testa. In seeds with physical dormancy, germination is prevented by the lack of imbibition of water (Baskin & Baskin 1989). When the seed coat finally becomes permeable, usually in only specific areas (Baskin & Baskin 1989), water is imbibed by the seed after which the seed is then capable of germinating over a wide range of temperature and light environments (Baskin & Baskin 1984). Seeds with physical dormancy occur in the seed banks of predictable (Narang & Bhardwaj 1974) and unpredictable (Auld 1986) habitats.

Seed size not only influences dispersal, but also germination, emergence, vegetative growth and sometimes even productivity (Black 1959). Seed size in legumes is constrained by successional status, dispersal strategy, seed predation and ecological aspects of seed germination and seedling establishment (van Staden *et al.* 1989). Most seeds fall in leptokurtic distributions in relation to the plant (Levin & Kerster 1974). Seed mortality is often random and independent of the density of siblings or distance from the plant (Howe & Smallwood 1982). Dispersal is advantageous in avoiding disproportionate seed and seedling mortality near the plant (Janzen 1970), colonizing disturbances (Baker 1974) or locating microhabitats suitable for establishment and growth. In modern plant biology, seed dispersal is one of the central topics, having numerous implications for both the ecology and biogeography of plant communities (Guitian & Sanchez 1992).

The present investigation concentrated on determining whether or not mopane diaspores are dispersed by epizoochory, and if not, what other agents could be responsible for dispersal?

MATERIALS AND METHODS:

A cattle crush facility (1,2m x 15m) at Onderstepoort (Pretoria, South Africa) was used for the experiment. Twenty seeds (pod covering removed) and twenty diaspores of *C. mopane* were laid out at regular intervals (every 2,5m). Soil was used to cover the concrete surface of the cattle crush, so simulating the sandy soil surface diaspores of *C. mopane* fall onto in the field, the mopane veld usually being a veld type devoid of a substantial grass sward. The experimental portion of the crush measured 10m, of which five sites (0m; 2,5m; 5,0m; 7,5m;

10m) served as reference points. The seeds and diaspores laid out at the respective sites were all coloured differently facilitating identification upon retrieval, so aiding the measuring of dispersal distances of seeds and diaspores from their reference points. Sixteen cattle passed through the crush once the seeds and diaspores had been placed at the respective sites, the cattle moving through the crush to a holding pen at the other end. Following this the seeds and diaspores were collected and counted. The hooves of the cattle and the soil in the holding pen were checked for both seeds and diaspores of *C. mopane*. The dispersal distances of seeds and pods moved were recorded. This experimental procedure was repeated four times, new undamaged seeds and diaspores being used for every treatment.

To test whether or not water may be a dispersal agent of diaspores of *C. mopane*, a tub (1m x 0,5m) was filled with water to a depth of 0,1m. The masses of 50 diaspores were recorded, after which the diaspores were dropped into the water. The number of diaspores floating (F) and the number that had sunk (S) were recorded at every five minute interval for an overall period of 20 min. The surface area and volume of each diaspore was also calculated. The surface area of a diaspore of *C. mopane* was determined according to the following equation derived from assuming the one half of the diaspore to be half an ellipse, while the other half's shape was that of half a kidney:

$$\textbf{Surface Area} = ab \quad \frac{\pi}{3} + \frac{\sqrt{3}}{2}$$

a: half the length of the long axis of the diaspore.

b: half the length of the short axis of the diaspore.

The volume of the diaspores was determined by placing a seed in a measured volume of water and then recording the difference, the volume displaced being the volume of the seed.

RESULTS:

TABLE 29: THE NUMBER OF DIASPORES MOVED BY EPIZOOCHORY

TR	REFERENCE POINTS ALONG CRUSH														
	0,0m			2,5m			5,0m			7,5m			10,0m		
	LO	RE	MV	LO	RE	MV	LO	RE	MV	LO	RE	MV	LO	RE	MV
1	20	20	-	20	19;1	-	20	19;1	-	20	18;2	-	20	13;7	2
2	20	13;7	2	20	16;4	-	20	19;1	-	20	15;5	-	20	13;7	-
3	20	17;3	-	20	16;4	-	20	16;4	2	20	16;4	-	20	16;4	-
4	20	13;7	1	20	16;4	-	20	10;10	5	20	13;7	-	20	20	-

(**KEY**: **TR**: Treatment; **LO**: Number of seeds/diaspores laid out; **RE**: Number of seeds/diaspores recovered, the number behind reflects the number that were completely destroyed by the animals hooves; **MV**: The number of seeds/diaspores moved.)

TABLE 30: THE NUMBER OF SEEDS MOVED BY EPIZOOCHORY

TR	REFERENCE POINTS ALONG CRUSH														
	0,0m			2,5m			5,0m			7,5m			10,0m		
	LO	RE	MV	LO	RE	MV	LO	RE	MV	LO	RE	MV	I.O	RE	MV
1	20	15;5	3	20	17;3	-	20	11;4	1	20	19;1	-	20	13;7	2
2	20	13;7	-	20	18;2	2	20	15;5	-	20	16;4	-	20	14;5	-
3	20	12;7	-	20	17;3	-	20	17;2	-	20	17;3	-	20	15;5	2
4	20	15;5	2	20	15;5	-	20	17;3	-	20	17;3	-	20	16;4	-

TABLE 31: DISTANCES SEEDS AND DIASPORES WERE MOVED FROM MARKED POINTS

	SEEDS		DIASPORES	
TR	REF.PT	DISTANCES	REF.PT	DISTANCES
1	0m	0,8m; 1,15m;1,05m	10m	4,0m; 1,3m
	5m	1,0m		
	10m	2,3m; 1,35m		
2	2.5m	1,7m; 0,65m	0m	1,2m; 0,9m
3	10m	2,4m; 1,1m	5m	1,5m; 1,2m
4	0m	3,0m; 0,95m	0m	1,2m
			5m	0,4m; 0,4m; 0,8m;0,85m; 1,25m

In all 400 seeds and 400 diaspores were used to test whether or not epizoochory is indeed the mode of dispersal of *C. mopane*. Only 12 diaspores were moved in total, this being either from being kicked or from adhering to the hooves of some individuals who had stood in the defaecations of individuals in front of them so rendering their hooves a suitable substrate for adherence. In the majority of cases those diaspores tramped on were damaged, often being broken open to reveal the seed inside which often, as a result of the pressure applied by the hoof, was completely destroyed. Of the 400 seeds laid out, only eight could not be recovered, and this may be directly attributable to the seeds having been destroyed by the tramping action of hooves. Twelve seeds were moved in total. The maximum distance a seed and a diaspore were moved was 3,0m and 4,0m respectively.

TABLE 32: TABLE OF VALUES OF MEASUREMENTS RECORDED FOR FIFTY DIASPORES OF *COLOPHOSPERMUM MOPANE*

DIASPORE MASS	00 MIN F	00 MIN S	05 MIN F	05 MIN S	10 MIN F	10 MIN S	15 MIN F	15 MIN S	20 MIN F	20 MIN S	$\bar{X}$ SURF AREA	$\bar{X}$ VOLUME
0,31±0,34	50	00	50	00	50	00	50	00	50	00	2,3±0,2	0,29±0,01

DISCUSSION:

The resin glands on the seed surface though making the seeds slightly sticky to the touch, do not serve to make the seed sticky enough for it to be able to adhere to the hoof of a mammalian ungulate that steps on the seed. In addition, the pressure exerted by a hoof when an animal stands on the seed/diaspore, causes extensive structural damage, seemingly rendering subsequent dispersal should it occur, relatively useless. The mopane does not have the seedcoat-imposed dormancy of the mimosoid legumes eg. members of the genus *Acacia*, the testa of whose seeds has to be damaged or broken down before water imbibition can occur, so setting the scene for germination. When a diaspore did adhere to the hoof of one of the experimental subjects used, the diaspore was immediately dislodged with the next step. The only time a diaspore ever adhered to a hoof was when the hoof acquired an agent facilitating attachment eg. wet faeces on the hoof, however, even under such circumstances the dispersal distances of diaspores never exceeded 4,0m. Thus epizoochory as the mode of dispersal of diaspores of *C. mopane* is conclusively disproved.

Studies conducted on seed dispersal mechanisms in many different types of plant communities find exozoochory as a mode of dispersal to be low (Sorenson 1986; Wilson *et al.* 1990; Guitian & Sanchez 1992), in keeping with the very small percentage of exozoochorous taxons in the flora as a whole (Guitian & Sanchez 1992). Plants utilizing exozoochory as a dispersal means are generally herbaceous (Rockwood 1985), generally being less than one metre high so as to maximize the number of contacts they might experience with dispersal vectors (Hawthorn & Hayne 1978; Lacey 1981; Sorenson 1986). Such characteristics usually typify a nitrophile community (Sorenson 1986; Guitian & Sanchez 1992), and indicate to diaspores being maintained on the plant and bearing structural appendages such as barbs or hooks to facilitate attachment. The above requirements are not met by either the diaspore morphology nor the sporophyte morphology of *C. mopane*.

Fruit and seed morphology often indicate the general means of dispersal (Ridley 1930; van der Pijl 1972). Seeds without obvious modifications for dispersal may be regularly scattered in rainwash (Bullock 1976). According to Howe & Smallwood (1982), seeds dispersed by water show either one or a few of the following adaptations; a resistance to sinking, utilization of surface tension and a low specific gravity. Most of the above adaptations are derived from the seedcoat, modifications usually including a small size, being unwettable and possessing hairs or slime, airspaces, cork or oil.

Results obtained in the flotation experiment (Table 32) conducted on diaspores of *C. mopane* definitely indicate water as a major vector in the dispersal biology of this caesalpinioid species. Every diaspore remained afloat for 20 minutes, and when removed from the tub, the moisture on the diaspore coat immediately ran off due to the resinous nature of pods of *C. mopane*. The mopane veld of the NTGR is very devoid of grass and so most rain falling, even the slightest shower, results in sheetflow of some kind across the soil surface. After rain has fallen diaspores can be found collected together, often being deposited together in piles, in the wake of the run-off. This further substantiates flotation as the real mode of dispersal of diaspores of *C. mopane*.

Howe & Smallwood (1982) cite as general adaptations to wind dispersal, seeds being light and having high surface area to volume ratios. Field observations showed that accompanying the strong winds (downdrafts) preceding thunderstorms in the NTGR was much movement of diaspores. The diaspores are generally light, possess a high surface area to volume ratio and in addition, have uneven edges. The undulating nature of the pod of *C. mopane* will allow air to move under it, lifting it and in so doing exposing the flat thin seed to the heavy winds. This allows for the seed to be dispersed by winds for quite some distance.

The structure and behaviour of seeds and pods of many legumes are a direct result of combined selective forces for seed dispersal and for protection from seed predators (van Staden *et al.* 1989). Small seeds will pass through an animal's gut easily, and escape mastication, but larger seeds much like those of *C. mopane* very rarely escape mastication and are either destroyed or experience such structural damage prior to entering the gut that endozoochory as a mode of dispersal of the mopane must be ruled out. In addition, seedlings of the mopane are never seen germinating in the faeces voided by animals.

Seedlings from large seeds show greater seedling vigour (Black 1956; Twamley 1967), however, the initial advantage in growth possessed by large seeds ceases to be significant when the leaf area index (leaf area to ground area) of seedlings approximates the value of four (Black 1957), and this may well be when the newly germinated seedlings of *C. mopane* experience the mass-damping off for which they are renowned (van Wyk 1972; Coates-Palgrave 1977; van Wyk 1984).

OBSERVATIONS ON THE FEEDING PREFERENCES OF GOATS *Capra hircus* WHEN OFFERED FOUR DIFFERENT MOPANE FOOD TYPES

INTRODUCTION:

Acceptability of a plant as food for a herbivore is determined by a combination of feeding incentives and deterrents (Buchsbaum *et al.* 1984). Selection processes whereby herbivores evaluate browse include not only looking at the plant, but also smelling and tasting it (Oh *et al.* 1968; Frost 1981). Freeland & Janzen (1974) have put forward a hypothesis which states that mammalian herbivores include a wide variety of plants in their diet to reduce the levels of secondary compounds entering their bodies. This assumes that herbivores can recognise foods on the basis of their toxic properties, that they can sense the level at which the compounds become toxic, and that they can regulate their diet to keep the concentrations of such compounds below toxic levels (du Toit *et al.* 1991). These abilities could either be learned (Provenza & Balph 1990) or genetically determined (Alcock 1984). Instinctive responses must presumably involve recognising the secondary metabolite (Provenza *et al.* 1990).

Ruminants are known to be able to detect subtle changes in food toxicity and have been recorded as being known to make adjustments in their feeding behaviour based on post ingestive consequences (du Toit *et al.* 1991). Browsers such as goats supposedly instinctively recognise secondary metabolites, especially condensed tannins, as most woody plants have condensed tannins in their leaves (Bate-Smith & Metcalf 1957; Cooper & Owen-Smith 1985; Cooper *et al.* 1988). On the other hand, many plants with relatively high levels of condensed tannins in their leaves are indeed very palatable (Riggs *et al.* 1988; Nunez-Hernandez *et al.* 1989), and so it may be argued that the diverse array of condensed tannins (Clausen *et al.*

1990), combined with the odours of various plants resulting from the volatile components of their browse, make it highly unlikely that goats can recognise and avoid plants containing condensed tannins (Provenza & Balph 1990; Provenza *et al.* 1990).

Possible ungulate feeding preferences for different food parts of *C. mopane* were to be investigated using goats as study subjects. Goats were chosen as they are easy animals to handle and observe in captivity, and because they are selective intermediate feeders, choosing a mixed diet (Hofmann 1989). Impala, the most abundant ungulate species of the NTGR (5748 or 57.48/ha^2 in 1991, le Roux 1991), are also selective intermediate feeders (Hofmann 1988,1989), and thus possess a digestive anatomy similar to goats (Hofmann 1973).

The purpose of the present investigation was to use goats as an indicator of the feeding preferences impala would probably show for mopane, this hopefully furthering our understanding of the relationship between impala and mopane trees of the NTGR. Moreover, this investigation would also allow for the testing of whether goats do indeed serve as direct monitors of browse quality, the preferences reportedly being for food items having little fibre and few condensed tannins (Hofmann 1989).

MATERIALS AND METHODS:

The study was conducted at the Experimental Farm of the University of Pretoria. Three goats were housed in the experimental enclosure which measured 10m x 12m. Fresh green mopane leaves, senescing mopane leaves, developing green pods and dry pods were collected at the NTGR. Collected samples were sealed in plastic bags and kept under cool conditions whilst being transported back to the site where the goats were being housed. The feeding choice experiment was run 48 h after the material had been collected. The method employed was to set out the four lots of samples in a row, about 1m from each other, so ensuring correct records of what food item was being fed upon. Records were made of the time that the animals were active around the layout site, as determined by one or more animals venturing to within 1,5m of the food site. Sniffing at a sample was then recorded as an interest bout for that sample, and was scored as such. Similarly, records of all feeds and sniffs were recorded for the respective samples, until all the goats were outside the 1,5m radius around the feeding site. The period of interest was then deemed to have ended, and the overall period of activity was recorded. An animal sniffing at a sample but not feeding was defined as being a rejection, whilst feeding after having sniffed that sample was defined as an acceptance. Finally, the number of attention bouts the various samples received were counted, and converted to proportions of the entire interest bout by dividing the number of attention bouts for that sample by the total number of attention bouts for all samples during the period of interest.

KEY:

SN: SESSION
GL: GREEN LEAVES
GP: GREEN PODS
SL: SENESCING LEAVES
DP: DRY PODS

RESULTS:

TABLE 33: GOAT FEEDING PREFERENCES OF FOUR MOPANE FOOD TYPES, RESULTS EXPRESSED AS THE PROPORTION OF THE FEEDING SESSION EACH FOOD TYPE EXPERIENCED

OBS SN	DURATION (min)	PROPORTION TOTAL ATTENTION GIVEN SL	GL	DP	GP	TOTAL
1	15	0,33	0,36	0,14	0,17	1,0
2	05	0,58	0,42	0,00	0,00	1,0
3	03	0,67	0,22	0,00	0,11	1,0
4	05	0,64	0,29	0,07	0,00	1,0
5	02	1,00	0,00	0,00	0,00	1,0
6	09	0,31	0,54	0,15	0,00	1,0
7	03	0,80	0,20	0,00	0,00	1,0
8	05	0,40	0,40	0,00	0,20	1,0
9	04	0,50	0,25	0,25	0,00	1,0
10	06	0,50	0,00	0,00	0,50	1,0
11	11	0,27	0,36	0,10	0,27	1,0
12	02	0,25	0,75	0,00	0,00	1,0
13	03	0,00	0,33	0,00	0,67	1,0

TABLE 34: TABLE OF VALUES EXPRESSING THE REJECTIONS AND ACCEPTANCES EACH FOOD TYPE OFFERED EXPERIENCED, PROPORTIONATELY

SN	REJECTION				ACCEPTANCE			
	SL	GL	DP	GP	SL	GL	DP	GP
1	0,57	0,53	0,50	0,71	0,43	0,47	0,50	0,29
2	0,71	0,20	0,00	0,00	0,29	0,80	0,00	0,00
3	0,67	1,00	0,00	1,00	0,33	0,00	0,00	0,00
4	0,56	1,00	1,00	0,00	0,44	0,00	0,00	0,00
5	1,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
6	0,75	0,29	0,50	0,00	0,25	0,71	0,50	0,00
7	0,75	1,00	0,00	0,00	0,25	0,00	0,00	0,00
8	0,50	0,75	0,00	1,00	0,50	0,25	0,00	0,00
9	1,00	1,00	1,00	0,00	0,00	0,00	0,00	0,00
10	0,67	0,00	0,00	1,00	0,33	0,00	0,00	0,00
11	0,67	1,00	1,00	1,00	0,33	0,00	0,00	0,00
12	1,00	0,67	0,00	0,00	0,00	0,33	0,00	0,00
13	0,00	1,00	0,00	1,00	0,00	0,00	0,00	0,00

TABLE 35: STATISTICAL DIFFERENCES BETWEEN THE NUMBER OF ACCEPTANCES (A) AND THE NUMBER OF REJECTIONS (R)

	$\bar{X}$±S.D.	RDL	RGL	RDP	RGP	ADL	AGL	ADP	AGP
R DL	0,68±0,26	N/S				***			
R GL	0,65±0,40						**		
R DP	0,31±0,43				N/S			N/S	
R GP	0,44±0,50							*	
A DL	0,24±0,18						N/S		
A GL	0,20±0,29								
A DP	0,08±0,19								N/S
A GP	0,02±0,08								

FINAL RANKED ORDER:

REJECTIONS:	ACCEPTANCES:
1: senescing leaves	1: senescing leaves
2: green leaves	2: green leaves
3: green pods	3: dry pods
4: dry pods	4: green pods

Table 33 shows the proportion of total attention each of the four mopane food samples received in the thirteen observed interest bouts. Overall, dry mopane leaves received the most attention from the goats, followed by green mopane leaves, green mopane pods and lastly dry mopane pods. The proportion of attention each food sample received per bout is further divided up into two subcategories, feeding and non-feeding interest bouts (Table 34). The two respective values of the initial value given in Table 33, though expressed as proportions, give direct indications of the percent each subcategory comprises of the original value. The ranked orders displayed at the base of Table 34 show that under the subcategory of non-feeding, dry leaves ranked highest, followed by green leaves, green pods and dry pods. Under the subcategory of feeding, dry leaves again ranked highest, followed by green leaves, dry pods and green pods.

Thus, dry mopane leaves rank highest on the attention scale (Table 33), and enjoyed both the highest number of acceptances and rejections (Table 34). Green mopane leaves which possess many volatile compounds and whose dominant smell resembles turpentine, rank second on the attention scale, and received both the second highest number of acceptances and rejections. Green pods, ranking third on the goat attention scale, received the third highest number of rejections, but the least acceptances. Dry pods, ranking fourth on the attention scale, received the most number of rejections, but the least number of acceptances.

The results in Table 35 show that no significant differences (p>0,05) exist between the number of rejections experienced by the dry leaves and green leaves, dry pods and green pods, nor any differences (p>0,05) between the number of acceptances experienced by dry leaves and green leaves, and dry pods and green pods. There are however, significant differences between the number of acceptances and rejections experienced by dry leaves (p<0,001), green leaves (p<0,01) and green pods (p<0,05). No difference exists between the number of rejections and acceptances for dry pods. Dry leaves experienced both the greatest overall proportion of rejections and acceptances, followed by green leaves. Dry mopane pods experienced a greater number of acceptances when compared with new green pods, the green pods experiencing a greater number of rejections than did the dry pods.

TABLE 36: MEAN VALUES OF THE CHEMICAL COMPOSITION OF GREEN (G) AND SENESCING (S) MOPANE LEAVES OFFERED

	CP	NI	EN	CT	TP	PP	NDF	ADF
G	9,7±0,3	1,6±0,04	19,1±0,4	80,1±1,9	176,3±2,7	69,8±5,7	39,3	32,2
S	3,6±0,2	0,6±0,03	18,5±0,2	68,4±1,0	249,5±8,1	74,9±5,8	35,5	30,2
SIG	***	***	***	***	***	***		

These results show the highly significant differences (p<0,001) which exist between the first six parameters investigated for the two mopane leaf types. The green mopane leaves offered to the goats had significantly more crude protein, nitrogen and available energy (N=20). The senescing leaves had significantly fewer condensed tannins (N=10), but significantly more total phenolics (N=10). Senescing leaves have less fibre (ADF and NDF), based on the organic matter content, than do the young leaves.

DISCUSSION:

It is generally accepted that condensed tannins are more widely distributed in plants than are hydrolyzable tannins (McLeod 1974; Bernays *et al.* 1989). Feeny & Bostock (1968) found that in browsed oak leaves the largest changes in tannin levels were associated with the condensed tannin content. Secondary metabolites are not distributed evenly throughout the plant, either quantitatively or qualitatively (McKey 1979; Rathcke 1985; Coley 1988), varying spatially, geographically or temporally (Moreno-Black & Bent 1982), this differential plant chemical content resulting in differential herbivory (Wisdom 1985). A secondary compound may well help against generalist herbivores, whereas specialist herbivores might use the compound as a feeding stimulant (Simms 1990). The ecological trade-offs which may result from these contrasting responses could cause stabilizing selection on the level of that compound in the plant tissue (Simms & Rausher 1989). Natural products with defensive properties do not protect all plants against all predators, but instead act as filters, screening out many herbivores which would otherwise have fed on the plant (Burnett *et al.* 1977).

Condensed tannins appear to be an important factor in the food choice of animals possessing a ruminant-like digestion (Oates *et al.* 1977; McKey *et al.* 1981), although not in animals with single stomachs (Milton 1979; Calvert 1985). For non-ruminants such as the equids, food passage rates are much less influenced by dietary quality (Parra 1978). Thus optimal diet selection adaptations for a non-ruminant should involve maximizing the ingestion rate of the most critical nutrient over a wider range of dietary qualities than would be the case for a non-ruminant (Owen-Smith & Novellie 1982).

Dunham (1980), using a tame impala, conducted an experiment on ten plant species to determine the mean bite rates and mean food rate intakes. His results revealed that for mopane the mean bite rate was the lowest, whilst the mean food rate intake was the highest, indicating the ease with which browsers could utilize mopane due to its relatively large leaves and absence of spinescence (van Wyk 1972).

Goats are highly selective for food types that have a low fibre content (R. Hofmann *pers. comm.*)[2]. The senescing mopane leaves which the goats mostly selected for, had the lowest fibre content. Senescing mopane leaves not only have little fibre, but also few condensed tannins. The goats seemed able to differentiate between the leaf qualities as far as the above two parameters are concerned, preferring the food with less fibre and fewer condensed tannins. This result is consistent with the known literature on goat feeding behaviour (Owen-Smith & Cooper 1987), and questions the suggestion that goats cannot instinctively recognise the presence of condensed tannins in plants (Provenza & Balph 1990; Provenza *et al.* 1990).

The food choice test was conducted at the end of October, so the leaf classes collected would fall seasonally, under spring. Investigations conducted into the seasonal palatability of green and senescing mopane leaves have shown that for spring, green mopane leaves are at their least palatable, while the senescing leaves were at their most palatable, hence their receiving the greatest acceptance.

No differences existed between the number of acceptances and rejections for dry mopane pods, dry pods ranking third overall on the final acceptance scale followed by green pods, and dry pods ranking last on the final rejection scale, preceded by green pods. The green pods have a very definite turpentine smell and have numerous resinous compounds present in them, factors that are probably responsible for the very low acceptance, plants and/or plant parts having very definite odours, often being rejected by ruminants (Frost 1981).

During the dry season, water in the NTGR becomes increasingly restricted to pools along

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the Limpopo, Shashe and two small internal rivers (Walker *et al.* 1987). During the extreme drought the NTGR experienced from 1981 to 1984, Walker *et al.* (1987) recorded a catastrophic mortality of grazing ungulates, some populations being reduced by 10-20% of their pre-drought densities. Impala however, were unaffected. Impala being mixed feeders, possess the ability to switch to browse when the grass sward is severely depleted. Walker *et al.* (1987) hypothesize that the persistence of foliage on *Acacia tortilis* and other evergreen shrubs, together with the fallen leaves of deciduous species, were responsible for impala persisting through the drought. The leaves of *C. mopane* are nutritious even when dry, being eaten by animals in this condition (Kelly & Walker 1976). The present study questions the above hypothesis of Walker *et al.* (1987) which implicates *A. tortilis* as largely being the means of salvation for many ungulates, especially impala, over drought periods in the NTGR. Young mopane leaves flush independently of rain, and the palatability of this phenophase far exceeds that of other phenophases of this woody plant species. Furthermore, *A. tortilis* had little or no leaf material present during the current drought, the worst ever, few trees other than mopane trees, even producing new leaves.

The definite preference goats displayed for senescing mopane leaves, and the nutritive value of the young mopane leaves present on the hedged mopane trees, probably serve as the two most important factors responsible for the maintenance of the impala population of the NTGR during stressful environmental conditions. Furthermore, the dependence of ungulates on the mopane leaf litter scattered around the bases of most mopane trees, has been highlighted. Though reports have hinted at the possible importance of fallen mopane leaves for herbivore ecology, the ecological significance of this highly utilisable resource, it is believed, has been grossly under-estimated in the past.

CHAPTER

SIX

THE RELATIONSHIPS BETWEEN *COLOPHOSPERMUM MOPANE* AND INSECTS

PLANT APPARENCY, INSECTS, ELEPHANTS AND THE DYNAMICS OF A BOTSWANA MOPANE SAVANNA

INTRODUCTION:

Elephant damage to mopane woodland usually takes the form of broken stems and branches (Anderson & Walker 1974; Guy 1981; O'Connor & Campbell 1986), yet because few mopane trees die the biomass remains relatively unaltered (Guy 1981). Windthrow and lightning are also occasionally responsible for both felling and breaking large branches off mopane trees.

When it is considered, that many, if not all of those trees damaged by elephants will ultimately die from the breakdown of their wood by other organisms, the tremendous impact of elephants on their habitat can be appreciated (Thompson 1975). It thus follows that the interactions between elephants and woodlands is of perennial concern for wildlife management and research organizations (Buechner & Dawkins 1961; Glover & Sheldrick 1964; Lamprey *et al.* 1967; van Wyk & Fairall 1969; Laws *et al.* 1970; Caughley 1983; Cumming 1983; Pellew 1983; Owen-Smith 1983). Most elephant studies have preferred to concentrate on the intensity of destruction, a phenomenon for which this megaherbivore is so renowned, and the resultant management strategy that should be employed to curb their effect in the given area.

The present study was originally initiated to investigate the effect elephants were having on the mopane trees of the NTGR, and found that elephants were instrumental both in creating and maintaining the niche requirements of insect species utilizing mopane trees. In this chapter the extent of this interdependence is examined.

MATERIALS AND METHODS:

Field observations revealed the confinement of the distribution of *Messinea conica* to the terminal parts of the branches. Very definite differences in the appearance of the scale insects larvae were apparent, so records of whether or not zonation was evident in the development of *M. conica* were made. Thirty mopane trees whose branches had the ant/scale insect association on their branches were studied. In total, 127 branches were used for the data collected. Four developmental stages were defined, the operational definitions for each stage being:

STAGE 1 (S1): This is the youngest stage, and is characterized by a vast number of tiny brown nymphs, this morph being the only morph present in this zone.

STAGE 2 (S2): This is the second youngest stage, characterized by the presence of tiny brown nymphs, but small pyramidal-shaped nymphs also occur, very sparsely however.

STAGE 3 (S3): This was defined as the third zone of maturation, being characterized by the pyramidal shaped nymphs being both larger and far more abundant than in the previous stage. The tiny brown nymph morph is still present, but very sparsely.

STAGE 4 (S4): This was defined as being the mature stage of the nymphs of *M. conica*. Only the pyramidal-shaped nymph morph now occurs, individuals being much larger than in the previous stages, now less numerous, and at an obviously lower density.

Records of the following parameters were made: the length of each of the identified stages present on a branch; the distance from the start of the scale insects to the growth tip of the mopane branch; and the distance from the beginning of each defined stage to the terminal growth point of the branch.

The distribution of the ant-scale insect association on the branches of the mopane trees of the NTGR showed a definite concentration on the lower levels of the trees (usually below

3m above ground level). To test whether or not this anti-herbivory mechanism exhibited some form of stratification, a sample of twenty five large (taller than 5m) mopane trees who's branches had the association, were investigated. A 3,5m long metal pole was used, three intervals of 1m each being marked off along its length. This facilitated records as to the presence/absence of ants and scale insects in the defined zones when the pole was placed in an upright position against the tree trunk. The zones for recording purposes were defined as follows:

ZONE 1: 0-1m

ZONE 2: 1-2m

ZONE 3: 2-3m

ZONE 4: 3m+

In each zone for each tree, the number of branches possessing the ant/scale insect association were counted, as was the overall number of branches in that zone. A branch was defined as having a diameter less than 40mm but not greater than 10mm. The number of branches with the anti-herbivory association in the tree's given zones was expressed as a percentage of the total number of branches recorded for the zones.

Mopane bees *Trigona* spp. were found to nest in damaged areas on the trunks of mopane trees. The bees often cohabited a trunk with ants of the genus *Crematogaster*. These factors required that *C. mopane* trees possessing trunks with mopane bee nests inside, be investigated. Data were collected from a sample size of sixty five such mopane trees. Records were made of the presence or absence of ant nests in the same trunk as the bee nest, the locality of the bee nest, and the probable cause of the damaged area should the bee nest be found in a damaged portion of the tree trunk.

With elephants being absent outside the NTGR, it was necessary to check trees outside the NTGR's borders to record whether or not a damaged part of a mopane tree's trunk is a prerequisite as a nest site for mopane bees. The presence/absence of bees in the areas and the sites of mopane bee nests was also recorded. Three sites were chosen, all outside the boundary fence of the NTGR. Site 1 was located 500m from the NTGR boundary; Site 2, 5km from the NTGR boundary; and Site 3, 10km from the NTGR boundary. A fairly detailed description was compiled for each site. At each site one hundred trees were checked for the presence/absence of the following parameters:

1: Presence of a mopane bee nest.

2: Presence of ants and scale insects on the branches of the tree.

3: Presence of an ant nest in the hollow trunk.

4: Presence of damaged areas on trees.

An investigation was conducted into the response of *Crematogaster* spp. ants and *Trigona* spp. bees when a disturbance was applied to the trunk of the mopane tree in which both species were nesting. The response of both species was recorded, it being noted upon applying the disturbance whether or not the species disappeared and sought refuge, or appeared in an effort to face the agent of disturbance.

Records were kept of the seasonal occurrence of ants and scale insects on the branches of *C. mopane* trees. Six hundred trees were sampled during spring, summer and autumn. The sampling procedure was to walk through the veld in random manner sampling every third tree encountered. The presence/absence of ants and scale insects was recorded and the percent occurrence calculated from the data.

RESULTS :

TABLE 37: SEASONAL OCCURRENCE OF *MESSINEA CONICA* AND *ARYTAINA MOPANE* ON MOPANE TREES

SN	N	No. WITH *MESSINEA*	%	No. WITH *ARYTAINA*	%
SP	600	108	18	492	82
SU	600	48	08	552	92
AU	600	03	0,5	243	40,5
WI	600	00	00	00	00

The ant-scale insect (anti-herbivory) association on thin terminal branches has an 18% occurrence in spring when the new mopane leaves are emerging, declining to 8% in summer, and further decreasing to 0,5% in autumn when the leaves begin to show the first signs of senescence. In winter *M. conica* are absent from the branches of *C. mopane*. The anti-herbivory mechanism, in the form of ants, is thus at its most abundant over the spring leaf flush stage, tapering off as the seasons progress and as simultaneously the output of new leaf material and requirements for the protection of the new leaves, decreases.

TABLE 38: THE MEAN LENGTHS OF THE FOUR SCALE INSECT STAGES (ST) ON BRANCHES AND THEIR RESPECTIVE DISTANCES FROM THE GROWTH POINTS

			SIGNIFICANCE					SIGNIFICANCE			
ST	N	$\bar{X}$ LENGTH	S1	S2	S3	S4	$\bar{X}$ DISTANCE	S1	S2	S3	S4
1	59	10,49±7,3	-	N/S	N/S	N/S	5,61±4,7	-	**	***	***
2	76	10,59±4,8	-	-	N/S	N/S	9,49±7,3	-	-	***	***
3	23	9,28±4,5	-	-	-	N/S	19,15±10	-	-	-	*
4	10	11,75±3,0	-	-	-	-	26,40±8,8	-	-	-	-

No differences ($p>0,05$, Mann-Whitney Tests) exist between the lengths of any of the four identified developmental stages. However, definite differences ($p<0,05$) do exist between the distances from the branch growth point to the point at which each identified scale insect stage begins. Results show each stage of maturation to begin further back along the branch from the growth point.

TABLE 39: THE MEAN PROPORTIONS OF BRANCHES WITH THE ANTI-HERBIVORY MECHANISM IN THE DEFINED ZONES, AND THE DIFFERENCES (MANN-WHITNEY TESTS) BETWEEN THE ZONES

ZONE	N	No TREES WITH AHM	%	$\bar{X}$ PROP. PER TREE	SIGNIFICANCE Z1	Z2	Z3	Z4
1	25	13	52	0,22±0,25	-	**	N/S	***
2	25	25	100	0,40±0,17	-	-	***	***
3	25	13	52	0,15±0,20	-	-	-	**
4	25	03	12	0,03±0,09	-	-	-	-

Significance values: ***, <0,001; **, <0,01; *, <0,05; N/S, non-significant).

Highly significant differences (p<0,01) exist between the number of branches carrying ants and scale insects in Zones 1 and 2, 1 and 4, 2 and 3, 2 and 4, and Zones 3 and 4. No difference exists between Zones 1 and 3. Resplendent in the mean values of the number of branches in each zone carrying the anti-herbivory mechanism is a very definite trend. The number of branches carrying ants increases from Zone 1 to Zone 2, thereafter steadily decreasing to a virtual absence in Zone 4. The anti-herbivory mechanism exhibits a definite vertical stratification, being concentrated in Zones 1,2 and 3, these three zones comprising the primary browse levels of mammalian ungulates. This is further substantiated by Zone 2 having ants present in every tree sampled, followed by Zones 1 and 3 having the mechanism present in 52% of all trees sampled, followed finally by Zone 4 having the mechanism present in only 12% of the trees sampled.

TABLE 40: RECORDS OF THE BEHAVIOUR PATTERNS EXHIBITED BY *CREMATOGASTER* SPP. ANTS AND *TRIGONA* SPP. BEES AFTER DISTURBANCES WERE APPLIED TO THEIR NESTING SITES

	ANTS			ENTER	BEES	
N	APPEAR	DISAPPEAR	SWARMING	BEE NEST?	APPEAR	DISAPPEAR
10	10	00	10	04	00	10

Every time the disturbance was applied to the trunk, the bees would immediately disappear only being visible deep within the nest entrance. In contrast, each time the ants would immediately appear, raising their abdomens in alarm, and beginning to swarm, individuals peeling out from every conceivable hollow in the main trunk until within a matter of minutes the entire trunk and most of the tree's branches possessing scale insects were covered by the angry ant mass. On four occasions ants were actually recorded passing along the tubular entrance to the bee nest, and disappearing into the hollow stem area housing the bee brood chambers and honey sites. On no occasion did the bees even attempt to stop the ants from passing into their nest.

TABLE 41: DATA PRESENTING MOPANE BEE NEST SITE CHOICE WITHIN AND OUTSIDE (S1,S2,S3) THE RESERVE, AND THE PRESENCE/ABSENCE OF ANT NESTS IN THE SAME HOLLOW TRUNK

SITE	N	No TREES DAMAGED	No.WITH BEE NEST	%	No.IN TRUNK	No.IN DAMAGE	No.SHARING WITH ANTS	%
RES	65	65	65	100	65	65	36	55,4
S1	100	50	02	02	02	02	00	00
S2	100	97	20	20	20	20	20	100
S3	100	33	01	00	01	01	01	100

Of the sixty five mopane bee nests sampled within the NTGR, thirty six (55,4%) shared the hollow tree trunk with an ant colony. In all cases the bees' nests were encountered in damaged areas on the main stem of the mopane tree. The sites utilized were usually where a large branch had been broken away from the main stem, the most likely cause being elephants, and where a definite opening into the inside of the termite-hollowed main stem existed. The above result confirms that the anti-herbivory mechanism is not confined to the mopane trees within the NTGR's boundaries. The presence of ants on a tree is directly related to the presence of the scale insects on that tree's terminal branches, and not to the presence/absence of nesting sites. An increase in the number of bees' nests in the hollow trunks of trees in an area whose mopane trees have ants on their branches (compare Site 2 with Sites 1 & 3), parallels the result obtained for the NTGR, thus suggesting that mopane bees prefer to nest in a mopane tree whose hollow trunk has an ant colony inside it. A tree having ants and scale insects on its branches does not necessarily imply that the ants will utilize the trunk as a nesting site. Often however, it is impossible for them to do so, especially if the tree is undamaged and does not have a hollow trunk.

DISCUSSION:

Coexistence of species in a community may be attributed to the joint effects of adaptation to biotic and abiotic interactions. Plant apparency influences the exposure of plants to herbivores (Chew & Courtney 1991). The availability of the host plant for herbivores is affected by resource availability and environmental stress, which may profoundly influence plant growth form, phenology, abundance, competitive ability and plant investment in antiherbivore defense (Grime 1977; Chapin 1980; Coley *et al.* 1985). Apparency also affects the likelihood of discovery by highly specific herbivores (Feeny 1975; Rhoades & Cates 1976). Mechanisms of antiherbivore defense usually occur either quantitatively or qualitatively. Quantitative defenses are effective against all herbivores, being especially effective in late successional plant species which tend to exist in pure stands as do mopane trees. These plants are bound to be found in ecological time due to their being apparent to herbivores, and so they invest in heavy chemical defenses which appear to be more or less universally effective (Price 1984). Such plants however, do undergo changes in the palatability of their browse and so additional defense mechanisms may be employed, often these defenses occurring in the form of physical anti-herbivory mechanisms, usually as ants.

Qualitative defenses, typifying early succession plants, are not very effective against herbivores in general, the policy employed here being one of being "unapparent" or hard to find. This not being the case in stands of mopane trees due to their being numerous and accessible to herbivores, indicates quantitative defenses as the adaptation typifying a mopane savanna. However, plant apparency need not only be of a chemical nature. The present study shows plant apparency to be present in stands of mopane trees, this apparency resulting from various trees having different insect associations, some trees assisting herbivory whilst other trees have physical mechanisms which actively deter herbivory.

Mopane is a host plant for a few endemic insect species, one of the endemics being the mopane psyllid *Arytaina mopane* (Homoptera, Psyllidae) a monophagous insect (Ernst & Sekhwela 1987). Psyllids are little bugs about the size of aphids and resemble tiny cicadas. Female psyllids are recorded as laying their eggs at the tips of young shoots, usually on the edges of young tender leaves. Psyllid eggs take about a week to hatch, sluggish nymphs emerging, which initially creep about, but soon settle down to feed after which they will rarely move unless overcrowding demands it. *Arytaina mopane* occurs on the branches of mopane trees in the NTGR, this species being a phloem feeder as are all other Psyllidae (Petty 1925, Hodkinson 1974). The larvae of *A. mopane* construct a scutcheon-like cover which protects the developing insect (Ernst & Sekhwela 1987). These leaves often cover the entire leaf surface so reducing photosynthetically active light perception (Ernst & Sekhwela 1987), and increasing the palatability of the leaf (van Wyk 1972). Larvae of *A. mopane* develop on the young expanding mopane leaf, the young leaf soon becoming completely covered by the sugar-rich lerps. These lerps have no starch, high amounts of monosaccharides (results in an increase in palatability) and water-insoluble carbohydrates, high concentrations of potassium and very low concentrations of calcium and magnesium (Ernst & Sekhwela 1987). Trees utilized by *A. mopane* had lerp-covered leaves scattered over most of their canopies. These trees can be regarded as patches for consumption within stands of mopane, this resulting in only partial prey consumption by browsers (Astrom *et al.* 1990).

Messinea conica (Hemiptera; Coccoidea; Coccidae) commonly called the mopane scale, often appears very insignificant, sometimes as mere specks adhering to twigs (juveniles), to pyramidal structures (fully mature females) whose diameter approximates 2mm. Females and males of *M. conica* are distinguished by the males being oval-shaped while the females are always round. Soft scales such as *M. conica*, being protected only by their own thickened skin, give off a great deal of honey-dew, which often attracts ants. No literature is available on the life cycle of *M. conica*, and similarly the ecology of this insect has not been documented. The development of the larval stages reveals a definite zonation in the stages of maturation along the length of a mopane twig.

Messinea conica has developed an association with the mopane tree through its utilizing the sap moving in the phloem tissue of the thin outer twigs of branches. It is hypothesized that it is due to its mouthparts being so small, that this insect is forced to feed off the thin outer twigs of the branch, its mouthparts being incapable of penetrating down to the conducting tissues of twigs whose diameter exceeds 7mm (N= 100). The outermost developmental zone, or that zone closest to the growth point, is the youngest zone, Zone 1. Posterior to that zone in a definite hierarchy, are the other zones, the most mature zone of *M.*

conica, Zone 4, the zone of mature females, being furthest from the growth point. This definite staggering of zones in relation to maturation, probably results from the differing sizes of mouthparts. It is hypothesized that the youngest individuals have the smallest mouthparts, and so are forced to feed on the very thin outermost twigs so confining them to the ends of the twigs. Adults possessing better developed mouthparts capable of deeper penetration, can feed further back. Thus the larval distribution of this insect is confined to the outermost growth points of the mopane tree.

According to Barnes (1976) the part of a branch most likely to experience herbivory is the very end of the branch, the growth point. It thus seems that the staggered development of *M. conica* on mopane branches, with adults being furthest from the growth point, the point most likely to experience herbivory, may be an adaptation to ensure that herbivory takes its toll on the juveniles of and not on the sexually mature adults.

Larvae of *M. conica* develop on the mopane trees' branches in early spring just before the spring leaf flush, a period when mopane trees becomes extremely valuable to all mammalian herbivores. *M conica* lives out its developmental stages on these branches until with the onset of autumn, *M. conica* disappears, the shells of these scale insects being all that remains on the branches. The seasonality of *M. conica*'s occurrence on mopane branches in turn results in cocktail ants *Crematogaster* spp., ants regularly encountered on mopane trees, exhibiting identical seasonal trends.

The presence of *Crematogaster* ants on mopane trees is related to whether or not *M. conica* is present on the tree. Such associations are mutualistic, the ants obtaining a readily available food source (Holldobler & Wilson 1990), while the tended species obtains protection (Pierce & Eastal 1986; Schupp 1986; Buckley 1987). Ants, according to Letourneau (1983), make use of plants either for shelter and/or nutrients. *Crematogaster* ants are renowned for their cleaning behaviour, this often resulting in the removal of potential herbivores in their earliest developmental stages (Fiala *et al.* 1989). The number of homopterans however, are known to increase in the presence of ants (Ito & Higashi 1991). Triangular relationships amongst plants, homopterans and ants are thus indeed complex (Ito & Higashi 1991).

Crematogaster ants are chiefly arboreal (Tho 1978; Fiala *et al.* 1989) nesting mostly in hollow tree trunks. Species of the genus are very fond of sugary substances and are often found attending aphids, coccids and other hemipterans which exude honeydew (Tho 1978; Skaife 1979; Fiala *et al.* 1989; Volke 1992), hence their attendance of a scale insect on the branches of mopane trees.

These ants are recognised by their habit of raising their abdomens when alarmed, the petiole being joined posteriorly to the abdomen, this joint being very flexible so allowing the ant to cock its gaster, hence the name (Skaife 1979). The defense mechanism employed by *Crematogaster* ants is not to actively sting the foe though all myrmicines do possess stings, but to use the spatulate sting to smear a poisonous fluid onto the foe whilst simultaneously biting in a frenzied fashion (Skaife 1979). The presence of *Crematogaster* ants on mopane trees in the NTGR, conferred an anti-herbivory mechanism (AHM) upon mopane trees, the protection mechanism resulting from a three way association between the ants, the scale insects, and the mopane tree.

The confinement of *M. conica*'s distribution to the outermost part of the canopy of mopane trees, in turn means that the ants are confined to the outermost part of the canopy, their being concentrated around the new growth points of the mopane tree's branches. Due to the pugnacious disposition of these ants, mopane trees thus possess an effective AHM, these ants deterring herbivory by browsing ungulates due to their physically climbing onto and biting at the mouthparts of the browser.

Ito & Higashi (1991) state that ants may contribute greatly to plants by protecting growing points which are the most important for any species of plant. Non-defoliating insects such as sap suckers, rarely result in conspicuous damage to plants (Vranjic & Gullan 1990), nevertheless considerable reductions in leaf production, leaf size and even seed production are known to occur in plants infested with homopterans (Dixon 1971a,b; Newberry 1980a,b,; Becerra & Venable 1989). Plants infested with sap sucking insects are known to allocate more dry matter to the leaves, often at the expense of the roots (Vranjic & Gullan 1990). This condition would result in a decrease in both the value and palatability of the browse. So it appears that homopterans often not only confer protection on plants through their associations with ants, but also through their reducing browse quality.

Furthermore, the *Crematogaster* ant - *M. conica* association is not only terminal in its distribution on mopane branches, but also stratified vertically. Results show a concentration of ants on mopane trees in the range Zone 1 to Zone 3, this implying that the AHM's vertical distribution is concentrated around the primary browse level of most African ungulates *i.e.* 0,5m - 2,5m above ground level. There is a sharp decline in the occurrence of ants and scale insects in Zone 4 (above 3m a.g.l.), a feeding height few African browsing ungulates can achieve.

The AHM was however not present on every mopane tree in the NTGR. The percent of trees possessing this mechanism varying from 18% in spring, to 8% in summer, to 0,5% in autumn, to 0% in winter. Those mopane trees whose branches had the AHM present, had few lerp-covered leaves when compared with those mopane trees whose branches had no AHM.

Many legumes possess extrafloral nectaries, which according to Becerra (1989) may function to defend plants from ant homopteran mutualisms by weaning ants onto a diet of nectar controlled by the plant. Mopane trees have no nectaries, nor any extrafloral nectaries, and so protection is afforded through *M. conica*, an insect whose purpose parallels that of an extrafloral nectary. Phloem fluids are known to directly affect the survival, growth and reproduction of homopterans (Auclair 1963; Dixon 1985), and so host plants can affect the fitness of their herbivores (Cushman 1991), but it is more difficult to produce chemical defenses against sap feeders than against chewing herbivores (Becerra 1989), hence the probable development of the association with *M. conica*.

Elephants, tear down large branches from trees exposing the auburn-coloured heartwood either directly or indirectly through splits in the sapwood, which develop as the sapwood dries out. This exposed heartwood is utilized as a food source by termites, especially *Macrotermes* and *Hodotermes* species which hollow out the heartwood of the tree. The termites never appear to enter the heartwood of the tree from underground *i.e.* the root area, so it seems the only entrance is via a damaged area on the aerial portions of the tree. When all the heartwood has been removed the termites disperse leaving behind a hollow but living tree. Mopane bees utilize the hollow stems of such large mopane trees.

Mopane bees, or more commonly known as stingless bees, belong to the genus *Trigona* (Apidae) and are members of the "social bees" of which there are about 500 species in the world. These bees are tiny, being amongst the smallest of bees, some of them measuring only 3mm in length. The nests of *Trigona* were always concentrated in the main trunk of the tree. A noticeable characteristic of these nests, is that the waxy tubular entrance always protruded from the trunks of trees sampled both inside and outside the NTGR, these damaged areas being the site of entry into the trunk. Inside the NTGR, the damaged area selected as a nesting site was usually directly attributable to elephants and their branch-braking habits. The possibility of such sites being created by branches being torn down by very heavy winds or lightning should not be discounted, but the chances are slight.

As *Trigona* cannot sting due to their stings being vestigial, their mode of defense is to swarm out of their nest if disturbed, buzzing about the face of the foe in a very irritating manner. They concentrate their efforts around the ears, nasal openings, mouth and eyes, and do occasionally bite freely. *Trigona* nest in hollow tree trunks and in holes in walls and rocks.

One African species of *Trigona* has been recorded nesting inside the nest of a species of cocktail ant (Skaife 1979). It was not uncommon to find both *Trigona* and *Crematogaster* ants nesting in the same hollow mopane tree trunk.

Observations in the NTGR showed that *Crematogaster* ants and *Trigona* cohabited peacefully in the same mopane tree trunk, *Trigona* individuals never attempting to deter a *Crematogaster* individual from passing along their tubular entrance into the nest. The presence of a *Crematogaster* nest in the same trunk as a *Trigona* nest may well be of great selective advantage for *Trigona*. *Crematogaster* ants definitely confer protection on the *Trigona* nest, as this bee species possesses no definite means of protecting the nest other than by physical constraints such as the narrow entrance to the nest which may exclude certain sized predators, but definitely not all.

Each time a disturbance was applied to a hollow mopane tree trunk containing nests of both species of insect, the ants would immediately raise their abdomens in alarm. If disturbed this ant genus is known to exude a sticky white fluid which has a strong unpleasant odour, from glands on the tip of the abdomen (Skaife 1979). This means of chemical communication soon alerts the other individuals of the colony, both on neighbouring branches and in the nest in the hollow trunk. The ants swarm out of the trunk spreading all over the surface of the trunk in a random manner. Soon this movement spreads to the branches and these too become a swarming mass of angry ants. Shortly after the disturbance, some ants were always to be found either in or around the entrance to the *Trigona* nest. *Trigona* individuals disappeared every time a disturbance was applied near their nest.

Bees of the genus *Trigona* and subgenus *Trigona* possess volatile materials in their mandibular glands which are used as alarm substances and as marking pheromones (Johnson & Wiemer 1982). Studies have shown that volatile compounds such as nerol, 2-heptanol and 2-nonanol are recognised as alarm substances (Johnson & Wiemer 1982; Johnson *et al.* 1985).

When a disturbance was applied to only the entrance of the bee nest, the ant response shortly after was similar to that mentioned above, some *Crematogaster* individuals appearing from inside the trunk and immediately moving to the bee nest entrance. It is hypothesized that the ants will respond to an alarm substance released by the bees, due to both species being highly evolved in the recognition of chemical messages in the form of volatiles. Even the smallest disturbance to the bee nest resulted in the defenders of the nest, *Crematogaster* ants, emerging to attack the intruder. Two tree trunks containing nests of both *Trigona* and *Crematogaster* ants were sawn open manually so avoiding creating excessive damage as would have resulted from using a chainsaw. It was apparent in both cases that the nests of the two insect species were indeed separate and the only means by which *Crematogaster* ants could gain entry into the *Trigona* nest, was by entering through the waxy entrance protruding from the tree trunk.

The findings within the NTGR are paralleled in the study conducted outside the NTGR. The *Crematogaster-Trigona* association in hollow trunks is also resplendent in trees outside the NTGR. Furthermore, as the number of ants encountered in hollow tree trunks increases as in Site 2, the number of nests of *Trigona* correspondingly increases. Due to elephants having been absent from the areas beyond the borders of the NTGR for many years, the availability of nesting sites for *Trigona*, in the form of hollow mopane tree trunks, is much lower. The utilization of elephant-damaged areas by *Trigona* reveals the importance of elephants in creating some of the niche requirements of this insect, and in maintaining its association with the mopane tree.

Trigona bees are often seen attending the relatively inconspicuous flowers of the mopane tree, some collected specimens being covered in pollen. These bees thus appear to serve as a pollen vector both within and between stands of mopane, and may assist in the pollination of mopane trees, trees which are probably pollinated by wind predominantly.

Trigona bees are often seen collecting resin oozing from a damaged area on a mopane tree trunk which resulted from elephants tusking the tree in an attempt to remove bark. These actions both expose and damage the cambial layer of the tree resulting in the resin oozing from the wound. The nesting material of *Trigona* is called cerumen, a dark coloured mixture of light wax, produced between the dorsal segments of the abdomen. Cerumen is used to block up cracks and crevices, and also to construct the curious tubular entrance to the nest often seen protruding from a portion of the main trunk. It has been suggested that the sticky funnel at the entrance prevents ants and other unwanted insects from entering. Sentries remain on guard at the entrance to the nest during the day, as is the case with the honey bee. As darkness approaches, the bees close up the funnel with a temporary plug of celumen. Both the brood consisting of irregular clusters of oval-shaped cells and cocoons supported by celumen, and the honey of *Trigona* are relished by Africans (Skaife 1979). When the inner bark of the turpentine tree *Syncarpia glomulifera* is damaged, it exudes a resin, this serving as an attractant for worker bees of two *Trigona* spp. bees, who then collected the resin in their pollen baskets (Milborrow *et al.* 1987).

The trees outside the NTGR are however, not completely undamaged. Local inhabitants chop branches from mopane trees to use as firewood. So doing, they simulate elephant damage, exposing the heartwood. Termites utilize the heartwood, this serving to begin the ecological interactions surrounding the hollowness of the mopane tree. Thus local inhabitants contribute towards maintaining Trigona nesting sites beyond the NTGR's borders.

Crematogaster ants were absent both on and in mopane trees from late Autumn (April) to late winter (July) due to the seasonality of *M. conica*. Over this period the *Trigona* nest is far more vulnerable to predation, than when the ants are present. It may well be that *Trigona* nests are constructed in hollow mopane trees whose branches are utilized by *M. conica* on an annual basis, *M. conica* returning to the tree in early spring, associated with this being the return of *Crematogaster* ants and protection for the *Trigona* nest. Such a situation would reduce the annual predation pressure that the *Trigona* nest would be exposed to.

Finally, it is concluded that the impact elephants have on plants, in this case mopane trees, needs to be given more detailed attention, and many aspects of proposed "destruction" should be carefully investigated before management decisions for the overall improvement of the area, are implemented.

FACTORS RESPONSIBLE FOR THE EXCLUSION OF CATERPILLARS OF THE MOPANE MOTH (SATURNIIDAE) FROM THE MOPANE VELD OF THE NORTHERN TULI GAME RESERVE, BOTSWANA

INTRODUCTION:

Caterpillars of the mopane moth *Imbrasia belina* have been absent from the NTGR for almost the last twenty years, the last record of their occurring within the boundaries of the NTGR being in 1969. However, the caterpillars have not disappeared from the entire Tuli Block, often being encountered in summer and early autumn on both the South African and Botswana sides of the NTGR, but never in the NTGR. It has become apparent to many of the wardens in the area that the NTGR seems to be an area of local extinction, the occurrence of caterpillars often circumventing the NTGR but never entering it.

Colophospermum mopane (Caesalpinioideae, Leguminosae) is a host plant for a few endemic invertebrate species, two of the endemics being monophagous insects (Ernst & Sekhwela 1987). One of these is the mopane moth *Imbrasia* (*Gonimbrasia*) *belina* (Westwood) whose caterpillars feed predominantly on the leaves of mopane trees (Pinhey 1975; Skaife 1979; Oberprieler 1986,1990). The leaves of the mopane are only utilized as larval food in a comparatively small area of the distribution range of the species, namely the extreme northern Transvaal, north-eastern Botswana, northern Namibia and parts of Zimbabwe and Mocambique (Oberprieler 1986).

The mopane tree indirectly serves as a source of food to the Tsonga people, as they use the caterpillars as a food source, either roasting or drying the caterpillars after the contents of the gut have been extruded (Liengme 1981). Dried mopane moth caterpillars are high in protein yet, in comparison with the protein from other products of animal origin, digestibility of this protein was found to be relatively low (Dreyer & Wehmeyer 1982). It is speculated that the poor protein digestibility may be due to the fact that some insects have nitrogenous compounds present such as chitin, a compound that cannot be hydrolysed during digestion because large mammals lack the enzyme chitinase (Dreyer & Wehmeyer 1982).

The caterpillars, colloquially known as "mopane worms", occur in summer (Liengme 1981), and prefer fully developed mopane leaves to young leaves when feeding (R. Oberprieler *pers. comm.*)[1]. Sometimes the outbreaks of caterpillars in southern Africa are sufficiently vast to defoliate stands of trees (van Wyk 1972; Bernays & Janzen 1988), on occasion up to three times in a single growing season (Barnes 1982).

Imbrasia belina, an emperor moth, belongs to the family Saturniidae (Skaife 1979). Saturniid adults have only rudimentary mouthparts and apparently do not feed, harvesting all their water and nutrient resources while they are caterpillars (Holm & de Villiers 1983; Janzen 1984). Caterpillars of all saturniid species feed on the foliage of dicotyledonous woody plants, feeding externally on the leaf blades of mature foliage (Janzen 1984). Saturniidae use host-plants whose foliage is rich in phenolics, especially tannins, yet poor in alkaloids (Janzen 1984; Janzen & Waterman 1984). These plants however,do not appear conspicuous in the phytochemistry literature as producers of directly toxic small molecules (Bernays & Janzen 1988).

The purpose of the present investigation was to determine what factors could have been and possibly still are responsible for the absence of caterpillars from mopane trees of the NTGR.

STUDY SITES:

Two sites were used for the present study, one in the NTGR, the other site 35km north of Bobonong, a small town lying to the south of Phikwe, some 140km by road from the

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NTGR boundary. The vegetation structure at both sites falls within the broad classification of Mopane Veld (Acocks 1975). Neither site has been subjected to any definite ecological management.

MATERIALS AND METHODS:

Leaf samples were collected from both sites. Only mature green leaves were collected for comparison of their chemical compositions. The methods used to analyze the plant material are described under the general methods section.

The following data were recorded for 600 trees at the NTGR site and 200 trees at the Bobonong site:

a) Basal diameter.

b) Presence of any structural damage to the tree.

c) Presence of ants and scale insects on the branches of the mopane tree.

RESULTS:

TABLE 42: TABLE PRESENTING CHEMICAL RESULTS OBTAINED FOR LEAF SAMPLES FROM THE TWO CHOSEN SITES

SITE	PARAMETER	N	$\bar{X}$±S.D.	SIGNIFICANCE
RESERVE	CP	20	12,9±0,5	
BOBONONG		20	15,4±0,2	***
RESERVE	NI	20	2,10±0,08	
BOBONONG		20	2,50±0,04	***
RESERVE	EN	20	19,5±0,3	
BOBONONG		20	20,1±0,2	***
RESERVE	CT	10	70,9±1,0	
BOBONONG		10	48,5±1,9	***
RESERVE	PP	10	48,4±5,15	
BOBONONG		10	29,4±6,10	***
RESERVE	TP	10	192,3±6,9	
BOBONONG		10	44,8±3,8	***

(**Significance values:** ***, <0,001; **, <0,01; * <0,05; N/S non-significant)

The most striking difference between the mopane trees within the NTGR, and at Bobonong where caterpillars regularly occur, is the shape of the trees. The mean basal diameter values in Table 43 clearly indicate that the mopane trees at Bobonong are slender compared to the trees within the NTGR.

Significant differences (p<0,05, Mann-Whitney Tests; Table 42) exist between the chemical composition of the foliage of the two sites. The Bobonong site's leaves have a significantly lower (p<0,001) condensed tannin and total phenolic content, a poorer (p<0,05) protein precipitation capacity, and significantly greater (p<0,001) amounts of nitrogen, crude protein and available energy. These factors make the mopane leaves found at Bobonong, far more nutritious than those of the NTGR.

TABLE 43: TABLE OF COMPARATIVE DATA FOR THE TWO STUDY SITES' TREES.

SITE	N	$\bar{X}$ BAS.DIAM.	No DAMAGED	%	No WITH ANTS	%
BOB.	200	8,31±3,12	4	2,00	0	0,00
RES.	600	16,78±10,59	567	94,5	79	13,20

DISCUSSION:

The belt of mopane trees outside Bobonong where caterpillars occur abundantly on an annual basis is easily recognisable by remains of old fires (ash piles) under trees along the roadside where the caterpillars are roasted as a food source by local inhabitants and commercial harvesters.

The much smaller mean basal diameter of mopane trees at the Bobonong site possibly indicates that caterpillars are more successful where the mopane is tall and thin, this morph resulting from environmental constraints which edaphic and geological factors impose (Gertenbach 1987). Many mopane trees within the NTGR have resident ants (*Crematogaster* spp.) on them due to the ants attending a homopteran (*M. conica*) which is present on the trees' branches. The absence of the homopteran on mopane trees at the Bobonong site, indicates that ant predation on young caterpillars may be an important factor influencing caterpillar occurrence.

Adult moths, active mostly at night, lay their eggs on the newly-developed green leaves of the mopane tree. Eggs are most likely to be preyed upon by parasitic wasps and not by ants, as the eggs of *I. belina* are too hard for ants to bite into (R. Oberprieler *pers. comm.*). However, the scouring effect the ants would have on the tree's foliage as a direct result of their movements, would result in the young larvae (up to 3cm in length) being preyed upon as ants are known to effectively reduce the number of lepidopteran larvae (Ito & Higashi 1991). Assassin bugs would also prey on the young caterpillars, while birds and possibly some mammal species would feed on the older instars.

Edaphic factors may also play a role. In the areas where caterpillar exoskeletons were encountered, the soil was always rather fine in texture. In contrast, in the NTGR, the soil is very coarse and the surface of the ground rocky. When the caterpillars are fully developed they leave the mopane trees and burrow into the soil relatively close to the bole of a tree. It is hypothesized that difficulties encountered whilst burrowing may contribute to their local absence, soil structure not being conducive for efficient burrowing and pupation in the soil.

Plant chemistry is known to affect the biology of saturniids (Bernays & Janzen 1988). Any plant that invests in defenses, especially in leaves, will reduce its losses to herbivores (Coley *et al.* 1985), the quality of browse being determined largely by its nutrient, chemical and mechanical properties (Jachmann & Bell 1985). When herbivores exert sufficient selective pressure on their hosts, hosts do not respond passively to damage (Rhoades 1979; Baldwin & Schultz 1983; Teague 1989; Lundberg & Astrom 1990), but evolve defenses, termed inducible defenses (Hendrix 1988; Edelstein-Keshet & Rausher 1989), such as toxic chemicals, protective physical features and nutrient deficiencies that tend to reduce or at least discourage attack (Bate-Smith 1971; Freeland & Janzen 1974; Arnold & Hill 1975; Coley

1986; Karban *et al.* 1989; Lundberg & Astrom 1990; Ras 1990). Thus the value of a host plant tissue for herbivores is a function of its nutrient and secondary compound contents (Rosenthal & Janzen 1979). Two leaf characteristics shown to influence the food value of leaves for insects include nitrogen content (Feeny 1970) and polyphenolic (especially tannin) content (Feeny 1970; Haukioja & Niemela 1978). Studies suggest that in the insect gut, tannin-protein precipitation may be reversed or even prevented (Berenbaum 1983; Martin & Martin 1984).

Lepidopterans are known to be selective in avoiding phenolics and related compounds in leaf material, as these influence their fitness (Crawley 1983; Hill & Pierce 1989). Having found the mopane leaves in the caterpillar belt to be so nutritious, it appears that these lepidopterans may proliferate in areas where mopane trees' leaves have higher nitrogen and crude protein contents, and where the availability of the crude protein to the larval insect is not reduced by the presence of many tannins, phenolics and a high browse protein precipitation value. Furthermore, the preponderance of caterpillars in mopane stands whose leaves have low phenolic contents, appears to be in agreement with the newly developed school of thought that adult moths may well be capable of perceiving browse quality by assessing the volatile compounds leaves are releasing (R. Oberprieler *pers. comm.*).

Game reserves are, in essence, islands confining animals within their boundaries, the area never being alleviated of the browsing pressures it experiences due to the natural migration patterns of many large mammalian ungulates having been disrupted by fences. This results in the area being utilized year in and year out by species competing for survival within the environmental constraints the reserve imposes upon them. A known response of plants experiencing continual herbivory is to concentrate the carbon compounds they generate from photosynthesis into distasteful compounds such as tannins and phenolics, in so doing attempting to deter browsing (Zucker 1983). This may well be the case in the NTGR where the mature mopane phenophase is not highly palatable when compared with that from the trees where the caterpillars occur. Edaphic factors may well contribute to this poorer palatability, but the effect of such factors on the palatability of mopane phenophases has not yet been determined.

It is hypothesized that, as the herbivore numbers increased, especially those of the larger herbivores known to utilize the mopane extensively *eg.* elephants and eland, due to the protection afforded within the NTGR, an increased browsing pressure resulted. The trees responded to the increased herbivory by producing more secondary compounds in their leaves, so attempting to reduce herbivory. Increasing the number of defenses probably only occurred in the mature mopane leaves, as younger developing leaves, use the products of products derived from photosynthesis for growth, not protection. This attempt to decrease palatability, along with the ever-increasing numbers of browsing ungulates in the NTGR, probably resulted in the quality of the mature leaves deteriorating further. With this being the leaf class the caterpillars focus their attention on, the nutritive gain must have been reduced and though the effects on larval biology are unknown, it does not seem ludicrous to think them adverse.

Caterpillars have dramatic effects where they occur, defoliating vast stands of mopane trees often required by browsing animals. The mature green mopane leaf on trees in the NTGR is seasonally, at its most palatable, in late summer and early autumn, the period when caterpillar outbreaks are expected. Defoliation over this period, especially in times of drought when food is extremely scarce, would remove a much needed food source for mammalian herbivores and set up an ecological situation of great concern for managers.

CHAPTER

SEVEN

CONCLUSION

In conclusion, it may be said that the local extinction of caterpillars of the mopane moth *Imbrasia belina* probably resulted first and foremost from the preponderance of ants on trees in the NTGR and may have been further assisted by edaphic factors a deterioration in browse quality of the phenophase selected by these caterpillars. However, it is believed that their absence may be ecologically advantageous both with respect to mammalian herbivore numbers within the NTGR, and the tourist trade, the carrying capacity of the mopane trees of the NTGR never being reduced to the very low values that might prevail in the event of mass defoliation by the caterpillars.

CONCLUSIONS DERIVED FROM THE OBJECTIVES SET AT THE BEGINNING OF THE STUDY:

1: Mopane trees have been exceedingly maligned in their ecological importance for mammalian ungulates. This is substantiated by the subtle changes the phenophases of this tree species undergo in their chemical composition. Each change in palatability of a phenophase, either for the better or worse, is complemented by changes in the palatabilities of the other phenophases, so that an overall balance for the good of herbivores in general, is maintained.

2: Implications are that the spectrum of volatile compounds an ungulate is exposed to, do possibly serve as an indicator of browse quality. The highly nutritious young mopane leaves on hedged mopane trees, have far greater concentrations of "nutritious volatile compounds", and far lower concentrations of "distasteful volatile compounds", than do the mature, far less palatable mopane leaves.

3: The impact elephants and eland are having on the area may not be aesthetically pleasing, but their activities are responsible for a mopane morph which is robust, comes into leaf early, keeps on producing new leaves even in the presence of heavy utilization, and which proves to be an available, palatable resource in the NTGR for mammalian ungulates when food is scarce. Eland are largely responsible for the hedged effect of many mopane trees within the NTGR, a phenomenon previously thought to result solely from elephants. Eland may well be utilizing the twig bark over the early spring period before the emergence of the highly palatable young green mopane leaves, to obtain sufficient moisture at a time when moisture is usually very scarce. The change in twig bark palatability from spring to summer, this being an increase in palatability, sees a vast increase in the number of branches removed. This results from the return of elephants to the areas of hedged mopane trees which are now in leaf. Eland concentrate their attention on new young growth whose bark can be peeled off more easily than the bark on older growth, whose nature is very dissected, making it difficult to be removed in strips. Elephants exhibit no definite preference for the new bark of young branches.

4: It is hypothesized that elephants will only utilize the stem bark of mopane trees over periods when the amount of crude protein the animal is taking in is low (eg. in winter). Stem bark probably serves as an available resource from which the crude protein dietary intake can be supplemented. The resilience of the mopane tree to debarking is evident from a specimen with 95% of its stem bark removed, showing no die back of growth tips, nor visible signs of mass leaf senescence. In the past far too much emphasis has been placed on the impact elephant bark-stripping is having on mopane trees. The mopane tree is very robust and is capable of tolerating incredible punishment imposed upon it by large mammals. The removal of a portion of the stem bark from a tree does not imply that the mopane tree will succumb. The resilient nature of the mopane tree is hypothesized as resulting from the possibility that elephants may have to rely on these trees in times of need, and the resultant heavy utilization could result in mass destruction and die-offs should this resilience factor not exist.

5: Epizoochory as the mode of dispersal of mopane diaspores is conclusively disproved. Water is probably the major vector of mopane diaspores, yet wind probably also assists in the dispersal biology of this caesalpinioid legume.

6: Goats are highly selective for food types that have a low fibre and condensed tannin content. Dry mopane leaves which the goats mostly selected for, had the lowest fibre content and the fewest condensed tannins. This result is consistent with the known literature on goat feeding behaviour, and questions the suggestion that goats cannot instinctively recognise the presence of condensed tannins in plants. Goats do thus serve as indicators of browse quality. Senescing mopane leaves are believed to be of extreme value in maintaining the impala population of the NTGR when adverse conditions prevail.

7: The impact elephants have on plants, in this case mopane trees, needs to be given more detailed attention, and aspects pertaining to the supposed "destruction" elephants wreak, should be carefully investigated before management decisions are implemented. *Trigona* bees are often seen collecting resin oozing from a damaged area on a mopane tree trunk which resulted from elephants tusking the tree in an attempt to remove bark. These tusking-actions both expose and damage the cambial layer of the tree resulting in the resin oozing from the wound. Moreover, the utilization of elephant-damaged areas by termites and *Crematogaster* spp. ants, further reveals the importance of elephants in creating some of the niche requirements of insect species associated with mopane trees. Plant apparency comes to the fore as spring approaches, vast stands of mopane trees, all appearing homogeneous, actually having very different biologies. The differences are directly attributable to the insect associations trees within mopane stands have.

8: The local extinction of caterpillars of the mopane moth *Imbrasia belina* probably resulted first and foremost from the preponderance of ants on mopane trees in the NTGR, and may have been further assisted by edaphic factors and a possible deterioration in browse quality of the phenophase they select for. However, it is believed that their absence may be ecologically advantageous both with respect to mammalian herbivore numbers within the NTGR, and the tourist trade, as the carrying capacity of the mopane trees of the NTGR is never reduced to the very low values that might prevail in the event of mass defoliation by these caterpillars.

CHAPTER

EIGHT

PHILOSOPHICAL

CONSIDERATIONS

EVOLUTIONARY ASPECTS

The biology of *Colophospermum mopane* and its relationships with the fauna that utilize this tree are indeed intricate, suggesting a long history of co-evolution of this tree species with its mammalian and insect fauna.

Messinea conica, the mopane scale, is an insect whose development and biology appears solely centred around the mopane tree. These insects, capable of exuding honeydew, function for the mopane tree as would an extrafloral nectary on an acacia tree. This insect association probably evolved due to the absence of extrafloral nectaries on the mopane tree. The evolutionary advantage of such a development was that an anti-herbivory mechanism prevailed, this resulting from the scale insect being attended by ants belonging to the genus *Crematogaster*. This alleviates the plant's physiological demands on herbivory deterrents which the plant itself would have to produce. Such compounds are energetically costly to produce, requiring much of the carbon derived from photosynthesis. Having an active and not a passive means of defense, means that more carbon compounds derived from photosynthesis can be mobilized to the growth points of the plants, and to biological processes other than phenolic production and the synthesis of distasteful compounds.

The mopane psyllid *Arytaina mopane* is an insect whose larval biology is confined to the mopane tree. The larvae of this psyllid harvest the sugar-rich substances from a developing mopane leaf and then secrete a sugar-rich lerp around themselves. This increases leaf palatability and encourages herbivory. Herbivory, especially concentrated herbivory, results in the improvement in the palatability of a browse. Those plants aiding herbivory have probably done so in order that ecological relationships between mammalian herbivores and the mopane veld be maintained, not all plants actively discouraging herbivory.

The striking differences in the biology of individual mopane trees within mopane stands, especially in their apparency, again indicates that this tree has co-evolved over a long period of time with both its mammalian and insect herbivores. It is hypothesized that the plants mediated much of the evolution between themselves and their insect component, this resulting in the two mediating many of the processes between browsing ungulates and this tree.

Elephants indeed appear to play a key role in the biological processes surrounding mopane trees, almost so much so, that elephants could be raised to the ecological status of a **keystone species** within this veld type. So much of the damage this megaherbivore inflicts on the mopane tree has proved to be extremely important, damaged areas being utilized by insects both for food in some instances, and shelter. These are both niche requirements of a species, and so elephant impact is extremely important in the maintenance of some of the niche requirements of certain insect species utilizing mopane trees.

The mopane tree is extremely resistant to wood-boring arthropods, their entry into the tree only being facilitated by the exposure of a mopane tree's heartwood. Where only the bark is removed, usually through the tusking-action of elephants, in so doing exposing the yellowish sapwood beneath, no wood-borer activity is evident. It thus appears as if the sapwood has a chemical composition which actively excludes these wood-boring insects. Monoterpenes (C10H6), a major class of secondary compounds present gymnosperms (Radwan & Crouch 1974), have been shown to play a role in both the selection and colonization of trees by wood-boring arthropods (Wood 1973), certain volatiles serving both to attract and repel insects (Vite & Pitman 1969; Moeck 1970; Phillips 1990). Mopane trees are flowering plants and thus fall within the Anthophyta, but their resistance to wood-boring insects, a phenomenon so often associated only with the gymnosperms, possibly suggests the retention of certain primitive characteristics in the mopane tree. Moreover, the insignificant flowers of the mopane tree point towards wind as being the chief vector of pollen, wing being the agent by which pollen of gymnosperms is mostly dispersed. Although the above two factors implicate the mopane tree as possibly being a more primitive member of the Anthophyta, this is questionable.

A compound leaf organisation implies an advanced evolutionary condition, the leaves of the mopane tree being alternate and compound (Coates-Palgrave 1988). Interestingly enough, between the two large leaflets the vestigial remains of a third leaflet can be seen. It is hypothesized that this third leaflet is indicative of the remains of what was once a compound leaf organisation paralleling the arrangement resplendent in some of the mimosoid legumes eg. the genera *Acacia* and *Albizia*, where leaflets are organised into pairs of pinnae along a common rachis. The reasons behind this reduction in the number of leaflets are far from clear, however, this condition may result from herbivore utilization. The leaflets of the mopane tree due to their large size and absence of protective structure such as prickles and spines, are easily obtained by herbivores. The present study and brief notes in reports have indicated the value of the mopane tree for the maintenance of mammalian herbivore body condition during stressful environmental conditions. Thus the dependence of mammals on this tree has become apparent, and it is believed that natural processes have accommodated this through the leaves being highly accessible, the resilience of the tree to heavy utilization and the apparency within mopane stands. Thus this tree species though possessing what appear to be primitive conditions, may well be a subtle blended of characteristics resplendent in both gymnosperms and angiosperms, the blend being such that the ecological relationships between this tree species and its herbivores reveal the very intricate workings of nature.

ACADEMIC IMPLICATIONS

Architecture and life form both contribute to the physiognomy (outer appearance) of vegetation, and each vegetation type has its own physiognomy. A vegetation type that extends over a large region is called a formation. In the southern African subregion, savannas would be regarded as being a formation, and within them exist associations. The mopane veld, a vegetation type often characterising extensive areas of semi-arid savannas, would thus be regarded as an association. An association has the following attributes: i) it has a relatively fixed floristic composition, ii) it exhibits a relatively uniform physiognomy and iii) it occurs in or as a relatively consistent type of habitat.

The International Biological Programme (IBP) was created in 1960 due to the novel research promoted by alliances. Although the IBP ended in 1974, the publications resulting from the programme continued to appear until the 1990's. The IBP emphasized the **biome** - the sum of plant and animal communities coexisting in the same region. This perspective stimulated research on the role of plants in energy transfer, ecosystem stability and evolutionary ecology. It has often been said that one of the most exciting aspects of evolutionary ecology to receive attention is the nature of plant herbivore relationships. Although hard data on co-evolved intricacies are being generated slowly, a vast body of speculative theory is growing fast. It is believed that the present study highlighting the intricate relationships between herbivores, both mammalian and insect, and the mopane tree will add to this data base and generate new ideas as far as large-mammal management policies are concerned.

Competition results from organisms utilizing the same resource, and from this, overlapping niches stem. In the light of the present study having discovered the immense number of associations between *Colophospermum mopane* and insects, the idea that elephant damage may be very important in alleviating interspecific competition between insects may not be absurd. Coexistence demands that species must evolve ecological differences, but the pressure on such evolution would be reduced in the face of continual niche creation and maintenance by an outside agent, in this case elephants.

Herbivory is usually thought of as a negative interaction on the part of plants, a one-way flow of benefits to the consumers. This now appears to be questionable. Dyer & Bokhari (1976) found that grasshoppers feeding on blue grama grass stimulated new shoot growth beyond that of mechanical clipping. Results from the present study elicited a rapid regrowth of mopane leaves following mammalian browsing, and continual utilization results in the browse quality being improved. Thus future research should take cognisance of the fact that mammals may be able to regulate the environment around their requirements, and should this be conclusively proved in other vegetation types, the management policies of today may prove to be incorrect or inadequate. This study on the mopane tree may have far reaching implications, especially when one considers that most of southern Africa's elephant populations are now confined to areas where the mopane tree is often the dominant woody species (N. Owen-Smith *pers. comm.*)[1], and thus of vital importance in the conservation strategy for this megaherbivore.

As guardians of nature, we the scientists whose task it is to determine the dynamics of an ecosystem through hands-on management practices should never err in our quest for new discoveries and the revamping of our often preconceived ideas, as our imperfection as guardians is often unwillingly resplendent in the very chaos we all too often create.

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MANAGEMENT

IMPLICATIONS

MANAGEMENT IMPLICATIONS

Managers and the management committee of the NTGR have never implemented culling, largely due to their being opposed to it, and because the animals within the NTGR belong to the people of Botswana and not to the landowners. Consequently they have been described as having taken no action, in essence being criticized by Walker *et al.* (1987) due to their inability to act. This study's results implicate elephants and other large herbivores as being vitally important in the ecology of the NTGR, and supports Dublin *et al.* (1990) who states that elephants alone should not be blamed solely for woodland damage.

Culling 25% of an elephant population has very little effect upon the trend of tree numbers, and only when 75% of the population is removed, will an increase in the tree population result (Barnes 1983b). The issue is as Walker *et al.* (1987) aptly state "are reductions in animal numbers essential in order to avoid progressive deterioration in habitat condition, or are the episodes of apparent overgrazing or over-browsing an intrinsic and readily reversible feature of vegetation-large herbivore interactions?" Culling is advocated largely because there is very little literature available which provides concrete evidence that herbivorous mammals actively manage the resources which they utilize (Gordon & Lindsay 1990). Darling (1960) considers the elephant's function in an ecosystem to be one of path-making, tree-felling, pan making and seed dispersal, and that the influence of elephants is profound in keeping the browse in such a condition so that other animals can use it. Though very basic, these ideas, especially the maintenance of browse, have substance, the present study confirming the maintenance hypothesis. The results obtained and the conclusions derived imply a condition in the NTGR which is representative of the alternative hypothesis proposed by Caughley (1976). This hypothesis states "the relationship between elephants and plant systems can be viewed as a stable limit cycle in which elephants increase while thinning the vegetation and then decline until reaching a low density which allows the resurgence of the vegetation".

Elephants have been regarded as having a negative long-term effect on plant communities, their activities resulting in disturbance, and the loss of biological diversity. The present study was conducted when the density of elephants in the NTGR was 0,63 animals/km^2, a density regarded as exceeding the carrying capacity.

These megaherbivores, largely assisted by eland, are responsible for the areas of extensive mopane hedges within the NTGR. These hedges, previously regarded with some trepidation as possible indicators of already impending ecological disorder, are very important. Being constantly browsed results in their having a resilience far exceeding that of less-browsed mopane trees, this being evident in their flushing far earlier, and independently of rain. Furthermore, they are also capable of seed production and so the large mammal impact is not as severe as might have been surmised. Moreover, the nutritional quality of the young leaves on the heavily browsed trees' leaves is very high, and the continual browsing also forces these trees to continually put out new leaflets so maintaining this food source. In the event of debarking occurring, the mopane tree immediately responds and new bark is soon generated under the resinous coating covering the damaged area, this process being termed a wound regeneration response.

Elephant damage on trees serves as sites for insect colonization, and of extreme importance is the utilization of elephant-damaged areas on a mopane tree's trunk by mopane bees, these hymenopterans probably serving as a rather important vector of pollen of this tree species.

The absence of caterpillars of the mopane moth from the NTGR is not a cause for grave concern, especially as it appears that mopane trees are central to the ecology of the NTGR, and mass defoliation by these caterpillars during an outbreak would remove this much needed food resource for mammals.

In the light of findings from the present study and the unveiling of many of the intricate workings of this tree species, especially the mammal-insect relationships, the impact elephants are having, must be regarded as positive. Thus, the culling of elephants in the NTGR, an area whose major vegetation component are *Colophospermum mopane* trees, cannot at present be advocated. Should elephant numbers continue to increase to the point where conservators within the area become concerned that possible irreparable veld damage is imminent, the capture and sale of elephants to other conservation areas is advocated. This policy allows for the stocking of areas lacking elephants, generates income for the NTGR and with the present ban on ivory, prevents the now senseless practice of culling a highly marketable commodity in Africa. However, it would be most interesting to allow the system to continue as at present so that the relationships between elephants and vegetation, and the population dynamics of the two, may be monitored in an attempt to discern whether or not elephants are the destructive agents they are proposed to be, or whether they are responsible for processes which we do not yet understand nor have discovered.

Finally, it is my belief that because the NTGR has hardly been tampered with by managers, and the area left much to its own ecological path, the discoveries in the present study were possible. I applaud the land-owners of the NTGR for not having meddled with the system, and hope that this ecological contribution to the NTGR will provide landowners and visitors alike with the key by which they too may discover the ecology surrounding mopane trees of the NTGR.

SUMMARY

OPSOMMING

SUMMARY

Relationships between herbivores and *Colophospermum mopane* of the Northern Tuli Game Reserve, Botswana were investigated.

- As a form of browse the mopane has been grossly underrated in the past, this study revealing young leaves especially, to be of a high nutritional value. These young leaves serve as an emergency food supply for mammalian herbivores in the NTGR, highlighting the importance of this tree species for game over periods of severe food shortage prior to spring rains.

- Gas chromatography was used to investigate the volatile compounds of both young and mature green mopane leaves, in an attempt to correlate known feeding with the volatile chemistry of the two phenophases. Young leaves, far more palatable than the mature leaves, had a greater variety of compounds identified which are known to assist rumen microbial fermentation processes. It is hypothesized tentatively, that an ungulate may well perceive the quality of a phenophase of a browse type, merely by the volatile spectrum it experiences when sniffing the food item.

- Mopane hedges, extensive areas encountered within the NTGR, often regarded as being indicative of ecological disorder, are, quite on the contrary, of extreme ecological importance. Branch browsing by elephants and eland, induce trees to come into leaf up to one month before their less-damaged riverine counterparts. These young leaves are

highly palatable, this condition resulting from the heavy browsing pressure the hedges are exposed to. This resource is available to all herbivores, the hedged form concentrating browse at an accessible level.

- A seasonal investigation into the removal of stem bark by elephants, found no bark to be removed from any of the large trees marked for the purpose of this study. This total absence of debarking for the period of the study is probably due to the drought which forced most of the elephants out of the mopane dominated areas, their concentrating on the Shashe and Limpopo riverine fringes where resources were more plentiful. In an experiment simulating elephant debarking, it was found that the tolerance of the mopane tree to debarking is immense, this tree species being capable of seed production with up to 95% of its stem bark removed.

- Epizoochory as the mode of dispersal of diaspores of *Colophospermum mopane* is conclusively disproved. Water and wind, the former especially, are agents of dispersal.

- Goats are highly selective for food types that have both a low fibre and condensed tannin content. Senescing leaves, the phenophase the goats mostly selected for, had both the lowest fibre and condensed tannin contents. Goats seem able to differentiate between forage qualities as far as the above two parameters are concerned. Green mopane pods have a very definite turpentine smell as well as numerous resinous compounds, factors which may be responsible for the very low acceptance of this food item. It is hypothesized that mopane is the woody tree species responsible for the maintenance of the impala population of the NTGR during stressful periods, especially drought. This is largely assisted by senescing leaf material which serves an additional valuable resource for these ungulates to exploit.

- The damage elephants inflict on mopane trees is proven to be of extreme importance. Due to their destructive feeding habits, especially branch breaking, these megaherbivores often expose the dead heartwood of the tree. Termites bore into the heartwood of the tree, the eventual effect being a hollow stem, a condition well documented for the mopane in most botanical literature. This hollowness is of extreme importance in that it houses the nest of mopane bees, *Trigona* spp., this insect proving to be a pollen vector of the mopane. Mopane bees are only ever encountered in areas of elephant damage. Plant apparency occurs within stands of mopane within the NTGR, some trees actively encouraging herbivory, while others actively deter it. *Messinea conica*, a soft-scale, is present on the terminal portions of the branches of some trees. Due to its exuding honeydew, this scale is attended by ants of the genus, *Crematogaster*, and an effective anti-herbivory mechanism results. *Arytaina mopane*, a psyllid, utilizes leaves of those mopane trees lacking ants and scale insects. The larvae of this insect develop on the leaves of the mopane, the larvae secreting a sugar-rich lerp around themselves which increases the palatability of the leaf.

- Caterpillars of the mopane moth *Imbrasia belina* have been locally extinct from within the NTGR's borders since 1969. The reasons are hypothesized as the preponderance of ants (predation) on the trees within the NTGR, edaphic factors and possibly browse quality differences between mopane stands inside and outside the NTGR.

OPSOMMING

Die verwantskap tussen plant vretende diere en *Colophospermum mopane* van Noord Tuli Natuurreservaat in Botswana is ondersoek.

- As 'n vorm van takvoer was die mopanie in die verlede geheel en al onderskat. Met hierdie ondersoek is bepaal dat veral jong blare hoë voedingswaarde bevat. Die jong blare voorsien aan die voedsel behoefte van blaar vretende soogdiere in die natuurreservaat wat die belangrikheid van die mopanie boom beklemtoon wanneer voedsel, voor die reëns in die lente, skaars is.

- Met die ondersoek is gebruik gemaak van gas chromatografie en daar is bepaal dat jong blare meer smaaklike vlugbare stowwe bevat en dus bewys dat hoefdiere voorkeur aan hierdie tipe blare gee.

- Daar is groot gebiede mopanie lanings in die reservaat wat as ekologiese wanorde beskou word, terwyl die teendeel bewys is - dat dit van die uiterste belang is. Hierdie lanings, veroorsaak deur die weiding van olifante en elande, bot tot 'n maand vroeër as die minder beskadigde mopanie langs die rivieroewers. Die nuwe blare is smaaklik en hierdie bron van voedsel, tot beskikking van alle blaar vretende soogdiere op 'n bekombare hoogte, word dus intensief bewei.

- 'n Seisoenale studie om die ontbassing van bome deur olifante te bepaal, het gevind dat geen bas van die bome wat vir die doel gemerk is verwyder is nie. Dit mag te wyte

wees aan die droogte wat veroorsaak het dat die olifante uit die mopane veld na die Limpopo en Shashe rivieroewers beweeg het waar voedsel meer volop is. In 'n eksperiment wat ontbassing simuleer is gevind dat 'n mopane boom, na 95% van die bas verwyder is, nog steeds saad produseer.

- Daar is onweerlegbaar bewys dat die verspreiding van saad deur water en wind veroorsaak word en nie, soos algemeen aanvaar, deur aan die hoewe van diere te kleef nie.

- Bokke verkies voedsel bronne met 'n laë vesel en tannine inhoud. Droog wordende mopanie blare, die voedsel bron wat bokke die meeste geniet, het reeds hierdie twee eienskappe. Groen mopanie peule het 'n sterk terpentyn reuk en 'n gomagtige samestelling wat veroorsaak dat dit nie so geredelik gevreet word nie. Dit word aanvaar dat mopanie bome die rooibokke in die Reservaat onderhou wanneer daar min voedsel beskikbaar is, veral die droogwordende blare, wat as 'n belangrike voedsel bron dien.

- Olifante breek die mopanie en ontbloot die kernhout van die stam. Hierdie beskadiging van die boom is baie belangrik as die verwantskappe tussen die mopanie boom en ander herbivore behou wil word. Termiete betrek die beskadigde stam, wat hulle uithol deur die kernhout as voedsel te gebruik. Later dien hierdie holtes as nesplek vir die mopanie by. Hierdie by is verantwoordelik vir die bestuiwing van die mopanie en hulle neste word gewoonlik in gebiede, waar olifante die bome beskadig het, gevind. Diere vreet geredelik die bome wat die insek *Arytaina mopane* bevat, weens die suikerinhoud van die lerp wat die insek om hoom afskei, terwyl bome wat die insek *Messinea conica* bevat nie deur diere gevreet word nie. *Messinea conica* gee heiningdou af en as gevolg van die soetigheid word miere van die genus *Crematogaster* aangelok. Hierdie miere, wat gewoonlik aan die punte van die takkies gevind word, verhoed dat weiding plaasvind deurdat die monddele van die hoefdiere byt. Dus moedig sommige mopanie bome weiding aan terwyl ander dit, weens die teenwoordigheid van miere, afweer.

- Ruspes van die mopanie mot *Imbrasia belina* het sedert 1969 van die reservaat verdwyn waarskynlik as gevolg van die groter teenwoordigheid van die miere binne die reservaat as buite die reservaat, asook edafiese faktore. Die vermoede bestaan dat die mopanie buite die reservaat meer smaaklik as binne die reservaat is.

AREAS IDENTIFIED FOR POSSIBLE FUTURE RESEARCH.

1: Cane & Jonsson (1982) used a field device to document the volatile compounds *Collates* bees used as mate attractants and defensive secretions. The digging odours of *Collates canicularius* all contained linalool in the volatile fraction. Linalool also predominated in the materials collected from females of this bee species that were actively guarding the nest entrance. This volatile compound was found to be of mandibular gland origin. With linalool having been identified as a volatile component of the leaves of *Colophospermum mopane*, it would be very interesting to see whether or not linalool is present in the chemical signals given off by mopane bees (*Trigona* spp.).

2: Alpha copaene has been documented as being an attractant for the male Mediterranean fruit fly or Medfly (Teranishi *et al.* 1986; Fritz *et al.* 1988). The larvae of the psyllid *Arytaina mopane* (Psyllidae; Homoptera) develop on the leaves of *C. mopane*. Both the young and mature green leaves have substantial peaks for alpha copaene relative to the major peak (caryophyllene). Studies conducted on whether or not the psyllid responds to alpha copaene may prove to be important in the development of an understanding of the utilization of mopane leaves by this psyllid, whose overall role in nature is commonly regarded as one of increasing leaf palatability.

3: It is necessary that elephant-damage be carefully studied in other veld types to ascertain whether tree-damage supports insect communities in veld types other than mopane veld. This study questions the management policies employed for elephants over the last three decades or so, elephant culling very possibly having served as a curtain behind which conservationists could hide financial gain in the name of good management.

4: The ecology of mopane hedges within the NTGR needs further attention, especially as the removal of branches by eland. It is necessary to identify what dietary requirement(s) causes the eland to actually seek out the bark of mopane branches as this would aid to our understanding of the hedged effect of the mopane of the NTGR.

5: Chromatographic analysis performed on the volatile components of the leaves of the mopane show many monoterpene compounds to be present. Thus one can surmise that this is the case in any plant part associated with the mopane trees. Limonene was identified in the leaf volatile component and may well explain why boring beetles do not attack exposed areas of sapwood on a mopane tree's trunk. Limonene has been shown to be toxic and inhibitory to boring beetles (Smith 1965,1966), insects preferring trees which contain low concentrations of this toxin (Sturgeon 1979). Obviously this hypothesis is based on the assumption that the inhibitor limonene, a component of the tree's volatile spectrum, is also present in the woody parts. A major volatile component of the mopane leaf is alpha pinene. Beta pinene has also been identified, but at much lower concentrations. These two compounds are both constituents of pine oil, "pine oil" being a very loose term for a complex mixture of oleoresins and terpene hydrocarbons (Nijhölt 1980; Richmond 1985). The effect of alpha and beta pinene together with that of limonene may further enhance the inhibitory effect. Chromatographic analysis of the volatile components of the sapwood of *C. mopane*, and then comparing the results with the volatile component profiles of woody tree species which do experience boring by beetles, may well answer the question of why the mopane tree experiences no boring, more succinctly.

REFERENCES

REFERENCES

Acocks, J.P.H. 1975. Veld types of South Africa, 2nd Ed. *Mem. Bot. Surv. S. Afr.* No. 40. 1 - 128.

Aide, T.M. 1988. Phenological escape from herbivores in a tropical understorey community. *Nature* 336: 574 - 575.

Aide, T.M. 1991. Synchronous leaf production and herbivory in juveniles of *Gustavia superba*. *Oecologia* 88: 511 - 514.

Alcock, J. 1984. *Animal Behaviour: An Evolutionary Approach.* Sinauer Associates, Sunderland.

Anderson, G.D. & Walker, B.H. 1974. Vegetation composition and elephant damage in the Sengwa Wildlife Research Area, Rhodesia. *J. S. Afr. Wildl. Mgmt. Ass.* 4: 1 - 14.

Argall, J.F. & Stewart, K.A. 1984. Effects of decapitation and benzyladenine on growth and yield of cowpea (*Vigna unguiculata* L., Walp.). *Ann. Bot.* 54: 439 - 444.

Arnold, G.W. & Hill, J.L. 1975. Chemical factors affecting selection of food plants by ruminants. In: *Phytochemical Ecology*. J.B. Harbourne (Ed.). Academic Press, New York.

Astle, W.D. 1971. Management in the Luangwa valley. *Oryx* 11: 135 - 139.

Astrom, M., Lundberg, P. & Dannell, K. 1990. Partial prey consumption by browsers: trees as patches. *J. Anim. Ecol.* 59: 287 - 300.

Auclair, J.L. 1963. Aphid feeding and nutrition. *Ann. Rev. Ent.* 8: 439 - 490.

Auld, T.D. 1986. Population dynamics of the shrub *Acacia suaveolensis* (Sm.) Willd. : Fire and the transition to seedlings. *Aust. J. Ecol.* 11: 373 - 385.

Baker, H.G. 1974. The evolution of weeds. *Ann. Rev. Ecol. Syst.* 5: 1- 24.

Baldwin, I.T. & Schultz, J.C. 1983. Rapid changes in tree leaf chemistry induced by damage: Evidence for communication in plants. *Science* 221: 277 - 279.

Barbour, M.G., Burk, J.H. and Pitts, W.D. 1987. *Terrestrial Plant Ecology* (2nd. Edn.). The Benjamin/Cummings Publishing Company, Inc., California.

Barnes, D.L. 1976. A review of plant-based methods of estimating food consumption, percentage utilization, species preferences and feeding patterns of grazing and browsing animals. *Proc. Grassl. Soc. S. Afr.* 11: 65 - 71.

Barnes, D.L. 1982. Management strategies for the utilization of southern African savanna. In: *Ecology of tropical savannas.* B.J. Huntley and B.H. Walker (Eds.). Springer-Verlag, Berlin.

Barnes, R.F.W. 1982a. Elephant feeding behaviour in Ruaha National Park, Tanzania. *Afr. J. Ecol.* 20: 123 - 136.

Barnes, R.F.W. 1983a. The elephant problem in Ruaha National Park, Tanzania. *Biol. Cons.* 26: 127 - 148.

Barnes, R.F.W. 1983b. Effects of elephant browsing on woodlands in a Tanzanian National Park: Measurements, models and management. *J. Appl. Ecol.* 20: 521 - 540.

Baskin, J.M. & Baskin, C.C. 1984. Environmental conditions required for germination of prickly sida (*Sida spinosa*). *Weed Sci.* 32: 786 - 791.

Baskin, J.M. & Baskin, C.C. 1989. Physiology of dormancy and germination in relation to seed bank ecology. In: *Ecology of Soil Seed Banks.* M.A. Leck, V.T. Parker and R.L. Simpson (Eds.). Academic Press, New York.

Bate-Smith, E.C. 1971. Attractants and repellents in higher plants. In: *Phytochemical Ecology*. J.B. Harbourne (Ed.). Academic Press, New York.

Bate-Smith, E.C. & Metcalf, C.R. 1957. Leucoanthocyanins. III. The nature and systematic distribution of tannins in dicotyledonous plants. *J. Linn. Soc. Lond. Bot.* 55: 669 - 705.

Bax, N.P. & Sheldrick, D.L.W. 1963. Some preliminary observations on the food of elephants in the Tsavo Royal National Park (East) of Kenya. *E. Afr. Wildl. J.* 1: 35 - 40.

Becerra, J.X. 1989. Extrafloral nectaries: a defense against ant-homopteran mutualisms? *Oikos* 55: 276 - 280.

Becerra, J.X. & Venable, D.A. 1989. The role of ant-homopteran mutualisms in the evolution of extrafloral nectaries. *Oikos* 60: 105 - 106.

Benner, B.J. 1988. Effects of apex removal and nutrient supplementation on branching and seed production in *Thlaspi arvense* (Brassicaceae). *Am. J. Bot.* 75: 645 - 651.

Berenbaum, M.R. 1983. Effects of tannins on growth and digestion in two species of papilionoids. *Ent. Exp. Appl.* 34: 245 - 250.

Bernays, E.A. & Janzen, D.H. 1988. Saturniid and sphingid caterpillars : two ways to eat leaves. *Ecology* 69: 1153 - 1160.

Bernays, E.A., Cooper Driver, G. & Bilgener, M. 1989. Herbivores and plant tannins. *Adv. Ecol. Res.* 19: 263 - 302.

Black, J.N. 1956. The influence of seed size and depth of sowing on pre-emergence and early vegetative growth of subterranean clover (*Trifolium subterraneum* L.). *Aus. J. Agr. Res.* 7: 98 - 109.

Black, J.N. 1957. Seed size as a factor in the growth of subterranean clover (*Trifolium subterraneum* L.) under space and sward conditions. *Aust. J. Agr. Res.* 8: 335 - 351.

Black, J.N. 1959. Seed size in herbage legumes. *Herbage Abstr.* 29: 235 - 241.

Blair, R.M. 1971. Forage production after hardwood control in a southern pine-hardwood stand. *Forest Sci.* 17: 279 - 284.

Bobeck, B. & Dzieciolowski, R. 1972. Method of browse estimation in different types of forests. *Acta Theriol.* 17: 171 - 186.

Bonsma, J.C. 1942. Useful bushes and shrubs. *Fmg S. Afr.* 17: 251 - 262.

Bonsma, J.C. 1976. *Bosveldbome en weistreke.* J.L. Van Schaik Bpk. Pretoria.

Bryant, J.P., Chapin, F.S.,III. & Klein, D.R. 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos* 40: 357 - 368.

Buchsbaum, R., Valiela, I. & Swain, T. 1984. The role of phenolic-compounds and other plant constituents in feeding by Canada geese in a coastal marsh. *Oecologia* 63: 343 - 349.

Buckley, R. 1987. Interactions involving plants, homoptera and ants. *Ann. Rev. Ecol. Syst.* 18: 111 - 135.

Buechner, H.K. & Dawkins, H.C. 1961. Vegetation change induced by elephants and fire in Murchison Falls National Park, Uganda. *Ecology* 42: 752 - 766.

Bullock, S.H. 1976. Comparison of the distribution of seed and parent-plant populations. *Southwest Nat.* 21: 383 - 389.

Burger, B.V., le Roux, M. & Burger, W.J.G. 1990. *Headspace analysis: A novel method for the production of capillary traps with ultra-thick stationary phase layers.* HRC, Vol 13: 777 - 779.

Burnett, W.C.,Jr., Jones, S.B.,Jr. & Mabry, T.J. 1977. Evolutionary implications of herbivory on *Vernonia* (Compositae). *Plant Syst. Evol.* 128: 277 - 286.

Buss, I.O. 1961. Some observations on food habits and behaviour of the African elephant. *J. Wildl. Mgmt.* 25: 131 - 148.

Caldwell, M.M., Richards, J.H., Johnson, D.A., Nowack, R.S. & Dzurec, R.S. 1981. Coping with herbivory: photosynthetic capacity and resource allocation in two semi-arid *Agropyron* bunchgrasses. *Oecologia* 50: 14 - 24.

Calvert, J.J. 1985. Food selection by western gorillas in relation to food chemistry. *Oecologia* 65: 236 - 246.

Cameron, Q.N. & Lapoint, T.W. 1977. Effects of tannins on the decomposition of Chinese tallow leaves by terrestrial and aquatic invertebrates. *Oecologia* 32: 349 - 366.

Cane, J.H. & Jonsson, T. 1982. Field methods for sampling chemicals released by active insects. *J. Chem. Ecol.* 8: 15 - 21.

Cates, R.G. & Rhoades, D.F. 1977. Plant tannins - their role in forage quality. *Nutr. Abstr. Rev.* 44: 803 - 815.

Caughley, G. 1976. The elephant problem - An alternative hypothesis. *E. Afr. Wildl. J.* 14: 265 - 283.

Caughley, G. 1983. Dynamics of large mammals and their relevance to culling. In: *Management of large mammals in African conservation areas.* R.N. Owen-Smith (Ed.). Haum Publishers, Pretoria.

Chapin, F.S. 1980. The mineral nutrition of wild plants. *Ann. Rev. Ecol. Syst.* 11: 233 - 260.

Chenier, J.V.R. & Philogene, B.J.R. 1989. Field responses of certain forest Coleoptera to conifer monoterpenes and ethanol. *J. Chem. Ecol.* 15: 1729 - 1745.

Chew, F.S. & Courtney, S.P. 1991. Plant apparency and evolutionary escape from insect herbivory. *Am. Nat.* 138: 729 - 750.

Clausen, T.P., Provenza, F.D., Burritt, E.A., Bryant, J.P. & Reichardt, P.B. 1990. Ecological implications of condensed tannin structure: a case study. *J. Chem. Ecol.* 16: 2381 - 2392.

Clifford, P.E. 1979. Source limitation of sink yield in mung beans. *Ann. Bot.* 54: 811 - 813.

Coates-Palgrave, K. 1977. *Trees of southern Africa.* Struik Publishers, Cape Town.

Coates-Palgrave, K. 1988. *Trees of southern Africa* (Revised 2nd. Edn.). Struik Publishers, Cape Town.

Cody, M.L. 1991. Niche theory and plant growth form. *Vegetatio* 97: 39 - 55.

Coe, M.J., Cumming, D.H.M. & Phillipson, J. 1976. Biomass and production of large African herbivores in relation to rainfall and primary production. *Oecologia* 22: 341 - 354.

Cole, M.M. 1963. Vegetation and geomorphology in Northern Rhodesia: An Aspect of the distribution of the savanna of Central Africa. *The Geogr. J.* 129: 290 - 310.

Cole, M.M. 1967. Biogeography in an African setting. *S. Afr. Geogr. J. Jubilee Conf. Proc.* Durban. 369 - 393.

Coley, P.D. 1983. Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecol. Monogr.* 53: 209 - 233.

Coley, P.D. 1986. Costs and benefits of defense by tannins in a neotropical tree. *Oecologia* 70: 238 - 241.

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.

Coley, P.D. & Aide, T.M. 1991. A comparison of herbivory and plant defenses in temperate and tropical broad-leaved forests. In: *Plant-animal interactions: evolutionary ecology in tropical and temperate regions*. P.W. Price, T.M. Lewinsohn, G.W. Fernandes and W.W. Benson (Eds.). John Wiley & Sons, New York.

Coley, P.D., Bryant, J.P. & Chapin, F.S.,III. 1985. Resource availability and plant anti-herbivore defense. *Science* 230: 895 - 899.

Cooper, S.M. & 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. & 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.

Crawley, M.J. 1983. *Herbivory*. Univ. of California Press, California.

Croze, H. 1974a. The Seronera bull problem. *E. Afr. Wildl. J.* 12: 1 - 27.

Croze, H. 1974b. The Seronera bull problem II. The Trees. *E. Afr. Wildl. J.* 12: 29 - 47.

Cumming, D.H.M 1983. The decision-making framework with regard to the culling of large mammals in Zimbabwe. In: *Management of large mammals in African conservation areas*. N. Owen-Smith (Ed.). Haum Publishers, Pretoria.

Cushman, J.H. 1991. Host plant mediation of insect mutualisms: variable outcomes in herbivore ant interactions. *Oikos* 61: 138 - 144.

Dannell, K. & Huss-Dannell, K. 1985. Feeding by insects and hares on birches earlier affected by moose browsing. *Oikos* 44: 75 - 81.

Darling, F.F. 1960. *Wildlife in an African territory*. Oxford University Press, London.

de la Hunt, T.E. 1954. The value of browse shrubs and bushes in the Gwanda area, S. Rhodesia. *Rhod. Agr. J.* 51: 251 - 262.

de Villiers, P.A. & Kok, O.B. 1988. Eto-ekologiese aspekte van olifante in die Nasionale Etoshawildtuin. *Madoqua* 15: 319 - 338.

Demment, M.W. & Van Soest, P.J. 1985. A nutritional explanation for body size patterns of ruminants and non-ruminant herbivores. *Am. Nat.* 125: 641 - 672.

de Winter, B., de Winter, M. & Killick, D.J.B. 1966. *Sixty-six Transvaal Trees.* Voortrekkerpers Ltd.

Dietz, D.R. 1965. Deer nutrition research in range management. *Trans. N. Am. Wildl. Conf.* 30: 274 - 285.

Dixon, A.F.G. 1971a. The role of aphids in wood formation. I. The effect of the sycamore aphid, *Drepanosiphum platanoides* (Schr.)(Aphididae) on the growth of the sycamore, *Acer pseudoplatanus* (L.). *J. Appl. Ecol.* 8: 165 - 179.

Dixon, A.F.G. 1971b. The role of aphids in wood formation. II. The effect of the lime aphid, *Eucallipterus tiliae* L. (Aphididae) on the growth of lime, *Tilia vulgaris* Hayne. *J. Appl. Ecol.* 8: 393 - 399.

Dixon, A.F.G., 1985. *Aphid ecology.* Blackie, London.

Dougall, H.W. & Sheldrick, D.L.W. 1964. The chemical composition of a day's diet of an elephant. *E. Afr. Wildl. J.* 2: 51 - 59.

Dreyer, J.J. & Wehmeyer, A.S. 1982. On the nutritive value of mopane worms. *S. Afr. J. Sci.* 78: 33 - 35.

Dublin, H.T., Sinclair, A.R.E. & McGlade, J. 1990. Elephant and fire as causes of multiple stable states in the Serengeti-Mara woodlands. *J. Anim. Ecol.* 59: 1147 - 1164.

Dunham, K.M. 1980. The feeding behaviour of a tame impala *Aepyceros melampus*. *Afr. J. Ecol.* 18: 253 - 257.

du Toit, E.W., Wolfson, M.M. & Ellis, R.P. 1991. The presence of condensed tannins in the leaves of *Eulalia villosa*. *J. Grassl. Soc. S. Afr.* 8: 74 - 76.

du Toit, J.T. 1988. *Patterns of resource use within the browsing ruminant guild in the central Kruger National Park.* Ph.D. thesis. University of the Witwatersrand, Johannesburg.

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

du Toit, J.T., Provenza, F.D. & Nastis, A. 1991. Conditioned taste aversion: how sick must a ruminant get before it learns about toxicity in foods? *Appl. Anim. Behav. Sci.* 30: 35 - 46.

Dyer, M.I. & Bokhari, U.G. 1976. Plant animal interactions: studies on the effects of grasshopper grazing on blue grama grass. Ecology 57: 762 - 772.

Echeverri, F., Cardona, G., Torres, F., Pelaez, C., Quinones, W. & Renteria, E. 1991. Ermanin: An insect deterrent flavonoid from *Passiflora foetida* resin. *Phytochem.* 30: 153 - 155.

Edelstein-Keshet, L. & Rausher, M.D. 1989. The effects of inducible plant defenses on herbivore populations. I. Mobile herbivores in continuous time. *Am. Nat.* 133: 787 - 810.

Ellis, B.S. 1950. A guide to some Rhodesian soils. A note on mopane soils. *Rhod. Agr. J.* 47: 49 - 62.

Ernst, W.H.O., Kuiters, A.T., Nelissen, H.J.M. & Tolsma, D.J. 1991. Seasonal variation in phenolics in several savanna tree species in Botswana. *Acta Bot. Neerl.* 40: 63 - 74.

Ernst, W.H.O. & Sekhwela, M.B.M. 1987. The chemical composition of lerps from the mopane psyllid *Arytaina mopane* (Homoptera, Psyllidae). *Insect Biochem.* 17: 905 - 909.

Farentinos, R.C., Capretta, P.J. & Kepner, R.E. 1981. Selective herbivory in tassel-eared squirrels: role of monoterpenes in ponderosa pines chosen as feeding trees. *Science* 213: 1273 - 1275.

Feeny, P. 1968. Effects of oak leaf tannins on the hydrolysis of proteins by trypsin. *Phytochem.* 8: 2119 - 2126.

Feeny, P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology* 51: 565 - 581.

Feeny, P. 1975. Biochemical coevolution between plants and their insect herbivores. In: *Coevolution of animals and plants.* L.E. Gilbert & P.H. Raven (Eds.). University of Texas Press, Austin.

Feeny, P. 1976. Plant apparency and chemical defense. *Rec. Adv. Phytochem.* 10: 1 - 41.

Feeny, P. & Bostock, H. 1968. Seasonal changes in the tannin content of oak leaves. *Phytochem.* 7: 871 - 880.

Fiala, B., Maschewitz, U., Tho, Y.P. & Helbig, A.J. 1989. Studies of a south east Asian ant-plant association: protection of *Macaranga* trees by *Crematogaster borneensis. Oecologia* 79: 463 - 470.

Field, C.R. 1971. Elephant ecology in the Queen Elizabeth National Park, Uganda. *E. Afr. Wildl. J.* 9: 99 - 123.

Freeland, W.J. & Janzen, D.H. 1974. Strategies in herbivory by mammals: the role of plant secondary compounds. *Am. Nat.* 108: 269 - 289.

Fritz, G.L., Cunningham, R.T. & Warthen, J.D.Jr.. 1988. Structure-activity relationship of (+)- alpha-copaene analogs as male medfly attractants. *Abstr. Pap. Am. Chem. Soc.* 196(Sep): 73.

Frost, S.K. 1981. Food selection in young naive impala *Aepyceros melampus. S. Afr. J. Zool.* 16: 123 - 124.

Gertenbach, W.P.D. 1987. *n' Ekologiese studie van die suidelikste Mopanieveld in die Nasionale Krugerwildtuin.* Ph.D. thesis. University of Pretoria.

Gertenbach, W.P.D. & Potgieter, A.L.F. 1979. Velbrandnavorsing in die struikmopanieveld van die Nasionale Krugerwildtuin. *Koedoe* 22: 1 - 28.

Glover, P.E. & Sheldrick, D. 1964. An urgent research problem on the elephant and rhino populations of the Tsavo National Park in Kenya. *Bull. epizool. Dis. Afr.* 12: 33 - 38.

Goering, H.E. & van Soest, P.E. 1970. Forage fibre analysis. *U.S.D.A. Agr. Handbook No.* 379.

Goldstein, W.S. & Spencer, K.C. 1985. Inhibition of cyanogenesis by tannins. *J. Chem. Ecol.* 11: 847 - 858.

Goldstein, J.L. & Swain, T. 1965. The inhibition of enzymes by tannins. *Phytochem.* 4: 185 - 192.

Gordon, I.J. & Lindsay, W.K. 1990. Could mammalian herbivores "manage" their resources? *Oikos* 59: 270 - 280.

Grime, J.P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Nat.* 111: 1169 - 1194.

Guitian, J. & Sanchez, J.M. 1992. Seed dispersal spectra of plant communities in the Iberian Peninsula. *Vegetatio* 98: 157 - 164.

Guy, P.R. 1976. The feeding behaviour of elephant in the Sengwa Area, Rhodesia. *S. Afr. J. Wildl. Res.* 6: 55 - 64.

Guy, P.R. 1981. Changes in the biomass and productivity of woodlands in the Sengwa Wildlife Research Area, Zimbabwe. *J. Appl. Ecol.* 18: 507 - 519.

Guy, P.R., Mahlangu, Z. & Charidza, H. 1979. Phenology of some trees and shrubs in the Sengwa Wildlife Research Area, Zimbabwe - Rhodesia. *S. Afr. J. Wildl. Res.* 9: 47 - 54.

Hagerman, A.E. 1987. Radial diffusion, method for determining tannin in plant extracts. *J. Chem. Ecol.* 13: 437 - 449.

Hall, R., Klemme, D. & Nienhaus, J. 1985. *The H & R Book: Guide to Fragrance Ingredients.* Gloss Publishers, Berlin.

Hall-Martin, A.J. 1974a. Food selection by Transvaal Lowveld giraffe as determined by analysis of stomach contents. *J. S. Afr. Wildl. Mgmt. Ass.* 4: 191 - 202.

Hall-Martin, A.J. 1974b. A note on the seasonal utilization of different vegetation types by giraffe. *S. Afr. J. Sci.* 70: 122 - 123

Hall-Martin, A.J. 1984. Conservation and management of elephants in the Kruger National Park, South Africa. In: *The status and conservation of Africa's elephants and rhinos.* D.H. Cumming and P. Jackson (Eds.). IUCN.

Hall-Martin, A.J. 1992. Distribution and status of the African elephant *Loxodonta africana* in South Africa 1652-1992. *Koedoe* 35: 65 - 88.

Hall-Martin, A.J. & Basson, W.D. 1974. Seasonal chemical composition of the diet of the Transvaal Lowveld giraffe. *J. S. Afr. Wildl. Mgmt. Ass.* 4: 75 - 79.

Halls, L.K. & Harlow, R.F. 1971. Weight-length relations in flowering dogwood twigs. *J. Range Mgmt.* 23: 146 - 147.

Happe, P.J., Jenkins, K.J., Starkey, E.E. & Sharrow, S.H. 1990. Nutritional quality and tannin astringency of browse in clear-cuts and old-growth forests. *J. Wildl. Mgmt.* 54: 557 - 566.

Harper, J.L. 1989. The value of a leaf. *Oecologia* 80: 53 - 58.

Harrington, G.N. & Ross, I.C. 1974. The savanna ecology of Kidepo Valley National Park. I. The effects of burning and browsing on vegetation. *E. Afr. Wildl. J.* 12: 93 - 105.

Harrison, M.S.J. 1984. Notes on the origins of the dry zone of the Limpopo valley. *S. Afr. J. Sci.* 80: 333 - 334.

Haslam, E. 1979. Vegetable tannins. *Rec. Adv. Phytochem.* 12: 475 - 523.

Haukioja, E. & Niemela, P. 1978. Birch leaves as a resource for herbivores: seasonal occurrence of increased resistance in foliage after mechanical damage of adjacent leaves. *Oecologia* 39: 151 - 159.

Hawthorn, W.R. & Hayne, P.D. 1978. Seed dispersal and seed predispersal predation in the biennial compositae species *Arctium minus* (Hill) Bernh. and *A. lappa* L. *Oecologia* 34: 283 - 295.

Henderson, C.B. 1990. The influence of seed apparency, nutrient control and chemical defenses in *Dipodomys ordii. Oecologia* 82: 333 - 341.

Hendrix, S.D. 1988. Herbivory and its impact on plant reproduction. In: *Plant reproductive ecology: patterns and strategies*. Doust, J.L. and Doust, L.L. (Eds.). Oxford University Press, New York.

Henning, A.C. & White, R.E. 1974. A study of the growth and distribution of the *Colophospermum mopane* (Kirk ex Benth) Kirk ex. J. Leon. : The interaction of nitrogen, phosphorus and soil moisture stress. *Proc. Grassl. Soc. S. Afr.* 9: 53 - 61.

Hill, C.J. & Pierce, N.E. 1989. The effect of adult diet on the biology of butterflies. I. The common imperial butterfly, *Jalmenus evagorus*. *Oecologia* 81: 249 - 257.

Hodkinson, I.D. 1974. The biology of the Psylloidea (Homoptera: a review). *Bull. Ent. Res.* 64: 325 - 329.

Hofmann, R.R. 1973. The ruminant stomach (stomach structure and feeding habits of East African game ruminants). Vol. 2. *East Afr. Monogr. Biol.*, E.A. Lit. Bureau, Nairobi, pp 1 - 364.

Hofmann, R.R. 1988. Morphophysiological evolutionary adaptations of the ruminant digestive system. In: A. Dobson (Ed.). *Comparative aspects of physiology of digestion in ruminants*. Cornell University Press, Ithaca.

Hofmann, R.R. 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. *Oecologia* 78: 443 - 457.

Hogberg, P. & Piearce, G.D. 1986. Mycorrhizas in Zambian trees in relation to host taxonomy, vegetation type and successional patterns. *J. Ecol.* 74: 775 - 785.

Holldobbler, B. & Wilson, E.O. 1990. *The ants*. Springer-Verlag, Berlin.

Holm, E. & de Villiers, W.M. 1983. *Ons eie insekte*. Tafelberg.

Howe, H.F. & Smallwood, J. 1982. Ecology of seed dispersal. *Ann. Rev. Ecol. Syst.* 13: 201 - 228.

Huntley, B.J. 1982. Southern African Savannahs. In: *Ecology of tropical savannahs*. B.J. Huntley and B.H. Walker (Eds.). Springer-Verlag, New York.

Illius, A.W. & Gordon, I.J. 1992. Modelling the nutritional ecology of ungulate herbivores: evolution of body size and competitive interactions. *Oecologia* 89: 428 - 434.

Ito, F. & Higashi, S. 1991. An indirect mutualism between oaks and wood ants via aphids. *J. Anim. Ecol.* 60: 463 - 470.

Jachmann, H. 1988. Food selection by elephants in the "miombo" biome, in relation to leaf chemistry. *Biochem. Syst. Ecol.* 85: 216 - 243.

Jachmann, H. 1992. Movements of elephants in and around the Nazinga Game Ranch, Burkina Faso. *J. Afr. Zool.* 106: 27 - 37.

Jachmann, H. & Bell, R.H.V. 1985. Utilization of elephants of the *Brachystegia* woodland of the Kasungu National Park, Malawi. *Afr. J. Ecol.* 23: 245 - 258.

Jachmann, H. & Croes, T. 1991. Effects of browsing by elephant on the *Combretum/Terminalia* woodland at the Nazinga Game Ranch, Burkina Faso, West Africa. *Biol. Cons.* 57: 13 - 24.

Janzen, D.H. 1970. Herbivores and the number of tree species in tropical forests. *Am. Nat.* 104: 501 - 528.

Janzen, D.H. 1974. Tropical black water rivers, animals, and mast fruiting by the Dipterocarpaceae. *Biotropica* 6: 69 - 103.

Janzen, D.H. 1981. The defenses of legumes against herbivores. In: *Advances in legume systematics* (Part 2). R.M. Polhill and P.H. Raven (Eds.). Royal Botanic Gardens, Kew.

Janzen, D.H. 1984. Two ways to be a tropical big moth. Santa Rosa saturniids and sphingids. *Oxford Surv. Evol. Biol.* 1: 85 - 140.

Janzen, D.H. & Waterman, P. 1984. A seasonal census of phenolics, fibre and alkaloids in foliage of forest trees in Costa Rica: some factors influencing their distribution and relation to host selection by Sphingidae and Saturniidae. *Biol. J. Linn. Soc.* 21: 439 - 454.

Jarman, P.J. 1971. Diets of large mammals in the woodlands around Lake Kariba, Rhodesia. *Oecologia* 8: 157 - 178.

Jing, S.W. & Coley, P.D. 1990. Dioecy and herbivory: the effect of growth rate on plant defense in Acer negundo. *Oikos* 58: 369 - 377.

Johnson, L.K. & Wiemer, D.F. 1982. Nerol: An alarm substance of the stingless bee *Trigona fulviventris* (Hymenoptera: Apidae). *J. Chem. Ecol.* 8: 1167 - 1181.

Johnson, L.K., Haynes, L.W., Carlson, M.A., Fortnum, H.A. & Gorgas, D.L. 1985. Alarm substances of the stingless bee *Trigona silvestriana. J. Chem. Ecol.* 11: 409 - 416.

Joubert, S.C.J. 1984. Report on an ecological survey of the eastern Tuli Block. Unpubl. mimeograph, Northern Tuli Cons. Ass. 1 - 36.

Karban, R., Brody, A.K. & Schnathorst, W.C. 1989. Crowding and a plant's ability to defend itself against herbivores and disease. *Am. Nat.* 134: 749 - 760.

Kelly, R.D. & Walker, B.H. 1976. The effects of different forms of land use on the ecology of a semi-arid area in south-eastern Rhodesia. *J. Ecol.* 64: 553 - 576.

Kopooshian, H. & Isley, D. 1966. Seed character relationships in the Leguminosae. *Proc. Iowa Acad. Sci.* 73: 59 - 67.

Kursar, T.A. & Coley, P.D. 1991. Nitrogen content and expansion rate of young leaves of Rain Forest species: Implications for herbivory. *Biotropica* 23: 141 - 150.

Lacey, E.P. 1981. Seed dispersal in wild carrot (*Daucus carrota*). *Mich. Bot.* 20: 15 - 20.

Lamprey, H.F., Glover, P.E., Turner, M.I.M. & Bell, R.H.V. 1967. Invasion of the Serengeti National Park by elephants. *E. Afr. Wildl. J.* 5: 151 - 166.

Laws, R.M. 1969. Aspects of reproduction in the African elephant. *J. Reprod. Fert. Suppl.* 6: 193 - 217.

Laws, R.M., Parker, I.S.C. & Johnstone, R.C.B. 1970. Elephants and their habitats in North Bunyoro, Uganda. *E. Afr. Wildl. J.* 8: 163 - 180.

le Roux, C.J.G. 1980. *Vegetation classification and related studies in the Etosha National Park.* D.Sc. thesis. University of Pretoria.

le Roux, C.J.G., Grunow, F.O., Morris, J.W., Bredenkamp, G.J. & Scheepers, J.C. 1988. A classification of the vegetation of the Etosha National Park. *S. Afr. J. Bot.* 54: 1 - 10.

le Roux, P. 1991. *Results of 1991 aerial game census in the Northern Tuli Game Reserve, N.E. Tuli Block, Botswana.* Unpubl. Mimeograph.

Letourneau, D.K. 1983. Passive aggression: An alternative hypothesis for the *Piper-Pheidole* association. *Oecologia* 60: 122 - 126.

Levin, D.A. & Kerster, H.W. 1974. Gene flow in seed plants. *Evol. Biol.* 7:

Lewis, D.M. 1986. Disturbance effects on elephant feeding: evidence for compression in Luangwa Valley, Zambia. *Afr. J. Ecol.* 24: 227 - 241.

Lewis, D.M. 1987. Elephant response to early burning in mopane woodland, Zambia. *S. Afr. J. Wildl. Res.* 17: 33 - 40.

Lewis, D.M. 1991. Observations of tree growth, woodland structure and elephant damage on *Colophospermum mopane* in Luangwa Valley, Zambia. *Afr. J. Ecol.* 29: 207 - 221.

Liengme, C.A. 1981. Plants used by the Tsonga people of Gazankulu. *Bothalia* 13: 501 - 518.

Lind, P. 1974. *Shashe - Limpopo ranger's report,* 1973/1974. Unpublished mimeograph, Shashe - Limpopo conservation Syndicate, 1 - 111.

Lüdemann, F. 1960. Utilization of trees and inferior roughage during droughts. *The Meat Industry*: Jul. - Sep. 1966: 23 - 28.

Lundberg, P. & Astrom, M. 1990. Low nutritive quality as a defense against optimally foraging herbivores. *Am. Nat.* 135: 547 - 562.

Martin, J.S. & Martin, M.M. 1982. Tannin assays in ecological studies: lack of correlation between phenolics, proanthocyanidins and protein-precipitating constituents in mature foliage of six oak species. *Oecologia* 54: 203 - 211.

Martin, M.M. & Martin, J.S. 1984. Surfactants: their role in preventing the precipitation of proteins by tannins in insect guts. *Oecologia* 61: 342 - 345.

Martin, R.B. 1974. *Structure, biomass and utilization of vegetation in the mopane and miombo woodlands of the Sengwa Wildlife Research Area.* Certificate in Field Ecology, Research Report, University of Rhodesia.

Mattson, W.J. 1980. Herbivory in relation to plant nitrogen content. *Ann. Rev. Ecol. Syst.* 11: 119 - 161.

McKenzie, A.A. 1990. Co-operative hunting in the black-backed jackal *Canis mesomelas* Schreber. Ph.D. thesis. University of Pretoria.

McKey, D.B. 1979. The distribution of secondary compounds within plants. In: *Herbivores, their interactions with secondary plant metabolites.* G.A. Rosenthal and D.H. Janzen (Eds.). Academic Press, New York. pp. 55 - 133.

McKey, D.B., Gartlan, J.S., Waterman, P.G. & Choo, G.M. 1981. Food selection by black colobus monkeys in relation to plant chemistry. *Biol. J. Linn. Soc.* 16: 115 - 146.

McLeod, M.N. 1974. Plant tannins - their role in forage quality. *Nutr. Abstr. Rev.* 44: 803 - 815.

Meissner, H.H., Pietersen, L.M. & de Villiers, P.A. 1990. Quality of food and *ad libitum* intake by elephant and impala. *S. Afr. Soc. Anim. Prod. Cong. Abstr.* (Stellenbosch), March 27-29. Congress 29: L2. 21.

Milborrow, B.V., Kennedy, J.M. & Dollin, A. 1987. Composition of wax made by the Australian stingless bee *Trigona australis. Aust. J. Biol. Sci.* 40: 15 - 25.

Milton, K. 1979. Factors influencing leaf choice by howler monkeys: a test of some hypotheses of food selection by generalist herbivores. *Am. Nat.* 114: 362 - 378.

Moeck, H.A. 1970. Ethanol as the primary attractant for the ambrosia beetle *Trypodendron lineatum* (Coleoptera, Scolytidae). *Can. Ent.* 102: 985 - 995.

Mole, S., Butler, L.G. & Iason, G. 1990. Defense against dietary tannins in herbivores: A survey for proline rich salivary proteins in mammals. *Biochem. Syst. Ecol.* 18: 287 - 293.

Moreno-Black, G.S. & Bent, E.F. 1982. Secondary compounds in the diet of *Colobus angolensis. Afr. J. Ecol.* 20: 29 - 36.

Mould, E.D. & Robbins, C.T. 1982. Digestive capabilities in elk compared to white-tailed deer. *J. Wildl. Mgmt.* 46: 22 - 29.

Mundell, I. 1992. Botswana needs science help to help save plant and animal species. *Nature* 357: 184.

Mwalyosi, R.B.B. 1990. The dynamic ecology of *Acacia tortilis* woodland in Lake Manyara National Park, Tanzania. *Afr. J. Ecol.* 28: 189 - 199.

Narang, A.K. & Bhardwaj, N. 1974. Seed coat regulated germination in *Tephrosia appolina* DC. and its significance. *Int. J. Ecol. Env. Sci.* 1: 47 - 51.

Newberry, D. McC. 1980a. Interactions between the coccid, *Icerya seyshellarum* (Westw.), and its host tree species on Aldabra atoll. I. *Euphorbia pyrifolia* Lam. *Oecologia* 46: 171 - 179.

Newberry, D. McC. 1980b. Interactions between the coccid, *Icerya seyshellarum* (Westw.), and its host tree species on Aldabra atoll. I. *Scaevola taccada* (Gaertn.) Roxb. *Oecologia* 46: 180 - 185.

Nijhölt, W.W. 1980. Pine oil and oleic acid delay and reduce attacks on logs by ambrosia beetles (Coleoptera, Scolytidae). *Can. Ent.* 112: 199 - 204.

Niosh Manual (National Institute for Occupational Safety and Health) 2nd. Edn. Vol 1-7; (3rd. Edn). Vol 1 & 2.

Nott, T.B. & Stander, P.E. 1991. The monitoring of density and utilization of two tree species in the Etosha National Park, Namibia. *Madoqua* 18: 11 - 15.

Novellie, P., Hall-Martin, A.J. & Joubert, D. 1991. The problem of maintaining large herbivores in small conservation areas: deterioration of the grassveld in the Addo Elephant National Park. *Koedoe* 34: 41 - 50.

Nunez-Hernandez, G., Holecheck, J.L., Wallace, J.D., Galyean, M.L. Tembo, A. Valdez, R. & Cardenas, M. 1989. Influence of native shrubs on nutritional status of goats: nitrogen retention. *J. Range Mgmt.* 42: 228 - 232.

O' Connor, T.G. & Campbell, B.M. 1986. Hippopotamus habitat relationships on the Lundi River, Gonarezhou National Park, Zimbabawe. *Afr. J. Ecol.* 24: 7 - 26.

Oates, L.G. 1972. Food preferences of giraffe in Transvaal Lowveld mopane woodland. *J. S. Afr. Wildl. Mgmt. Ass.* 2: 21 - 33.

Oates, J.P., Swain, T. & Zantovska, J. 1977. Secondary compounds and food selection by Colobus monkeys. *Biochem. Syst. Ecol.* 5: 317 - 321.

Obermeijer, A.A. 1933. Notes on the distribution of *Copaifera mopane* Kirk. *S. Afr. J. Sci.* 30: 266 - 269.

Oberprieler, R. 1986. *Pinus radiata* D. Don: a new food plant record for *Imbrasia* (*Gonimbrasia*) *belina* (Westwood) (Lepidoptera: Saturniidae). *J. Ent. Soc. S. Afr.* 49: 168 - 169.

Oberprieler, R. 1990. Das Braune oder Mopane-Nachtpfauenauge *Imbrasia belina* (Westwood). *Mitteilungen Newsletter* 31: 132 - 149.

Oh, H.K., Sakai, T., Jones, M.B. & Longhurst, W.M. 1967. Effects of various essential oils isolated from Douglas fir needles upon sheep and deer rumen microbial activity. *Appl. Microbiol.* 15: 777 - 784.

Oh, H.K., Jones, M.B. & Longhurst, W.M. 1968. Comparison of rumen microbial inhibition resulting from various essential oils isolated from relatively unpalatable plant species. *Appl. Micro.* 16: 39 - 44.

Owen, D.F. 1990. The language of attack and defense. *Oikos* 57: 133 - 135.

Owen, D.F. and Weigert, R.G. 1976. Do consumers maximize plant fitness? *Oikos* 27: 488 - 492.

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. 1988. Plant palatability assessment and its implications for plant-herbivore relations. *J. Grassl. Soc. S. Afr.* 5: 72 - 75.

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

Owen-Smith, N. & Novellie, P. 1982. What should a clever ungulate eat?. *Am. Nat.* 119: 151 - 178.

Owen-Smith, R.N. 1983. Dispersal and the dynamics of large herbivores in enclosed areas: Implications for management. In: *Management of large mammals in African conservation areas*. N. Owen-Smith (Ed.). Haum Publishers, Pretoria.

Paige, K.N. & Whitham, T.G. 1987. Overcompensation in response to mammalian herbivory: the advantage of being eaten. *Am. Nat.* 129: 407 - 416.

Palmer, E. & Pitman, N. 1972. *Trees of Southern Africa.* A.A. Balkema, Cape Town.

Parra, R. 1978. Comparison of foregut and hindgut fermentation in herbivores. In: *The ecology of arboreal folivores.* G.G. Montgomery (Ed.). Smithsonian Institution, Washington. pp. 205 - 229.

Pellew, R.A. 1983. Modelling and the systems approach to management problems: The Acacia/elephant problem on the Serengeti. In: *Management of large mammals in African conservation areas.* N. Owen-Smith (Ed.). Haum Publishers, Pretoria.

Petty, F.W. 1925. New South African Psyllids. *S. Afr. J. Nat. Hist.* 8: 125 - 142.

Phillips, T.W. 1990. Responses of *Hylastes salebrosus* to the turpentine, ethanol, and pheromones of *Dendroctonus* (Coleoptera: Scolytidae). *Florida Ent.* 73: 286 - 292.

Phillips, T.W., Wilkening, A.J., Atkinson, T.H., Nation, J.L., Wilkinson, R.C. & Foltz, J.L. 1988. Synergism of turpentine and ethanol as attractants for certain pine-infesting beetles (Coleoptera). *Env. Ent.* 17: 456 - 462.

Pienaar, U. de V. 1983. Management by intervention: The pragmatic/economic option. In: *Management of large mammals in African conservation areas.* N. Owen-Smith (Ed.). Haum Publishers, Pretoria.

Pienaar, U. de V., Joubert, S.C.J., Hall-Martin, A.J., De Graaff, G. & Rautenbach, I.L. 1987. *Field Guide to the Mammals of the Kruger National Park.* Struik Publishers, Cape Town.

Pierce, N.E. & Eastal, S. 1986. The selective advantage of attendant ants for the larvae of a lycaenid butterfly, *Glaucopsyche lygdamus. J. Anim. Ecol.* 55: 451 - 462.

Pimentel, D. 1988. Herbivore population feeding pressure on plant hosts: feedback evolution and host conservation. *Oikos* 53: 289 - 302.

Pinhey, E.C.G. 1975. *Moths of southern Africa.* Tafelberg Publishers, Cape Town.

Price, M.L. & Butler, L.G. 1977. Rapid visual estimation and spectrophotometric determination of tannin content of sorghum grain. *J. Agr. Food Chem.* 25: 1268 - 1273.

Price, P.W. 1984. *Insect Ecology* (2nd Edn.). John Wiley & Sons, New York.

Provenza, F.D. & Balph, D.F 1990. applicability of five diet-selection models to various foraging challenges ruminants encounter. In: *Behavioral mechanisms in food selection.* R.N. Hughes (Ed.). NATO ASI Series G: Ecological Sciences Vol 20, Springer, Heidelberg.

Provenza, F.D., Burritt, E.A., Clausen, T.P., Bryant, J.P. Reichardt, P.B. & Distel, R.A. 1990. Conditioned flavour aversion: a mechanism for goats to avoid condensed tannins in blackbrush. *Am. Nat.* 136: 810 - 828.

Radwan, M.A. & Crouch, G.L. 1974. Plant characteristics related to feeding preference by black-tailed deer. *J. Wildl. Mgmt.* 38: 32 - 41.

Radwan, M.A., Crouch, G.L., Harrington, C.A. & Ellis, W.D. 1982. Terpenes of ponderosa pine and feeding preferences by pocket gophers. *J. Chem. Ecol.* 8: 241 - 253.

Ras, A.M. 1990. Die invloed van ontblaring en vog op die tanien- en prolifenolinhoud van *Portulacaria afra. J. Grassl. Soc. S. Afr.* 7: 139 - 143.

Rathcke, B. 1985. Slugs as generalist herbivores: Tests of three hypotheses on plant choices. *Ecology* 66: 828 - 836.

Rhoades, D.F. 1979. Evolution of plant chemical defenses against herbivores. In: *Herbivores, their interaction with secondary plant metabolites.* G.A. Rosenthal and D.H. Janzen (Eds.). Academic Press, New York.

Rhoades, D.F. & Cates, R.G. 1976. Toward a general theory of plant antiherbivore chemistry. *Rec. Adv. Phytochem.* 10: 168 - 213.

Richmond, C.E. 1985. Effectiveness of two pine oils for protecting lodgepole pine from attack by mountain pine beetle (Coleoptera, Scolytidae). *Can. Ent.* 112: 199 - 204.

Ridley, H.N. 1930. *The dispersal of plants throughout the world.* Ashford Publishers, Reeve.

Riggs, R.A. Urness, P.J. & Hall, T.A. 1988. Diets and weight responses of Spanish goats used to control gambel oak. *Small-Ruminant Res.* 1: 259 - 271.

Riney, T. 1982. Study and management of large mammals. John Wiley & Sons, New York.

Robbins, C.T., Hanley, T.A., Hagermann, A.E., Hjeljord, O., Baker, D.L., Schwartz, C.C. & Mautz, W.W. 1987a. Role of tannins in defending plants against ruminants: reduction in protein availability. *Ecology* 68: 98 - 107.

Robbins, C.T., Mole, S., Hagermann, A.E. & Hanley, T.A. 1987b. Role of tannins in defending plants against ruminants: reduction in dry matter digestion? *Ecology* 68: 1606 - 1615.

Robertson, J.B. & van Soest, P.E. 1981. The detergent system of analysis and its application to human foods. In: *The analysis of dietary fibre in food.* W.P.T. James & O. Theander (Eds.). Dekker, New York.

Rockwood, L.L. 1985. Seed weight as a function of life form, elevation and life zones in neotropical forest. *Biotropica* 17: 32 - 39.

Rosenthal, G.A. & Janzen, D.A. 1979. *Herbivores, their interactions with secondary plant metabolites.* Academic Press, New York.

Ruggiero, R.G. 1992. Seasonal forage utilization by elephants in central Africa. *Afr. J. Ecol.* 30: 137 - 148.

Rutherford, M.C. 1979. Plant-based techniques for determining available browse and browse utilization : A Review. *Bot. Rev.* 45: 203 - 228.

Sauer, J.J.C, Theron, G.K. and Skinner, J.D. 1977. Food preferences of the giraffe (*Giraffa camelopardalis*) in the arid bushveld of the western Transvaal. *S. Afr. J. Wildl. Res.* 7: 53 - 59.

Scholes, R.J. 1983. The regrowth of *Colophospermum mopane* following clearing. *J. Grassl. Soc. S. Afr.* 7: 147 - 151.

Schoonhoven, L.M. & Derksen-Koppers, I. 1976. Effects of some allelochemicals on food uptake and survival of a polyphagous aphid *Myzus persicae*. *Ent. Exp. App.* 19: 52 - 56.

Schroeder, L.A. 1986. Changes in the leaf quality and growth performance of Lepidopteran larvae. *Ecology* 67: 1628 - 1636.

Schroeder, L. & Malmer, M. 1980. Dry matter, energy, and nitrogen conversion by Lepidoptera and Hymenoptera larvae fed leaves of black cherry. *Oecologia* 45: 63 - 71.

Schultz, J.C., Nothnagle, P.J. & Baldwin, J.T. 1982. Seasonal and individual variation in leaf quality of two northern hardwood species. *Am. J. Bot.* 69: 753 - 759.

Schupp, E.W. 1986. *Azteca* protection of *Cecropia*: ant occupation benefits juvenile trees. *Oecologia* 70: 379 - 385.

Scriber, J.M. & Feeny, P. 1979. Growth of herbivorous caterpillars in relation to feeding specialization and to the growth form of their food plants. *Ecology* 60: 829 - 850.

Sheldon, S.P. 1986. Factors influencing the number of branches and inflorescences of *Potamogeton richardsonii* (A. Benn.) Rydb. *Aquat. Bot.* 24: 27 - 34.

Short, J. 1981. Diet and feeding behaviour of the forest elephant. *Mammalia* 45: 177 - 185.

Siegel, S. 1956. *Nonparametric statistics for the behavioral sciences.* McGraw-Hill, New York.

Simms, E.L. 1990. Examining selection on the multivariate phenotype: Plant resistance to herbivores. *Evol.* 44: 1177 - 1188

Simms, E.L. & Rausher, M.D. 1989. The evolution of resistance to herbivory in *Ipomoea purpurea*. II. Natural selection by insects and costs of resistance. *Evol.* 43: 573 - 585.

Skaife, S.H. 1979. *African Insect Life*. Struik Publishers, Cape Town.

Skarpe, C. 1990. Shrub layer dynamics under different herbivore densities in an arid savanna, Botswana. *J. Appl. Ecol.* 27: 873 - 885.

Skarpe, C. & Bergstrom, R. 1986. Nutrient content and digestibility of forage plants in relation to their phenology and rainfall in the Kalahari, Botswana. *J. Arid Environ.* 11: 147 - 167.

Skinner, J.D. & Smithers, R.H.N. 1990. *The Mammals of the Southern African Subregion* (2nd Edn.). University of Pretoria Press, Pretoria.

Smart, N.E.O., Hatton, J.C. & Spence, D.H.N. 1985. The effects of long-term exclusion of large herbivores on vegetation in Murchison Falls National Park, Uganda. *Biol. Cons.* 33: 229 - 245.

Smith, R.H. 1965. Effect of monoterpene vapours on the western pine beetle. *J. Econ. Ent.* 58: 509 - 510.

Smith, R.H. 1966. The monoterpene composition of *Pinus ponderosa* xylem resin and of *Dendroctonus brevicomis* pitch tubes. *Forest Sci.* 12: 63 - 68.

Smithers, R.H.N. 1986. *Land mammals of southern Africa: a field guide*. Macmillan Publishers, Johannesburg.

Sorenson, A.E. 1986. Seed dispersal by adhesion. *Ann. Rev. Ecol. Syst.* 17: 443 - 463.

Stafford, H.A., Smith, E.C. & Wieder, R.M. 1989. The development of proanthocyanidins (condensed tannins) and other phenolics in bark of *Pseudotsuga menziesii*. *Can. J. Bot.* 67: 1111 - 1118.

Stein, O.L. 1978. Early leaf ontogeny and the shoot apex of *Colophospermum mopane* (Leguminosae). *Am. J. Bot.* 65: 544 - 551.

Stenseth, N.C. 1981. Optimal food selection: some further considerations with special reference to the grazer-hunter distinction. *Am. Nat.* 117: 457 - 475.

Stuart, C.T. & Stuart, M.D. 1988. *Field Guide to the Mammals of Southern Africa.* Struik Publishers, Cape Town.

Sturgeon, K.B. 1979. Monoterpene variation in Ponderosa Pine xylem resin related to western pine beetle predation. *Evol.* 33: 803 - 814.

Swain, T. 1965. The tannins. In: *Plant Biochemistry.* J. Bonner and J. Varner (Eds.). Academic Press, New York. pp. 552 - 580.

Swain, T. 1979a. Tannins and lignins. In: *Herbivores, their interactions with secondary plant metabolites.* G.A. Rosenthal and D.H. Janzen (Eds.). Academic Press, New York. pp. 657 - 682.

Swain, T. 1979b. Phenolics in the environment. *Rec. Adv. Phytochem.* 12: 617 - 640.

Tainton, N.M., Bradsby, D.I. & Booysen, P. de V. 1985. *Common veld and pasture grasses of Natal* (4th Edn.). Shuter and Shooter Ltd., Pietermaritzburg.

Taylor, R.D. & Walker, B.H. 1978. Comparisons of vegetation use and herbivore biomass on a Rhodesian game and cattle ranch. *J. Appl. Ecol.* 15: 565 - 581.

Teague, W.R. 1989. Patterns of selection of *Acacia karroo* by goats and changes in tannin levels and *in vitro* digestibility following defoliation. *J. Grassl. Soc. S. Afr.* 6: 230 - 235.

Teague, W.R., Teague, R.C. & Walker, B.H. 1990. Simulating browse production and response of *Acacia karroo* to defoliation I. Model description and sensitivity analyses. *J. Grassl. Soc. S. Afr.* 7: 1 - 10.

Teague, W.R. & Walker, B.H. 1988. Growth patterns and annual growth cycle of *Acacia karroo* Hayne in relation to water stress I. Leaf and shoot growth. *J. Grassl. Soc. S. Afr.* 5: 85 - 95

Tempel, A.S. 1982. Tannin - measuring techniques : A Review. *J. Chem. Ecol.* 8: 1289 - 1298.

Teranishi, R., Buttery, R.G. Flath, R.A., Mon, T.R. & Stern, D.J. 1986. Medfly attractancy of alpha-copaene from different essential oils. *Abs. Pap. Am. Chem. Soc.* 192 (Sep): 48.

Terrill, T.H., Windham, W.R., Evan, J.J. & Hoveland, C.S. 1990. Condensed tannin concentration in *Sericea lespedeza* as influenced of preservation method. *Crop Sci.* 23: 197 - 200.

Tho, Y.P. 1978. Living in harmony. *Nature Malay.* 3: 34 - 39.

Thompson, P.J. 1960. A description of the growth habits of mopane in relation to soil and climatic conditions. *Proc. 1st Fed. Sci. Cong.* Salisbury, Rhodesia.: 181 - 186.

Thompson, P.J. 1975. The role of elephants, fire and other agents in the decline of a *Brachystegia boehmii* woodland. *J. S. Afr. Wildl. Mgmt. Ass.* 5: 11 - 18.

Tolsma, D.J., Ernst, W.H.O. & Verwey, R.A. 1987a. Nutrients in soil and vegetation around two artificial waterpoints in eastern Botswana. *J. Appl. Ecol.* 24: 991 - 1000.

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

Twamley, B.E. 1967. Seed size and seedling vigour in birdsfoot trefoil. *Can. J. Pl. Sci.* 47: 603 - 609.

van der Meijden, E., Wijn, M. & Verkaar, J. 1988. Defence and regrowth, alternative plant strategies in the struggle against herbivores. *Oikos* 51: 355 - 363.

van der Pijl, L. 1972. *Principles of Dispersal in Higher Plants* (2nd Edn.). Springer-Verlag, Berlin.

van Hoven, W. 1984. Tannins and digestibility in greater kudu. *Can. J. Anim. Sci.* 64 (Suppl.): 177 - 178.

van Rooyen, N., Theron, G.K. & Grobbelaar, N. 1981. A floristic description and structural analysis of the plant communities of the Punda Milia - Pafuri - Wambiya area in the Kruger National Park, Republic of South Africa. *J. S. Afr. Bot.* 47: 405 - 449.

van Staden, J., Manning, J.C. & Kelly, K.M. 1989. Legume Seeds - The Structure : Function Equation. In: *Advances in legume biology.* C.H. Stirton and J.L. Zarruchi (Eds.). *Monogr. Missouri Bot. Gard.* 29: 417 - 450.

van Wyk, P. 1972. *Trees of the Kruger National Park.* Vol.1. Purnell, Cape Town.

van Wyk, P. 1984. *Field guide to the trees of the Kruger National Park.* Struik Publishers, Cape Town.

van Wyk, P. & Fairall, N. 1969. The influence of the African elephant on the vegetation of the Kruger National Park. *Koedoe* 12: 57 - 89.

Viljoen, P.J. 1989. Habitat selection and preferred food plants of a desert-dwelling elephant population in the northern Namib Desert, South West Africa Namibia. *Afr. J. Ecol.* 27: 227 - 240.

Viljoen, P.J. & Bothma, du P., J. 1990. The influence of desert dwelling elephants on vegetation in the northern Namib desert, South West Africa/Namibia. *J. Arid Environ.* 18: 85 - 96.

Vite, J.P. & Pitman, G.B. 1969. Insect and host odours in the aggregation of the western pine beetles. *Can. Ent.* 101: 113 - 117.

Volke, W. 1992. Aphids or parasitoids: who actually benefit from the ant-attendance? *J. Anim. Ecol.* 61: 273 - 281.

von Breitenbach, F. 1965. *The Indigenous Trees of southern Africa.* Descriptive text, Part 2, Vol. III. Unpubl. Mimeograph.

Vranjic, J.A. & Gullan, P.J. 1990. The effect of a sap sucking herbivore (Homoptera: Eriococcidae), on seedling growth and architecture in *Eucalyptus blakelyi. Oikos* 59: 157 - 162.

Walker, B.H., Emslie, R.H., Owen-Smith, N. & Scholes, R.J. 1987. To cull or not to cull: Lessons from a southern African drought. *J. Appl. Ecol.* 24: 381 - 401.

Wandera, F.P., Dzowela, B.H. & Karachi, M.K. 1991. Production and nutritive value of browse species in semi-arid Kenya. *Trop. Grassl.* 25: 349 - 355.

Welker, J.M., Briske, D.D., Rykiel, E. & Goeschl, J. 1985. Carbon import among vegetative tillers of two bunchgrasses: assessment with carbon-11 labelling. *Oecologia* 67: 209 - 212.

Welker, J.M., Briske, D.D. & Weaver, R.W. 1987. Nitrogen-15 allocation among three tiller generations within the bunchgrass *Schizachyrium scoparium*: response to selective defoliation. *Oecologia* 74: 330 - 334.

Werger, M.J.A. & Coetzee, B.J. 1978. The Sudano-Zambezian Region. In: *Biogeography and ecology of southern Africa.* Werger, M.J.A. (Ed.). Junk, The Hague.

Weyerhauser, F.J. 1985. Survey of elephant damage to baobabs in Tanzania's Lake Manyara National Park. *Afr. J. Ecol.* 23: 235 - 243.

Wilson, M.F., Rice, B.L., & Westoby, M. 1990. Seed dispersal spectra: a comparison of temperate plant communities. *J. Veg. Sci.* 1: 547 - 563.

Wisdom, C.S. 1985. Use of chemical variation and predation as plant defenses by *Encelia farinosa* against a specialist herbivore. *J. Chem. Ecol.* 11: 1553 - 1565.

Wood, D.L. 1973. Selection and colonization of ponderosa pine by bark beetles. In: *Insect/Plant Relationships*. H.G. Van Emden (Ed.). Blackwell Scientific Publications, London.

Zucker, W.V. 1983. Tannins: does structure determine function? An ecological perspective. *Am. Nat.* 121: 335 - 365.

APPENDICES

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SL,	SENESCING LEAVES
GL,	GREEN LEAVES
TB,	TWIG BARK
SB,	STEM BARK
VYL,	VERY YOUNG LEAVES
YL,	YOUNG LEAVES
Yng.,	YOUNG

APPENDIX ONE

NUMBER OF LEAFLETS COUNTED ON THE MARKED BRANCHES:

SPRING LEAVES

14	54	18	25	9	37	28	37
12	5	13	38	26	18	46	12
25	21	10	19	17	4	28	8
36	14	13	10	10	46	10	14
25	31	5	9	12	42	2	40
10	6	21	35	16	39	0	18
25	4	21	45	49	40	13	24
4	0	20	29	27	62	19	24
13	21	14	37	16	24	28	9
25	23	12	24	18	39	57	54
46	12	6	16	24	15	19	41
45	13	23	50	20	29	12	28
23	1	18	25	16	52	27	46
21	4	25	19	29	13	4	18
12	21	17	13	27	8	12	58
14	5	36	12	18	13	13	58
23	8	24	29	41	16	10	25
10	19	18	13	29	21	15	29
2	24	34	18	58	8	14	24
5	13	21	39	39	13	21	35
15	25	12	19	27	4	31	71
26	21	10	26	10	40	15	39
12	18	25	34	4	25	24	30
14	38	12	64	16	19	30	67
10	3	13	19	23	16	7	51
2	7	24	24	69	35	20	26
0	14	19	18	24	46	19	19
12	2	46	25	13	18	24	10
14	13	21	31	51	39	12	15
2	10	13	16	26	28	29	6
36	24	20	22	69	46	18	23
25	15	28	16	41	52	25	12
21	22	13	21	39	21	6	15
13	45	25	34	21	26	8	5
11	52	14	19	58	17	1	4
42	34	34	26	37	25	15	12
36	11	15	19	29	42	10	16
24	8	26	18	59	19	19	3
9	26	19	43	69	27	29	14
54	15	35	50	18	34	15	8
21	39	21	49	68	38	5	13
36	14	8	28	25	60	12	21
26	54	25	30	26	56	16	9
21	24	34	14	24	21	9	8
31	31	13	10	31	19	21	26
8	26	24	68	24	14	14	13
11	31	19	41	19	49	26	24
9	12	29	24	24	43	15	13
16	11	41	16	16	70	12	24
21	2	45	28	29	43	28	28

SUMMER LEAVES

15	28	75	0	24	79	18
13	10	55	7	42	48	33
27	11	180	0	39	21	21
14	6	185	27	24	41	20
21	13	55	42	37	17	17
47	4	50	18	27	37	18
26	30	43	23	48	61	44
21	12	31	62	47	47	37
24	36	12	13	22	52	12
13	10	34	25	16	46	31
12	15	107	0	0	18	38
8	2	77	0	18	61	48
2	31	17	42	0	4	20
13	19	32	58	0	28	5
29	18	55	0	21	40	41
14	15	0	57	0	8	32
31	10	0	33	0	47	57
12	17	35	52	0	17	51
17	3	22	38	0	32	47
4	9	18	0	0	0	46
12	9	3	70	0	47	35
17	4	40	42	0	51	17
36	15	31	41	0	57	18
12	6	77	31	27	28	25
10	12	53	26	32	23	18
9	14	56	17	47	57	91
14	10	52	22	0	31	61
2	2	0	4	73	31	52
12	5	62	16	71	37	61
27	19	52	21	57	42	30
19	14	97	100	21	31	51
14	25	56	0	32	2	47
15	1	69	42	81	0	74
6	3	57	72	0	26	40
29	14	113	0	12	30	92
39	8	88	37	56	32	55
25	14	81	35	45	41	50
24	29	53	13	57	23	67
26	31	40	47	29	62	46
3	12	68	31	0	41	8
13	8	57	75	62	82	42
24	4	96	0	31	5	30
30	15	87	0	58	31	0
12	12	73	46	29	0	5
5	25	57	0	45	31	56
14	22	11	0	82	31	13
12	13	13	15	47	17	61
13	14	12	0	69	35	55
14	26	31	7	78	51	30
16	7	41	8	72	35	41

SUMMER LEAVES

20	0	57	0	0
35	42	36	0	4
9	31	22	0	0
30	33	15	5	1
0	20	0	0	0
55	0	55	68	9
47	0	24	33	81
77	0	13	38	47
62	45	11	63	0
51	67	71	24	3
12	13	52	0	45
0	7	35	0	18
17	8	51	6	39
12	4	22	8	65
11	5	51	0	49
35	12	31	0	26
5	26	42	42	77
0	32	0	18	2
0	24	7	22	6
57	18	47	7	0
18	0	82	0	33
62	19	58	1	47
35	41	0	22	13
48	22	73	18	40
22	8	61	0	17
46	37	24	0	5
42	37	22	4	3
40	0	31	13	18
62	30	0	3	4
40	41	0	0	0
68	22	0	1	0
42	18	0	0	37
41	20	4	0	5
31	27	18	0	12
0	15	0	0	32
0	13	22	68	21
62	25	5	6	15
0	25	22	62	8
57	40	21	57	3
48	21	28	17	9
49	8	86	2	17
85	11	23	0	25
112	5	35	0	23
27	18	11	0	47
8	32	19	0	15
90	19	15	4	22
88	6	37	0	6
57	27	45	2	8
80	13	0	0	2
40	30	77	0	42

AUTUMN LEAVES

52	0	24	35	17	20	13	38	0	0
41	0	18	36	25	31	11	15	0	2
88	0	38	31	16	7	10	23	0	0
126	24	20	25	14	17	21	14	0	4
34	32	0	0	3	0	9	0	0	0
20	20	44	37	0	37	0	45	14	0
48	5	17	55	37	22	0	8	5	70
16	32	48	41	27	55	0	16	6	55
10	8	25	61	7	62	48	9	31	0
6	17	0	25	27	31	75	40	8	1
116	0	0	17	20	13	7	31	4	35
48	14	20	31	27	46	9	17	0	7
13	30	0	0	20	7	6	24	35	16
40	48	0	24	36	30	4	15	0	0
48	0	13	0	4	17	4	30	0	25
32	48	0	5	11	18	6	0	0	10
18	40	0	42	27	67	8	0	27	4
36	40	0	0	51	19	20	0	8	12
25	13	0	28	22	42	3	0	7	33
9	0	0	45	88	15	13	0	2	0
6	45	0	36	32	10	36	0	22	15
24	16	0	51	21	35	6	0	13	10
18	32	0	41	24	0	21	0	18	0
30	20	10	31	27	0	11	0	17	8
32	16	13	52	17	20	4	0	0	4
36	24	30	51	60	30	47	22	12	10
32	15	10	31	0	13	42	31	0	11
0	20	0	40	47	43	0	18	13	34
16	17	22	0	48	42	34	2	36	12
32	12	0	17	17	41	37	0	7	16
88	64	15	23	46	45	10	27	26	2
45	16	20	31	26	17	0	41	0	12
40	20	55	0	47	0	7	16	24	3
48	0	31	10	55	32	22	18	30	4
72	13	5	12	50	0	13	0	12	12
41	30	45	20	61	0	14	18	56	7
52	25	0	0	60	24	12	5	0	0
32	15	61	5	37	1	18	18	48	6
30	0	0	31	48	0	21	4	35	1
35	56	0	15	0	22	10	14	27	5
40	0	13	52	48	29	8	39	0	10
52	0	32	0	51	52	13	0	5	15
48	0	56	22	30	67	3	8	0	10
56	0	62	37	39	22	7	7	1	13
40	0	30	0	51	8	24	2	9	7
11	7	72	25	0	57	11	7	8	20
7	24	62	17	48	128	4	13	0	13
7	10	66	0	39	45	17	24	0	10
4	0	46	40	20	0	20	0	1	32
10	0	51	33	35	37	13	41	8	0

MOISTURE CONTENT FIGURES:

WINTER

GL	TB	SB
30,4	32,8	5,8
34,6	35,7	2,3
36,1	34,9	4,6
31,4	29,8	4,2
32,8	29,8	3,5
31,6	38,3	2,7
33,8	36,0	2,5
37,3	37,2	2,8
32,1	34,7	3,7
31,0	33,8	3,8
29,4	33,1	2,7
30,7	35,2	3,9
33,8	33,7	5,7
33,2	29,6	3,6
32,8	30,3	4,3

SPRING

VYL	YL	GL	TB	SB
38,3	46,7	45,3	33,8	5,8
43,8	40,2	46,9	35,7	5,8
46,9	44,8	40,8	46,3	6,3
40,6	35,6	45,6	43,2	5,7
39,2	39,2	47,9	35,7	6,3
38,7	41,7	47,8	33,5	6,4
38,6	40,3	43,8	39,3	5,3
39,7	38,8	46,9	44,7	6,3
40,8	38,6	46,8	45,8	6,1
43,7	40,1	47,2	38,8	6,1
38,2	36,4	45,4	43,5	5,8
42,1	37,1	43,8	46,2	5,8
39,3	40,2	47,3	36,3	6,4
40,6	38,0	46,8	46,8	6,0
42,5	41,3	44,9	44,9	6,0

SUMMER

GL	TB	SB
39,0	36,9	7,7
37,1	34,9	7,9
45,3	37,3	6,9
47,4	38,8	7,5
46,0	37,7	7,5
38,6	38,9	7,8
46,3	33,7	7,9
36,7	38,8	8,0
36,2	39,5	8,3
46,1	36,5	7,9
45,7	40,3	7,8
43,6	43,7	8,3
44,8	39,8	8,2
47,4	38,4	7,7
45,5	39,9	7,5

AUTUMN

GL	TB	SB
47,2	36,7	7,1
45,3	38,5	6,0
44,8	36,4	6,5
36,7	43,2	7,0
35,9	42,9	5,8
39,1	41,0	5,8
38,6	37,7	6,3
44,3	38,6	6,7
42,5	34,3	6,7
41,9	39,7	5,9
40,6	34,6	6,1
40,5	37,9	6,0
38,1	43,3	6,8
40,3	36,1	5,8
41,1	35,3	6,3

NITROGEN CONTENT FIGURES:

	WINTER		
GL	SL	TB	SB
1,56	0,55	0,88	0,60
1,54	0,54	0,91	0,56
1,56	0,51	0,84	0,58
1,44	0,50	0,85	0,63
1,45	0,57	0,84	0,58
1,42	0,54	0,82	0,57
1,46	0,54	0,85	0,52
1,47	0,57	0,87	0,63
1,49	0,56	0,86	0,59
1,47	0,58	0,84	0,58
1,46	0,58	0,80	0,56
1,47	0,56	0,87	0,59
1,50	0,56	0.86	0,55
1,50	0,53	0,84	0,56
1,51	0,49	0,84	0,54
1,53	0,52	0,84	0,58
1,46	0,51	0,83	0,60
1,44	0,56	0,82	0,53
1,48	0,54	0,84	0,59
1,57	0,58	0,88	0,58

		SPRING			
VYL	YL	GL	SL	TB	SB
2,14	2,74	1,52	0,58	0,87	0,52
2,15	2,83	1,55	0,58	0,84	0,63
2,14	2,85	1,64	0,58	0,86	0,67
2,18	2,85	1,48	0,46	0,87	0,65
2,07	2,80	1,59	0,60	0,86	0,67
2,16	2,63	1,54	0,58	0,88	0,70
2,12	2,80	1,55	0,57	0,87	0,64
2,07	2,78	1,61	0,58	0,86	0,59
2,13	2,85	1,59	0,57	0,89	0,65
2,14	2,88	1,56	0,59	0,85	0,66
2,15	2,86	1,58	0,61	0,86	0,64
2,08	2,77	1,49	0,57	0,87	0,67
2,11	2,68	1,54	0,56	0,88	0,68
2,16	2,85	1,50	0,58	0,86	0,63
2,14	2,86	1,60	0,58	0,84	0,59
2,14	2,91	1,58	0,60	0,86	0,61
2,17	2,90	1,54	0,59	0,86	0,67
2,15	2,83	1,55	0,58	0,89	0,65
2,09	2,83	1,58	0,57	0,89	0,65
2,14	2,74	1,59	0,57	0,90	0,62

	SUMMER		
GL	SL	TB	SB
2,54	0,50	0,90	0,64
2,51	0,48	0,90	0,64
2,53	0,49	0,91	0,63
2,58	0,52	0,92	0,64
2,54	0,47	0,93	0,65
2,56	0,51	0,89	0,65
2,59	0,50	0,90	0,64
2,53	0,45	0,91	0,65
2,54	0,52	0,92	0,62
2,52	0,50	0,91	0,63
2,55	0,46	0,91	0,64
2,55	0,49	0,88	0,62
2,57	0,49	0,93	0,62
2,54	0,52	0,92	0,64
2,54	0,50	0,91	0,65
2,55	0,49	0,90	0,64
2,56	0,46	0,90	0,64
2,56	0,47	0,91	0,64
2,53	0,47	0,92	0,65
2,54	0,49	0,89	0,63

	AUTUMN			BOBONONG
GL	SL	TB	SB	
2,12	0,52	0,94	0,75	2,44
2,09	0,54	0,96	0,75	2,51
2,26	0,49	0,93	0,76	2,45
2,08	0,49	0,93	0,75	2,43
2,14	0,51	0,98	0,74	2,43
2,02	0,50	0,97	0,75	2,46
1,97	0,50	0,93	0,71	2,43
2,02	0,50	0,91	0,78	2,45
1,84	0,52	0,91	0,74	2,47
2,05	0,51	0,88	0,74	2,45
2,11	0,54	0,93	0,76	2,56
2,12	0,50	0,93	0,71	2,45
2,06	0,55	0,97	0,75	2,46
2,10	0,54	0,94	0,76	2,48
2,05	0,54	0,90	0,70	2,54
2,04	0,51	0,92	0,79	2,44
2,02	0,51	0,94	0,77	2,48
2,09	0,52	0,98	0,77	2,53
2,06	0,50	0,89	0,71	2,50
2,05	0,53	0,94	0,75	2,49

CRUDE PROTEIN CONTENT FIGURES:

WINTER			
GL	SL	TB	SB
9,77	3,43	5,49	3,75
9,64	3,36	5,66	3,49
9,74	3,21	5,23	3,64
8,99	3,10	5,32	3,94
9,06	3,54	5,28	3,62
8,90	3,38	5,12	3,59
9,10	3,41	5,34	3,26
9,16	3,56	5,44	3,92
9,29	3,49	5,37	3,71
9,19	3,64	5,22	3,64
9,15	3,60	4,99	3,49
9,20	3,52	5,45	3,72
9,36	3,51	5,41	3,42
9,37	3,32	5,26	3,48
9,43	3,05	5,23	3,38
9,56	3,26	5,28	3,64
9,15	3,21	5,16	3,76
9,02	3,52	5,10	3,32
9,23	3,39	5,30	3,70
9,79	3,64	5,49	3,48

SPRING					
VYL	YL	GL	SL	TB	SB
13,34	17,15	9,50	3,59	5,45	3,26
13,46	17,70	9,68	3,65	5,26	4,00
13,40	17,80	10,24	3,64	5,40	4,20
13,62	17,80	9,26	2,92	5,47	4,08
12,92	17,47	9,92	3,74	5,39	4,18
13,49	16,45	9,65	3,63	5,49	4,36
13,24	17,47	9,67	3,58	5,43	4,02
12,95	17,32	10,06	3,65	5,34	3,70
13,31	17,80	9,91	3,54	5,54	4,05
13,40	17,97	9,75	3,66	5,28	4,13
13,46	17,87	9,86	3,80	5,37	4,03
12,99	17,34	9,31	3,54	5,45	4,18
13,20	16,76	9,64	3,49	5,51	4,25
13,49	17,80	9,37	3,60	5,39	3,92
13,40	17,87	9,99	3,63	5,28	3,70
13,40	18,20	9,86	3,75	5,39	3,80
13,58	18,14	9,64	3,70	5,37	4,19
13,46	17,70	9,67	3,65	5,55	4,09
13,06	17,70	9,86	3,54	5,57	4,05
13,40	17,14	9,91	3,56	5,61	3,86

SUMMER			
GL	SL	TB	SB
15,90	3,15	5,59	4,02
15,70	2,98	5,60	4,03
15,79	3,09	5,66	3,91
16,12	3,23	5,72	3,98
15,87	2,94	5,82	4,04
15,98	3,16	5,59	4,09
16,18	3,10	5,64	4,03
15,84	2,84	5,71	4,08
15,89	3,22	5,77	3,85
15,74	3,12	5,66	3,92
15,94	2,78	5,68	4,02
15,93	3,05	5,49	3,86
16,05	3,09	5,82	3,87
15,87	3,26	5,72	4,02
15,87	3,15	5,66	4,07
15,96	3,04	5,63	4,00
16,01	2,87	5,62	3,98
16,00	2,93	5,66	4,03
15,81	2,94	5,76	4,07
15,88	3,09	5,54	3,91

AUTUMN				BOBONONG
GL	SL	TB	SB	
13,25	3,26	5,88	4,68	15,28
13,07	3,36	5,98	4,69	15,69
14,13	3,09	5,80	4,78	15,29
13,00	3,05	5,79	4,67	15,17
13,35	3,21	6,15	4,63	15,16
12,64	3,16	6,09	4,68	15,40
12,30	3,11	5,83	4,46	15,20
12,60	3,10	5,68	4,85	15,29
11,49	3,27	5,70	4,66	15,41
12,84	3,22	5,52	4,61	15,34
13,19	3,37	5,81	4,74	15,98
13,25	3,13	5,79	4,47	15,29
12,85	3,42	6,05	4,68	15,38
13,13	3,38	5,87	4,73	15,52
12,79	3,35	5,64	4,40	15,34
12,75	3,21	5,75	4,92	15,25
12,62	3,20	5,88	4,84	15,51
13,09	3,24	6,14	4,79	15,80
12,86	3,10	5,56	4,46	15,65
12,84	3,32	5,85	4,70	15,58

TOTAL PHENOLIC CONTENT FIGURES:

WINTER				SUMMER			
GL	SL	TB	SB	GL	SL	TB	SB
213,19	295,76	426,49	144,50	183,49	298,05	479,24	110,09
208,60	304,93	426,49	130,73	185,78	259,06	486,12	110,09
208,60	304,93	431,08	135,21	185,78	302,64	483,83	116,97
201,72	311,81	424,20	139,79	183,49	298,05	481,54	114,68
194,84	307,22	428,78	144,38	183,49	298,05	476,95	119,27
206,31	318,69	419,60	144,38	176,49	259,06	479,24	116,97
206,31	323,28	426,49	148,97	185,78	295,76	479,24	107,80
213,19	304,93	424,20	142,09	188,07	302,64	483,83	114,68
208,60	309,52	421,90	139,79	183,49	295,76	488,42	114,68
204,01	314,10	421,90	144,50	183,49	259,06	483,83	123,85

AUTUMN				BOBONONG
GL	SL	TB	SB	
199,54	268,23	440,25	128,44	43,46
194,95	270,53	437,96	130,73	45,76
194,95	270,53	435,66	126,15	45,76
201,83	279,70	440,25	123,85	48,05
183,49	270,53	433,37	126,15	41,17
181,19	272,82	435,66	133,03	38,87
197,25	261,35	437,96	126,15	45,76
197,25	272,82	431,08	130,73	52,64
192,66	275,11	435,66	130,73	43,46
199,66	272,82	437,96	128,44	43,46

SPRING					
VYL	YL	GL	SL	TB	SB
201,83	151,38	176,49	272,82	444,84	107,80
199,54	142,20	176,49	270,53	437,96	110,09
184,78	144,50	176,49	277,41	451,72	91,63
197,25	151,38	181,08	272,82	447,13	89,33
183,49	146,79	172,02	291,17	442,54	100,80
178,78	149,08	176,49	286,58	460,89	105,39
192,66	144,50	178,78	275,11	449,43	98,51
197,25	153,67	172,02	272,82	444,84	103,10
190,37	151,38	176,49	284,29	449,43	109,98
194,95	142,20	176,49	291,17	449,43	105,39

CONDENSED TANNIN CONTENT FIGURES:

	WINTER		
GL	**SL**	**TB**	**SB**
74,23	70,63	64,63	58,63
74,23	71,83	65,23	58,03
74,83	73,03	63,43	55,02
74,23	71,83	64,43	57,43
74,23	70,63	64,43	58,63
74,83	70,03	66,43	59,23
74,23	69,43	64,63	58,03
73,63	72,43	64,63	57,43
76,03	70,03	66,43	58,63
74,23	71,83	65,23	56,83

	SUMMER		
GL	**SL**	**TB**	**SB**
57,43	67,03	69,43	57,43
61,63	69,43	70,03	58,03
59,83	68,83	69,43	59,83
65,23	71,83	67,03	58,03
66,43	73,63	67,03	56,83
64,63	70,63	68,23	59,83
63,43	70,03	70,03	59,23
66,43	68,23	67,63	60,43
64,03	70,03	70,63	58,63
62,83	68,23	65,23	58,63

	AUTUMN		
GL	**SL**	**TB**	**SB**
68,83	70,63	67,03	58,63
70,63	73,03	66,43	59,83
70,63	71,83	67,03	60,43
71,83	71,23	71,83	59,23
70,63	69,43	67,63	59,23
71,23	70,63	68,23	58,03
71,23	70,63	66,43	59,23
71,23	71,83	66,43	59,83
72,43	69,43	68,83	59,83
70,03	71,23	66,43	59,23

BOBONONG
46,02
47,82
47,22
50,82
50,22
50,22
47,82
45,42
49,62
50,22

		SPRING			
VYL	**YL**	**GL**	**SL**	**TB**	**SB**
68,83	57,43	81,44	68,23	67,03	60,43
68,83	62,83	82,64	67,63	67,03	62,83
70,03	59,83	79,63	68,23	65,83	62,83
71,23	61,03	80,23	68,23	66,43	62,23
70,63	64,43	77,23	70,03	67,63	59,83
72,43	64,03	77,83	70,03	67,03	61,63
68,23	64,03	77,83	68,23	67,03	61,63
72,43	62,83	80,23	68,23	65,83	59,83
73,03	62,83	82,04	67,03	64,63	61,03
70,63	58,63	81,44	67,63	67,03	62,83

PROTEIN PRECIPITATION CAPACITY FIGURES:

WINTER

GL	SL	TB	SB
42,25	72,25	25,00	36,00
36,00	81,00	36,00	42,25
36,00	72,25	49,00	42,25
42,25	72,25	56,25	36,00
42,25	64,00	49,00	42,25
36,00	72,25	49,00	36,00
42,25	64,00	36,00	36,00
36,00	81,00	49,00	42,25
36,00	72,25	36,00	36,00
36,00	81,00	56,25	36,00

SUMMER

GL	SL	TB	SB
42,25	64,00	25,00	42,25
49,00	56,25	30,25	36,00
36,00	64,00	30,25	36,00
42,25	90,25	30,25	42,25
42,25	90,25	36,00	42,25
42,25	64,00	25,00	36,00
42,25	64,00	25,00	36,00
36,00	64,00	36,00	42,25
36,00	56,25	36,00	42,25
42,25	72,25	30,25	36,00

AUTUMN

GL	SL	TB	SB
42,25	64,00	25,00	56,25
56,25	72,25	36,00	49,00
49,00	90,25	49,00	49,00
42,25	56,25	56,25	42,25
49,00	72,25	49,00	56,25
49,00	56,25	36,00	49,00
49,00	72,25	36,00	56,25
49,00	56,25	49,00	49,00
42,25	72,25	49,00	49,00
56,25	72,25	56,25	42,25

BOBONONG
25,00
25,00
25,00
36,00
36,00
25,00
25,00
36,00
25,00
25,00

SPRING

VYL	YL	GL	SL	TB	SB
110,25	56,25	64,00	64,00	56,25	42,25
90,25	56,25	72,25	72,25	72,25	36,00
110,25	64,00	72,25	72,25	56,25	42,25
132,25	56,25	64,00	72,25	72,25	49,00
110,25	64,00	81,00	81,00	49,00	56,25
110,25	56,25	72,25	81,00	56,25	36,00
90,25	56,25	72,25	81,00	56,25	42,25
110,25	64,00	64,00	72,25	72,25	42,25
110,25	56,25	72,25	71,00	72,25	56,25
90,25	56,25	64,00	72,25	49,00	49,00

APPENDIX TWO

NUMBER OF BRANCHES REMOVED FROM FIFTY MARKED TREES IN ELEPHANT VALLEY:

WINTER		SPRING		SUMMER		AUTUMN	
No.Yng	No.Old	No. Yng	No.Old	No.Yng	No.Old	No.Yng	No.Old
2	8	2	8	1	6	1	5
5	5	5	5	2	4	2	4
5	5	5	5	2	5	1	5
7	3	6	3	4	1	3	1
3	7	3	7	1	7	0	6
9	1	9	1	6	0	6	0
9	1	8	1	7	0	7	0
7	3	5	3	4	3	3	3
6	4	6	4	2	2	2	2
7	3	6	3	6	3	5	3
7	3	7	3	6	3	6	3
6	4	5	4	5	3	5	3
8	2	8	2	5	1	3	0
6	4	5	4	4	4	4	3
9	1	8	1	5	0	5	0
5	5	5	5	4	4	2	4
6	4	4	4	4	4	3	4
5	5	5	5	3	3	3	3
8	2	6	2	4	2	3	2
5	5	5	5	3	3	2	2
5	5	5	5	4	4	4	4
6	4	5	4	3	4	3	4
6	4	6	4	6	4	3	4
3	7	3	7	3	7	3	7
8	2	7	2	7	2	5	2
8	2	8	2	4	1	4	1
7	3	5	3	1	2	1	2
7	3	7	3	7	3	5	3
5	5	5	5	5	5	4	3
5	5	4	5	4	3	4	3
7	3	5	3	5	3	5	3
6	4	6	4	4	3	3	3
4	6	3	6	2	4	2	4
5	5	5	5	5	5	2	4
2	8	2	8	0	7	0	6
1	9	1	9	1	5	0	5
4	6	2	6	0	6	0	5
9	1	9	1	5	1	5	1
5	4	4	3	4	3	3	3
6	4	6	4	5	4	3	3
4	6	3	6	3	6	2	6
6	4	6	4	5	4	2	4
6	4	5	4	2	3	2	3
7	3	6	3	5	1	5	1
7	3	7	3	7	3	7	3
4	6	2	5	2	5	1	5
4	6	4	6	1	6	1	4
5	5	4	5	3	5	3	5
5	5	5	5	2	3	0	3
9	1	8	1	7	1	6	1

TOTALS:

WINTER	SPRING	SUMMER	AUTUMN
10	10	7	6
10	10	6	6
10	10	7	6
10	9	5	4
10	10	8	6
10	10	6	6
10	9	7	7
10	8	7	6
10	10	4	4
10	9	9	8
10	10	9	9
10	9	8	8
10	10	6	3
10	9	8	7
10	9	5	5
10	10	8	2
10	8	8	7
10	10	6	6
10	8	6	5
10	10	6	4
10	10	8	8
10	9	7	7
10	10	10	7
10	10	10	10
10	9	9	7
10	10	5	5
10	8	3	3
10	10	10	8
10	10	10	7
10	9	7	7
10	8	8	8
10	10	7	6
10	9	6	6
10	10	10	6
10	10	7	6
10	10	6	5
10	8	6	5
10	10	6	6
10	7	7	6
10	10	9	6
10	9	9	8
10	10	9	6
10	9	5	5
10	9	6	6
10	10	10	10
10	7	7	6
10	10	7	5
10	9	8	8
10	10	5	3
10	9	8	7

PERCENT MASS OF TWIG MATERIAL IN ELEPHANT FAECAL SAMPLES:

WINTER	SPRING	SUMMER	AUTUMN
11,0	8,6	10,3	10,7
8,8	10,5	11,6	10,9
7,0	10,7	14,0	9,3
7,5	7,3	9,5	10,7
14,2	8,9	12,2	11,5
9,6	9,3	13,6	8,4
11,5		13,3	10,7
7,1		8,8	8,6
10,6		11,5	7,2
9,7		13,2	12,3
9,3		11,6	8,3
7,6		12,8	6,6
9,3		8,7	12,6
10,7		13,7	10,8
11,7		15,2	12,4

APPENDIX THREE

PERCENT BARK REMOVED FROM MARKED TREES:

MAJALE	JWALA1	JWALA2	JWALA3	JWALA3
1,90	7,55	0,00	0,00	0,00
0,00	0,00	0,00	0,00	2,12
0,00	0,00	4,71	0,00	0,00
0,00	0,00	1,10	0,00	0,00
3,35	16,49	0,00	3,78	0,00
1,69	0,00	0,00	0,00	0,00
9,88	0,00	0,00	0,00	4,18
0,00	24,79	0,01	1,04	0,00
10,46	0,00	0,00	15,52	4,87
1,48	19,43	0,00	0,00	0,00
5,92	0,00	0,00	3,38	0,00
0,00	0,00	1,09	0,00	0,00
0,01	0,00	0,00	0,00	0,00
0,00	0,00	0,00	0,73	10,22
7,21	7,53	0,00	0,00	23,34
0,00	4,09	0,00	0,00	35,79
0,00	6,71	28,08	16,55	28,94
0,00	0,00	0,00	0,00	0,00
13,26	15,91	1,60	0,00	0,00
2,37	5,76	1,52	0,00	6,56
0,00	3,10	3,31	0,00	3,87
0,00	0,01	0,00	0,00	5,03
2,57	14,23	1,68	0,00	14,76
0,00	8,48	0,00	0,00	4,61
4,08	50,18	0,00	0,00	0,00
0,00	7,96	0,00	0,00	0,01
0,00	0,00	0,00	0,00	0,01
2,33	4,22	0,00	3,60	36,11
5,57	13,74	0,00	4,60	9,20
0,00	12,68	5,52	0,00	17,32
6,09	0,00	0,00	0,00	0,00
0,00	0,00	4,71	0,00	12,37
0,00	0,00	0,00	2,43	5,06
0,00	21,63	0,00	0,00	0,00
0,00	0,00	0,00	0,00	7,02
3,06	14,70	0,00	0,00	0,00
0,00	0,00	0,00	4,05	16,32
0,00	0,00	0,00	9,06	0,00
13,83	0,00	1,96	0,00	0,00
0,01	0,00	0,00	0,00	0,00
1,02	0,00	0,00	0,00	0,00
5,92	0,00	0,00	2,22	0,00
14,25	0,00	0,00	0,00	0,00
0,00	0,00	2,48	0,00	0,00
0,00	0,00	0,00	0,00	3,11
0,00	0,00	0,00	7,90	1,67
9,64	0,00	2,68	7,25	5,57
4,66	0,00	0,00	69,19	0,00
5,32	0,00	3,65	0,00	0,00
6,28	0,00	0,00	5,60	0,00

APPENDIX FOUR

EPIZOOCHORY: MOPANE DIASPORES

SEEDMASS	SURF.AREA	VOLUME
0,35	4,12	0,29
0,32	5,08	0,30
0,31	5,36	0,27
0,30	4,70	0,29
0,28	5,12	0,30
0,36	4,90	0,28
0,37	4,68	0,29
0,39	5,08	0,27
0,29	4,72	0,27
0,26	4,36	0,27
0,26	5,18	0,28
0,29	4,17	0,29
0,30	4,30	0,30
0,32	4,68	0,29
0,31	4,44	0,30
0,28	4,34	0,30
0,36	4,06	0,28
0,32	4,02	0,28
0,32	4,68	0,28
0,36	5,16	0,30
0,31	5,18	0,30
0,21	4,34	0,28
0,31	5,30	0,27
0,35	4,16	0,30
0,27	5,48	0,28
0,30	4,02	0,28
0,29	4,30	0,29
0,31	4,34	0,30
0,32	5,50	0,28
0,33	5,36	0,27
0,30	4,68	0,28
0,30	4,28	0,28
0,31	4,10	0,29
0,26	4,08	0,29
0,33	4,72	0,31
0,36	4,18	0,29
0,35	4,70	0,28
0,36	4,32	0,29
0,32	4,66	0,29
0,34	4,68	0,28
0,30	4,18	0,27
0,27	4,20	0,28
0,28	4,30	0,28
0,28	4,68	0,29
0,30	4,02	0,29
0,31	4,12	0,29
0,25	4,38	0,28
0,32	4,72	0,30
0,30	4,28	0,29
0,32	4,16	0,29

APPENDIX FIVE

PROPORTION OF BRANCHES WITH ANTS (AHM) ON THEM:

ZONE1	ZONE2	ZONE3	ZONE4	B.DIAM TREE	HT. TREE
0,67	0,38	0,08	0,14	18,00	310,00
0,43	0,57	0,56	0,09	44,00	520,00
0,60	0,60	0,20	0,43	32,00	480,00
0,46	0,22	0,38	0,00	25,00	360,00
0,38	0,36	0,18	0,00	38,00	650,00
0,22	0,47	0,27	0,00	24,00	220,00
0,67	0,20	0,18	0,00	54,00	750,00
0,22	0,80	0,21	0,00	76,00	580,00
0,09	0,33	0,08	0,00	29,00	190,00
0,60	0,55	0,43	0,00	48,00	340,00
0,29	0,50	0,44	0,00	31,00	350,00
0,57	0,38	0,18	0,00	38,00	390,00
0,33	0,58	0,63	0,00	33,00	460,00
0,00	0,27	0,00	0,00	29,00	250,00
0,00	0,19	0,00	0,00	35,00	280,00
0,00	0,57	0,00	0,00	18,00	310,00
0,00	0,38	0,00	0,00	37,00	460,00
0,00	0,44	0,00	0,00	21,00	450,00
0,00	0,13	0,00	0,00	22,00	510,00
0,00	0,38	0,00	0,00	29,00	530,00
0,00	0,25	0,00	0,00	26,00	360,00
0,00	0,30	0,00	0,00	39,00	670,00
0,00	0,11	0,00	0,00	48,00	820,00
0,00	0,60	0,00	0,00	11,00	230,00
0,00	0,29	0,00	0,00	19,00	370,00

RECORDS OF THE DISTANCE (cm) THE AHM WAS FROM THE GROWTH POINT OF THE BRANCHES:

0,00
0,00
0,00
0,00
0,00
0,00
8,50
10,00
3,00
0,00
0,00
0,00
0,00
0,00
0,00
0,00
0,00
5,50
4,00
3,50
4,00
7,50
8,00
6,50
0,00
4,50

0,00
0,00
0,00
2,50
9,00
0,00
0,00
2,50
1,00
8,00
3,00
2,50
0,00
0,00
11,00
4,00
0,00
0,00
0,00
0,00
0,00
3,00
8,00
6,50
1,00
14,00

1,50
4,00
3,50
5,00
0,00
0,00
0,00
1,50
1,50
11,50
15,00
0,00
8,00
3,50
12,00
0,00
0,00
3,00
13,00
2,50
3,00
8,00
1,50
1,50
1,00

0,00
8,00
0,00
0,00
15,00
3,50
0,00
0,00
4,00
24,00
5,50
0,00
0,00
0,00
8,00
2,50
1,00
13,00
6,50
3,00
0,00
0,00
11,00
8,00
3,00

7,00
4,50
8,00
19,00
2,50
0,00
0,00
9,00
11,00
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