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THE RELATIONSHIP BETWEEN ELEPHANTS AND THE RIVERINE TREE COMMUNITIES OF THE NORTHERN TULI GAME RESERVE, BOTSWANA

MSc UP 1993

The relationship between elephants and the riverine tree communities of the Northern Tuli Game Reserve, Botswana.

by

John William Malan

Submitted in partial fulfilment
of the requirements for the degree of
M.Sc (Zoology)

in the
Faculty of Science
University of Pretoria
Pretoria

November 1992

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by

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ABSTRACT

The species composition, and relative impact of elephants, on the riverine tree communities in the Northern Tuli Game Reserve, Botswana, were investigated. Elephants showed a preference for *Acacia tortilis*, *A. nigrescens*, *A. albida* and *Schotia brachypetala*. *Croton megalobotrys* rarely showed bark damage. Debarking predisposes trees to mortality. Relatively high mortality rates were recorded for preferred species. The dominance of *C. megalobotrys* may be attributable to a relatively low mortality rate, associated with a low level of bark utilization, and an apparently high recruitment. The riverine tree communities seem to have a retrogressive succession pattern towards monospecific *C. megalobotrys* stands, facilitated by elephant activity. The energy, phenolic or crude protein content of bark does not explained the species preference of elephants. Species with strong and pliable bark were preferred. However, the bark of preferred species was not necessarily strong and pliable.

ACKNOWLEDGEMENTS

I would like to thank the Botswana government, and in particular the Office of the President and the Department of Wildlife and National Parks, for extending their permission to conduct this project. I would also like to thank the Northern Tuli Game Reserve Association and its members and Mashatu Game Reserve for allowing me access to certain areas in the Reserve, for the purposes of this study. I would also like to sincerely thank Ted Steyn for granting me permission to stay at Naledi.

I would like to express my gratitude towards Prof. J.D. Skinner, the University of Pretoria and the Foundation for Research Development for financial assistance.

My sincere thanks to Andrew McKenzie for his supervision of this project. His valuable comments and assistance in the field were essential to the completion of this study.

I would also like to thank Christopher Styles for his assistance in the field, his valuable comments and for making the trips to Botswana so enjoyable. The assistance of Peet van Dyk and Kieran Kanavan in the field is also greatfully acknowledged.

I would like to express my gratitude to Prof. Braam van Wyk for his botanical advice and for his invaluable contribution to one of the chapters in this thesis. I would like to thank Lynn Du Toit for her invaluable assistance with the tannin assay techniques. I would like to thank the Council for Scientific and Industrial Research, and in particular Stephanie Dyer, for the species identification of dead wood collected in the field.

My sincere thanks to Tanya McKenzie and the boys for the wonderful times at Naledi. I would also like to thank Nellie Senyatso and William Tukishi for their help.

Last, but not least, I want to thank my family and friends for their support.

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Chapter 1

INTRODUCTION

The threat posed by elephants to the conservation of African woodlands became apparent during the 1960s and 70s. Attention mainly focused on areas undergoing marked vegetation changes such as in Budongo (Laws 1970; Laws, Parker & Johnstone 1975), Tsavo National Park (Glover 1963; Leuthold 1977), Serengeti National Park (Lamprey *et al.* 1967) and Luangwa Valley National Park (Lawton 1971; Caughley 1976). Due to their relatively large size and high mean age of survival, elephants are able to make relatively massive interventions in an ecosystem which may be of a long term nature (Watson & Bell 1968).

However, elephants may play an important role in the ecosystem. By thinning out the mature closed canopy of trees the regeneration and recruitment of species such as *Acacia tortilis*, which are unable to grow in the shade, are encouraged (Mwalyosi 1990). The activity of elephants may also benefit other browsers. For example, elephants cause pollard growth of *Colophospermum mopane* trees (Lawton 1971) and, thereby, bring the browse level down for themselves and other browsers. It is, therefore, imperative that quantitative data with respect to vegetation utilization by elephants, which in the present study refers to bark utilization, are collected to facilitate the assessment of damage, the detection of trends and the application of sound management decisions. As Barnes (1983) contends: "The state of a park in 10 or 20 years' time depends upon the events of today. In order to understand tomorrow's ecological and management problems we must study those that exist today".

During the early 1950s an intense culling programme was carried out south of Francistown, Botswana (Lind 1974). From this information, it would appear that elephants have been in the area now referred to as the Northern Tuli Game Reserve (NTGR) for at least 40 years. In the late 1960s and early 1970s around 1500 elephants were reported in the Reserve, utilizing a range of approximately 2 500 km^2 which extended into the Bamangwato territory in the north-west, the Tuli Circle in Zimbabwe to the north-east, and southwards into South Africa (Page 1990). In 1981 this range was reduced to approximately 1 200 km^2, due to the erection of a fence along the Tuli Block backline in an attempt to control foot-and-mouth disease in the area and the implementation of a policy confining elephants to the farms east of the Motloutse River. From censuses conducted in the NTGR since 1984 (Le Roux 1989), the elephant population appears to have remained fairly stable at approximately 1 per km^2. This density varies between years largely due to the movement of elephants across the borders of the Reserve into neighbouring areas, particularly in dry years when resource availability is low. In 1989, for example, approximately 200 elephants moved across the Shashe River, ending up on Sentinel and Knottingham ranches in Zimbabwe (Le Roux 1989). The present study was undertaken following observations by McKenzie (1986), which indicated the need for an in-depth investigation of the impact of elephants on riverine tree communities of the NTGR. The impact of elephants on only the large trees in these communities was investigated as these constitute the most important structural component of the riverine forests. Apart from their aesthetic qualities, the loss of this component of the riverine communities in the NTGR may lead to a reduction in raptor nesting sites, food sources for small mammals and a major food source for elephants and other browsers. For the purpose of the present study, large trees have been defined as trees with a stem circumference measured just above basal swelling in excess of one metre. The term large, rather than mature, was used because certain tree species (such as *Xanthocercis zambesiaca*) which have a stem circumference of one metre may not be mature, whereas other species (such as *Croton megalobotrys*) which are mature may have a stem circumference of less than one metre.

The main objectives proposed at the start of this study were:

1) to determine the extent to which the species composition of the riverine tree communities in the NTGR, with respect to large trees, have changed in the recent past, and to assess the nature of these changes;

2) to determine the relative importance of elephants as agents of large tree mortality in the riverine tree communities of the NTGR;

3) to determine the present level of recruitment to the large tree component of the riverine communities in the NTGR;

4) to investigate the relationship between the preferential utilization of bark by elephants and the fracture properties of the barks of large riverine tree species in the NTGR; and

5) to investigate the relationship between the preferential utilization of bark by elephants and the content of crude protein, energy and secondary plant metabolites in the barks of large riverine tree species in the NTGR.

Objectives one to three, four and five are dealt with in chapters 3, 4 and 5 respectively. Chapters 3 and 4 are in the form of papers (manuscript format) submitted to scientific journals. Details of materials and methods, references etc., for all contributions to this thesis, are presented in the individual contributions. A synthesis of the principal findings of this study are presented, in the order of the objectives mentioned above, under "General discussion" in Chapter 6. A list of publications to which references have been made in those parts of the text, other than in the manuscripts of papers, is presented at the end of each chapter. The various parts of this thesis have some stylistic inconsistencies. These are, however, primarily due to differences in layout and style required by the various journals.

There is often concern over the use of the term "damage" when referring to utilization of plant material by herbivores (Anderson & Walker 1974). In the present study, damage not only implies excessive or possibly destructive vegetation utilization by elephants but also all easily noticeable signs of bark utilization, whether excessive or not.

Aerial photographs taken of the riverine tree communities in the NTGR allowed the identification of the position of each tree sampled in May 1991, October 1991 and February 1992. During a relatively short period of time (May 1991-Feb 1992) three sources of information concerning the impact of elephants on the riverine tree communities of the NTGR were obtained using these photographs: tree mortality prior to 1986, tree mortality between 1986 and May 1991, and the mortality and damage to trees between May 1991 and February 1992. The latter period forms part of an extended dry season due to the relatively low rainfall (96.5 mm) recorded for the period November 1991 to February 1992 (usually the rainy season).

Not only has the information derived from the present study revealed the relatively large impact of elephants on the riverine tree communities of the NTGR, but may form the basis of future studies in the Reserve should these communities continue to be monitored.

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Chapter 2

STUDY AREA

STUDY AREA

Introduction

The study was undertaken in the Northern Tuli Game Reserve (NTGR), a private game reserve in the eastern corner of Botswana. A brief description of the Reserve is given in chapters 3 and 4. A more detailed description, particularly with reference to the remaining chapters, is given here.

Location

The 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 meet (Fig. 1). The Reserve constitutes the north-eastern extremity of a 350 km strip of private land known as the Tuli Block. The Reserve 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 Reserve consists of nine original farms, some of which have been divided into several portions. With the exception of fences shown in Fig. 2, the farms are unfenced.

Fig. 1. Location of the Northern Tuli Game Reserve.

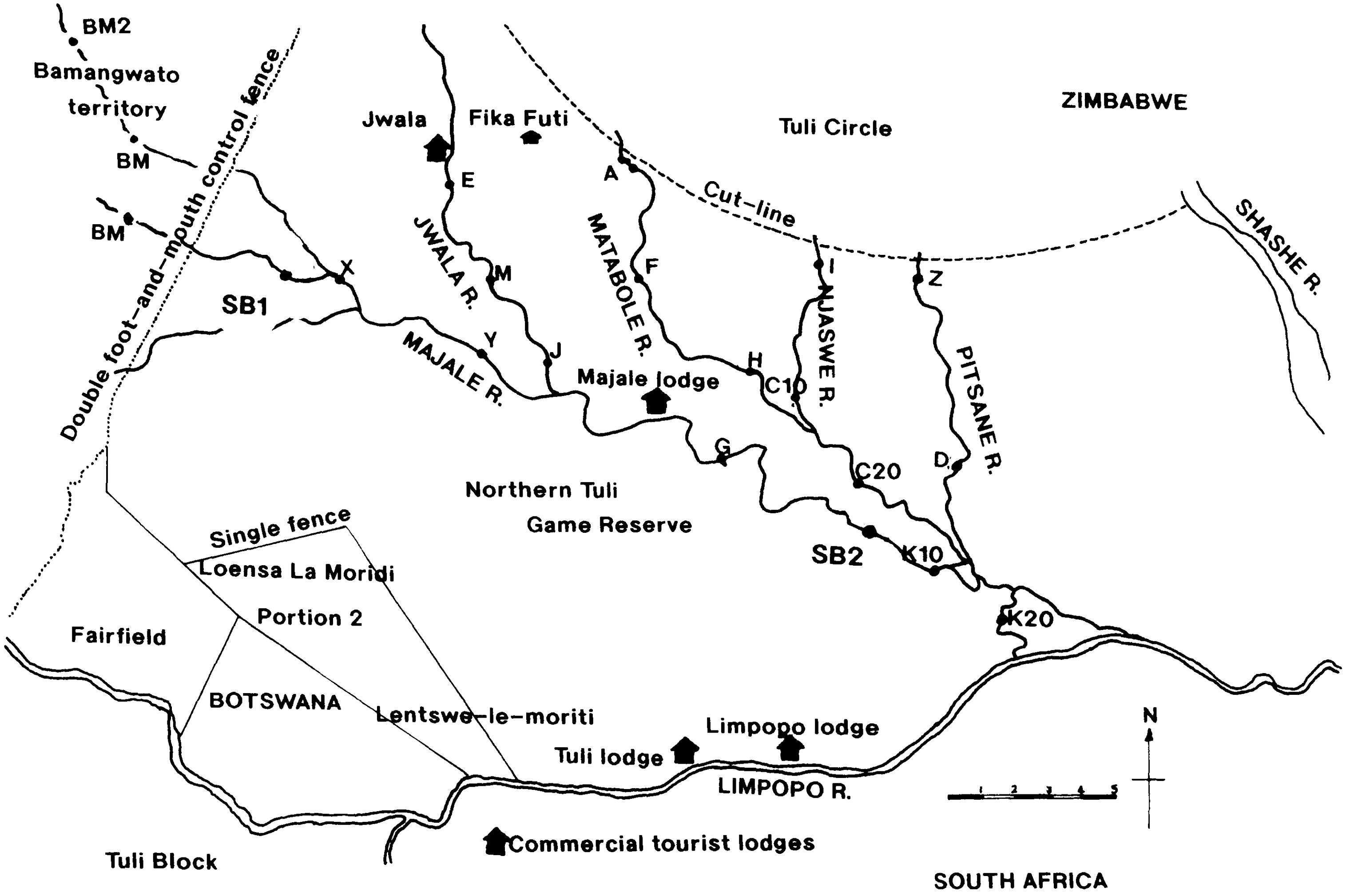

Fig. 2. Map of the study area showing the approximate location of the study sites located along the main rivers in the Northern Tuli Game Reserve.

Areas in the Reserve which are utilized for purposes other than as a conservation area include Fairfield, which is used for livestock farming, and Portion 2 of Loensa-la-Moridi incorporating the village of Lentswe-le-moriti, which is used for crop and pastoral production. The remainder of the Reserve is maintained as a private game reserve, comprising an area of approximately 65 000 ha. Together with the Tuli Circle Conservation Area, the total conserved area comprises approximately 100 000 ha.

The present study was undertaken at the sites depicted in Fig. 2, comprising a total of 16 sites in the NTGR and 3 sites outside the Reserve in the Bamangwato area.

Climate

The climate of the region incorporating the Reserve is semi-arid tropical with the rainfall being low and unpredictable (Harrison 1984). The long-term average rainfall is 369.5 mm (1965-1989), with peak rainfall years receiving up to 661 mm (1976) and low rainfall years receiving as little as 180 mm (1989). Rain mainly falls 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.

Ground surveys, for the purpose of the present study, were conducted during the dry season in May 1991, October 1991 and February 1992. For the rainy season that followed the 1991 dry season (Nov 1991-Feb 1992) only 96.5 mm rain was recorded (Pontdrift records, Department of Transport, Pretoria, South Africa).

Geology and soils

The description given here is derived from Joubert (1984) as described in McKenzie (1990).

The geological substratum of the Reserve is comprised of deep Clarens Sandstone formation overlain by Letaba and Sabi River basalt formations. Numerous east-west dolerite dikes intrude these strata.

The sandstone is only exposed along the southern extremities of the Reserve along the Limpopo and Motloutse rivers. The rest of the Reserve is dominated by basalt formations. Extensive alluvial plains occur along all the major rivers, including the lower Majale River.

Topography and drainage

The description given here is derived from McKenzie (1990).

The Reserve is extensively dissected by incisive drainage lines. Most of the Reserve is drained via the Majale River which terminates in the south-central portion of the Reserve where it enters the Limpopo River. Other minor rivers flow directly into the Motloutse, Limpopo and Shashe rivers. All these rivers flow only sporadically in summer and are dry, with the exception of 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 the sandstone formations in the south and west and by the dolerite dykes in other parts.

Vegetation

The vegetation of the Reserve falls within the broad classification of Mopane Veld (Acocks 1975). Characteristic trees in the riverine are mentioned in Chapter 3.

Prominent shrubs are *Diospyros lycioides* and *Acacia* *sweinfurthii.* The most characteristic grass species is *Enneapogon cenchroides*, with varying associations of *Setaria verticilliata*, *Cenchrus ciliaris*, *Urochloa mosambicensis*, *Cynodon dactylon*, *Panicum coloratum*, *Eragrostis* spp., *Aristida* spp. and *Digitaria* spp. *Sporobolus consimilis* occurs in discrete, seasonally indated, vleis.

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Chapter 3

THE RELATIONSHIP BETWEEN ELEPHANTS AND THE RIVERINE TREE COMMUNITIES OF THE NORTHERN TULI GAME RESERVE, BOTSWANA*

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* Submitted for publication in *African Journal of Ecology*

The relationship between elephants and the riverine tree communities of the Northern Tuli Game Reserve, Botswana.

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Summary

Bark damage to the large riverine trees in the Northern Tuli Game Reserve, Botswana, and the extent to which elephants have been responsible for changes in composition of the tree communities in this Reserve, was investigated. Species for which elephants had a preference included *Acacia tortilis*, *A. nigrescens* and in particular *Acacia albida* and *Schotia brachypetala*. Between 1986 and May 1991, a larger proportion of debarked individuals died than did undamaged individuals. Secondary damage from wood-borer insects contributed to this mortality, 80,5% of the debarked *Schotia brachypetala* trees investigated showing such damage. Unlike other species, *Croton megalobotrys* seems to be increasing in number. This is attributed to a relatively low mortality rate, likely to be associated with a low level of bark utilization by elephants, and what seems to be a high level of recruitment. It is suggested that there is a retrogressive succession pattern in the riverine tree communities of the Reserve towards monospecific stands of *C. megalobotrys*, which has been facilitated by the activity of elephants.

Key words: Trees, riverine, elephants, debarking, mortality, recruitment

Introduction

The striking effect that elephants have on their habitat is evident in many parts of eastern and southern Africa (Anderson & Walker 1974). Its relatively large size and high mean age of survival enable this species to make relatively massive interventions in an ecosystem which may be of a long-term nature (Watson & Bell 1968). It is, therefore, imperative that quantitative data on vegetation utilization by elephants are collected to facilitate the assessment of damage, detection of trends and application of sound management decisions.

Elephants in the Northern Tuli Game Reserve (NTGR) represent a "compressed" population, whose relative density may be considered excessive (Joubert 1984). From censuses conducted in the Reserve since 1984 (Le Roux 1989), the elephant population appears to have remained fairly stable at approximately 1 per km^2. Contrary to what Joubert (1984) suggests, both bulls and cows are responsible for bark damage to the trees in the NTGR (McKenzie 1986). In the process of bark removal, the cambial and secondary phloem tissues are torn away from the secondary xylem. This exposes the tree to wood-borer beetle and fungal attack, as well as affecting the carbohydrate supply link between the roots and leaves (Crawley 1983), often resulting in its death (Vesey-

Fitzgerald 1973; Afolayan 1975; Thomson 1975).

Large riverine trees are an asset to the NTGR, and, as such, enjoy conservation priority status (McKenzie 1986). A mortality rate in excess of their replacement rate would conflict with this status. Observations by McKenzie (1986) indicated the need for an investigation of the impact of elephants on the NTGR riverine tree communities. The large tree species preference by elephants in the NTGR, based on bark utilization, was therefore investigated in the present study. Only large trees were included in this study as these constitute the most important structural component of the riverine forests.

Field work for this study was conducted during the 1991 dry season, commencing in May 1991. During a relatively short period of time, using aerial photographs taken of the NTGR's riverine tree communities in 1986 (McKenzie 1986), three sources of information were obtained. These were: mortality prior to 1986; mortality and bark damage between 1986 and the start of the 1991 dry season (May); and bark damage and mortality that occurred during the 1991 dry season (May 1991-Feb 1992). The data are also important for future studies, should these communities continue to be monitored.

Study area

The NTGR lies in the eastern corner of Botswana between 21°55'S and 22°15'S, and 28°55'E and 29°15'E, where Botswana, South Africa and Zimbabwe meet (Fig. 3). The Reserve 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 veterinary control fence). The Reserve covers an area of approximately 60 000 ha, and is comprised of several privately owned farms which, with one exception, are unfenced.

Methods

Species composition and recruitment

A stratified sample of the NTGR's riverine tree communities, comprising 16 sites (Fig. 3), was examined in May 1991. Only sites along the main rivers in the Reserve were assessed; it is likely that elephant activity along the boundary rivers (Limpopo, Shashe and Motloutse) is subject to influence by human activity from adjoining populated areas. The first 200 large riverine trees, irrespective of state, encountered at each site, with the exception of site

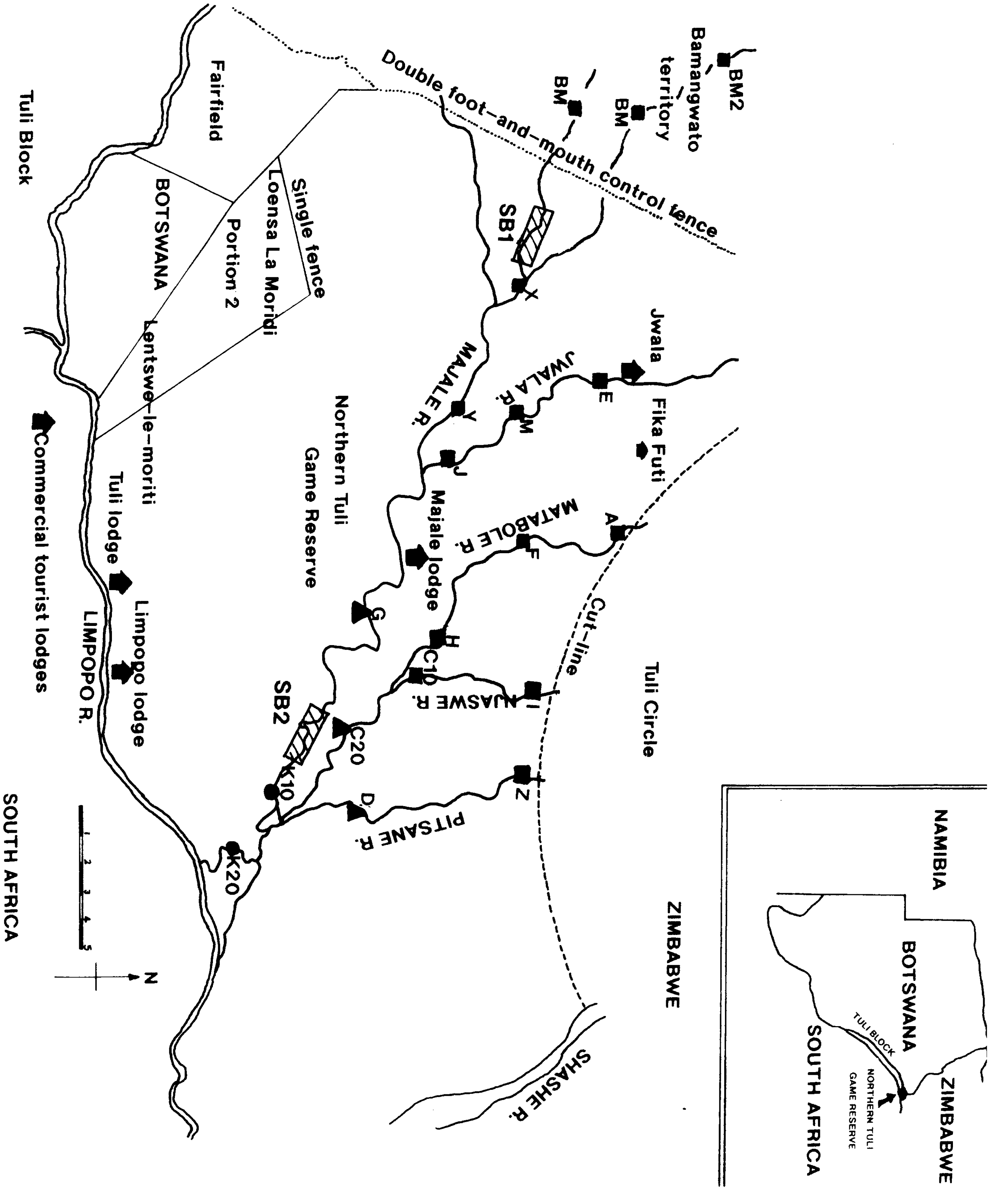


Fig. 3. Map of the Northern Tuli Game Reserve and surrounding areas showing the relative location of sites referred to in the text. ■ Northern zone, ▲ middle zone, ● southern zone. □ *Schotia brachypetala* sites

C10 (193 trees), were sampled. Large trees were defined as individuals with a stem circumference, measured just above basal swelling, equal to or exceeding 1 m.

A count of the number of recruitment class trees for the riverine species sampled was made. These were defined as individuals with a girth of less than 1 m and height equal to or exceeding 1 m. For comparative purposes, the species composition and number of recruitment class trees at three sites outside the Reserve (BM1, BM2 and BM3), located in the Bamangwato area (Fig. 3), were determined. For comparisons between the recruitment tree class components inside and outside the Reserve, only sites sampled in the northern zone of the Reserve were considered due to the similar species composition.

Bark utilization

In May 1991 the extent of debarking (also referred to as the percentage bark removed) of the large riverine trees was recorded. This was defined as the width of bark removed at the height where the greatest width of bark had been removed, expressed as a percentage of the trunk circumference at that height. This parameter was chosen because disruption of the vascular transport system between the roots and crown, as a result of bark removal, is likely to be proportional to the maximum width of bark removed. Relative to the time of sampling, the time of debarking in weeks (fresh damage) and/or months (recent damage), and/or years (old damage), was estimated. New damage mentioned in the text refers to trees with fresh and/or recent damage. These time criteria were confirmed as being reliably distinguishable from observations made on trees from which sections of bark had been removed by the investigator. Weeks-old damage was dark in colour (usually orange-red; sometimes yellow as in the case of *Croton megalobotrys*), and damp, due to the presence of sap, resin compounds and other exudates. Months-old damage was lighter in colour, less damp, and was usually accompanied by active bark healing and regeneration. Years-old damage was grey in colour and completely dry (bark regeneration no longer active). These time classes were used not to determine the precise time of debarking, but to provide a relative index of when debarking had occurred. Trees with damage inflicted during two or more of these time frames were recorded as trees showing repeated utilization. In October (usually the start of the rainy season) 1991 the trees sampled in May 1991 were revisited. Bark damage inflicted during the intervening period was recorded. Due to an extended dry season, these trees were revisited in February 1992 and assessed for bark damage inflicted since October.

Trees growing on cliff edges are inaccessible to elephants, while the trunks of trees on steep gradients, or in close proximity to other trees, may be only partially accessible (i.e., one side of the trunk may be accessible while the other side is inaccessible). In this study trees were recorded as "fully accessible", "partially accessible" or "inaccessible" to elephants, the former two being collectively termed "accessible".

Trees identified with weeks old damage in May 1991, October 1991 and February 1992 represented trees that were debarked during the month prior to each sampling period. Expressing the total number of trees identified with weeks old damage in May 1991, October 1991 and February 1992 as a percentage of the accessible living trees sampled, the rates of debarking in April/May 1991, September/October 1991 and January/February 1992, respectively, were calculated.

Preference ratios

Preference ratios (PR's) were calculated using the following equations as adapted from Petrides (1975):

$$PR = \frac{\text{Percentage utilization (U)}}{\text{Percentage availability (A)}}$$

where:

$$U = 100 \times \frac{\text{Number of trees of a particular species debarked at all sites sampled}}{\text{Number of trees of all species debarked at all sites sampled}}$$

and where:

$$A = 100 \times \frac{\text{Number of available trees of a species at all sites sampled}}{\text{Number of available trees of all species at all sites sampled}}$$

A preferred species was defined as one which is utilized proportionately more frequently than its availability in the environment suggests (Petrides 1975). Preference ratios were only calculated for species with ten or more individuals in the data set.

Schotia brachypetala sites

Observations made during the initial field survey suggested that the bark of *Schotia brachypetala* is particularly favoured by elephants. Two sites, one along the northern (SB1) and the other along the southern (SB2) section of the Majale River (see Fig. 3 for location) were quantitatively assessed for the impact of elephants on fully accessible large *S. brachypetala* trees. Twenty-five large trees, irrespective of state, were assessed for bark damage at each site. Visible evidence of wood-borer insect damage was also recorded. The extent of bark damage to these trees was not quantified.

Mortality

Dead trees with unequivocal signs of ringbarking, uprooting, or bark damage (determined from signs of bark regeneration or wood scarring), sometimes accompanied by the presence of wood-borer insect activity, were classified as trees with elephant damage.

Wood samples of dead trees, the identity of which could not be determined in the field, were taken and microscopically identified as described by Kromhout (1977). The time of death for these trees (pre-1986 or post-1986) was determined from low level black and white aerial photographs taken of thirteen NTGR sites (sites X, Y and Z excluded) in 1986 (McKenzie 1986). The annual mortality rates between 1986 and May 1991 (i.e., over five years) were calculated independently for each species using the equations:

$$UMR = 100 \times \frac{X}{5\,(X+N_u)}$$

and

$$EMR = 100 \times \frac{M}{5\,(M+N_e)}$$

where UMR = the mortality rate of tree without elephant damage; EMR = the mortality rate of trees with elephant damage; X = the number of undamaged trees that died between 1986 and May 1991; M = the number of trees unequivocally identified with signs of elephant damage that died during the same period of time; N_u = the number of accessible living trees that had no elephant damage in May 1991, and; N_e = the number of accessible living trees that had bark damage in May 1991.

Statistical tests

For the comparisons mentioned in the tables, differences were tested using a Fisher's exact G-test (Sokal & Rohlf 1981). Differences are assumed significant at the 5% level.

Mortality:

The following null hypotheses were tested:

1) There is no difference between the proportion of dead trees (death prior to May 1991) that had bark damage and the proportion of living trees debarked prior to May 1991.

2) There is no difference between the proportion of debarked trees that died (1986-May 1991) and the proportion of undamaged trees that died (1986-May 1991).

3) There is no difference between the proportion of single-stemmed debarked trees that died (1986-May 1991) and the proportion of multi-stemmed debarked trees that died (1986-May 1991).

Schotia brachypetala sites:

A Fisher's exact G-test was carried out to test the following null hypotheses:

1) The proportion of trees sampled at the southern site that had died does not differ significantly from the proportion of trees sampled at the northern site that had died.

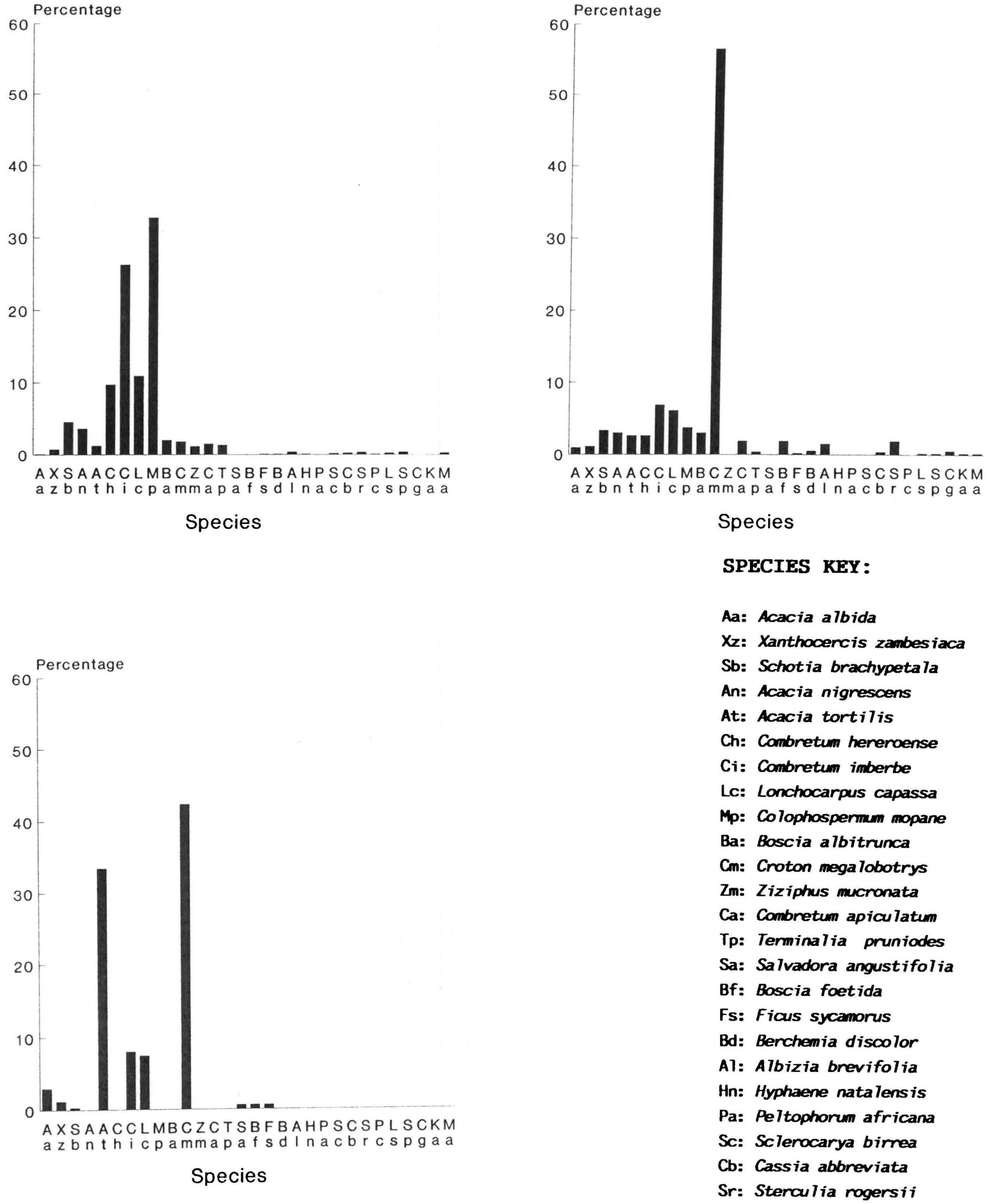
2) The proportion of accessible living trees at the southern site that had bark damage does not differ significantly from the proportion of accessible living trees at the northern site that had bark damage.

3) The proportion of debarked trees at the southern site that had wood-borer insect damage does not differ significantly from the proportion of debarked trees at the northern site that had wood-borer insect damage.

Results

Species composition

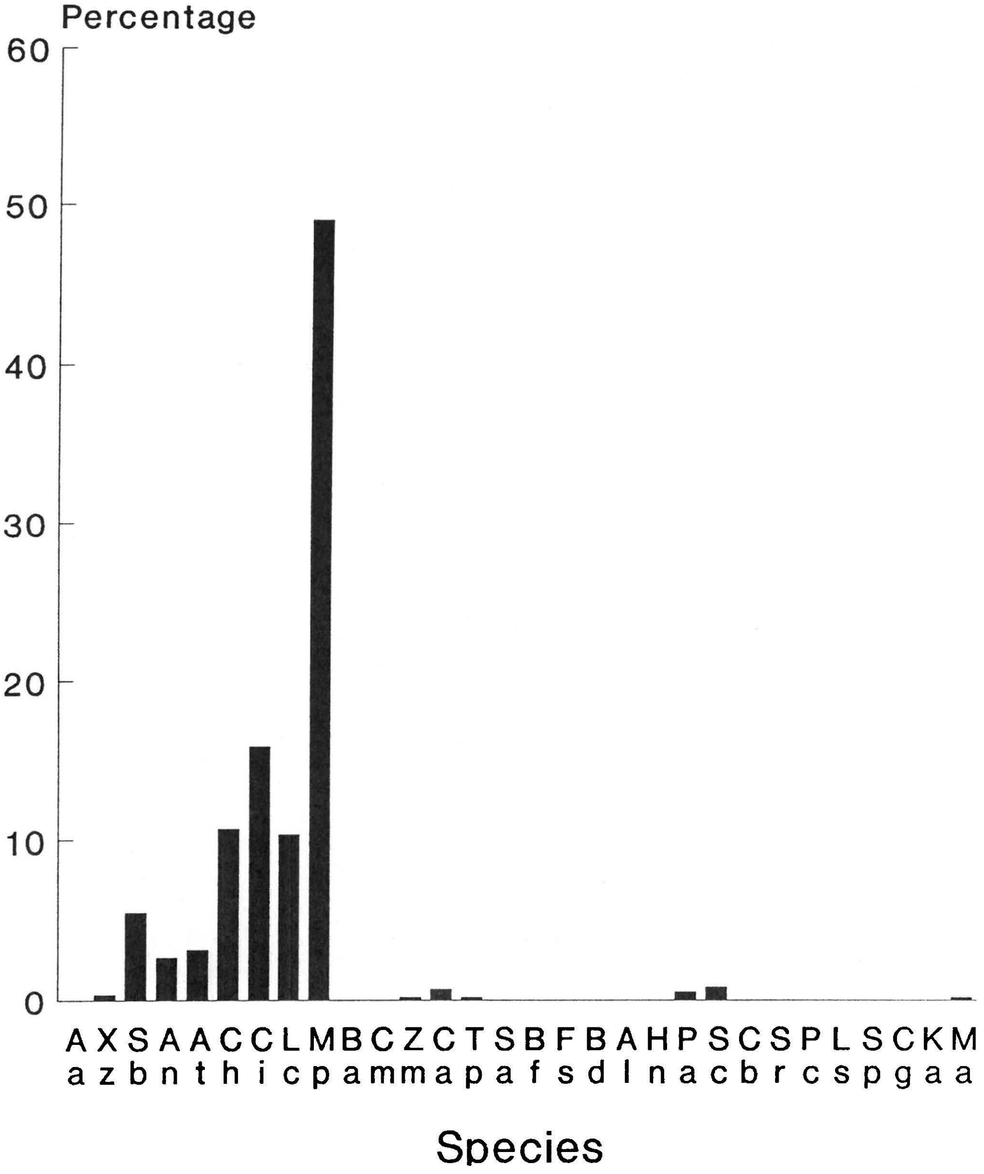
In May 1991, 2694 living large trees comprising 29 species were sampled. Species comprising 20% or more of the species composition at a site were defined as dominant. Using this parameter, sites were classified into three zones (Fig. 3): the northern zone, the sites of which are dominated by *Combretum imberbe* and/or *Colophospermum mopane*; the middle zone, the sites of which are dominated by *Croton megalobotrys*; and the southern zone, the sites of which are dominated by *C. megalobotrys* and *Acacia tortilis*. *Colophospermum mopane* is dominant at all sites outside the Reserve. The species composition at the sites inside and outside the Reserve are given in Figs 4a, b & c and Fig. 5 respectively.



SPECIES KEY:

Aa:	*Acacia albida*
Xz:	*Xanthocercis zambesiaca*
Sb:	*Schotia brachypetala*
An:	*Acacia nigrescens*
At:	*Acacia tortilis*
Ch:	*Combretum hereroense*
Ci:	*Combretum imberbe*
Lc:	*Lonchocarpus capassa*
Mp:	*Colophospermum mopane*
Ba:	*Boscia albitrunca*
Cm:	*Croton megalobotrys*
Zm:	*Ziziphus mucronata*
Ca:	*Combretum apiculatum*
Tp:	*Terminalia pruniodes*
Sa:	*Salvadora angustifolia*
Bf:	*Boscia foetida*
Fs:	*Ficus sycamorus*
Bd:	*Berchemia discolor*
Al:	*Albizia brevifolia*
Hn:	*Hyphaene natalensis*
Pa:	*Peltophorum africana*
Sc:	*Sclerocarya birrea*
Cb:	*Cassia abbreviata*
Sr:	*Sterculia rogersii*
Pc:	*Pappea capensis*
Ls:	*Lannea sweinfurthii*
Sp:	*Spirostachys africana*
Cg:	*Commiphora glandulosa*
Ka:	*Kirkia acuminata*
Ma:	*Markhamia acuminata*

Fig. 4. Species composition of the large riverine tree communities in the northern (a), middle (b) and southern (c) zones of the Northern Tuli Game Reserve (sample sizes are given in Appendix A).



SPECIES KEY:

Aa: *Acacia albida*
Xz: *Xanthocercis zambesiaca*
Sb: *Schotia brachypetala*
An: *Acacia nigrescens*
At: *Acacia tortilis*
Ch: *Combretum hereroense*
Ci: *Combretum imberbe*
Lc: *Lonchocarpus capassa*
Mp: *Colophospermum mopane*
Ba: *Boscia albitrunca*
Cm: *Croton megalobotrys*
Zm: *Ziziphus mucronata*
Ca: *Combretum apiculatum*
Tp: *Terminalia pruniodes*
Sa: *Salvadora angustifolia*
Bf: *Boscia foetida*
Fs: *Ficus sycamorus*
Bd: *Berchemia discolor*
Al: *Albizia brevifolia*
Hn: *Hyphaene natalensis*
Pa: *Peltophorum africana*
Sc: *Sclerocarya birrea*
Cb: *Cassia abbreviata*
Sr: *Sterculia rogersii*
Pc: *Pappea capensis*
Ls: *Lannea sweinfurthii*
Sp: *Spirostachys africana*
Cg: *Commiphora glandulosa*
Ka: *Kirkia acuminata*
Ma: *Markhamia acuminata*

Fig. 5. Species composition of the large riverine tree communities outside the Northern Tuli Game Reserve (sample sizes are given in Appendix A).

Recruitment

Ratios of the number of recruitment class trees to the number of large trees (only species with five or more large trees) are given in Table 1. The number of recruitment class trees (all sites) of only two species (*Acacia tortilis* and *Croton megalobotrys*) exceed the number of large trees. A similar pattern was found when considering only those trees in the northern zone of the Reserve. With the exception of *Schotia brachypetala*, the number of recruitment class trees outside the Reserve exceed the number of large trees.

The number of recruitment class trees at the three sites outside the NTGR (for species with five or more recruitment class trees) were compared with the number of recruitment class trees in the northern zone of the NTGR (see Appendix B). No difference ($U = 21$, $n_1 = 3$ and $n_2 = 11$, $P > 0.1$, Mann-Whitney *U*-test) was found for *Combretum imberbe*. Significant differences were found for *Lonchocarpus capassa* ($U = 0$, $n_1 = 3$ and $n_2 = 11$, $P < 0.05$, Mann-Whitney *U*-test), *Acacia nigrescens* ($U = 0$, $n_1 = 3$ and $n_2 = 11$, $P < 0.05$, Mann-Whitney *U*-test) and *Acacia tortilis* ($U = 1$, $n_1 = 3$ and $n_2 = 11$, $P < 0.05$, Mann-Whitney *U*-test), a larger number of recruitment class trees occurring outside the NTGR than in the northern zone of the Reserve.

Table 1. Number of recruitment class trees per 100 large trees sampled at all sites in the Northern Tuli Game Reserve, at the sites in the northern zone of the Reserve and at sites outside the Reserve.

	Inside					
	No. of trees at all sites		No. of trees in the northern zone		No. of trees outside	
Species	Large	Recruit/ 100 large	Large	Recruit/ 100 large	Large	Recruit/ 100 large
Croton megalobotrys	489	871	33	967	0	0*
Acacia tortilis	149	527	41	198	19	1547
Combretum imberbe	543	80	479	89	82	105
Combretum apiculatum	6	33	4	50	0	5*
Lonchocarpus capassa	257	27	199	32	62	121
Lannea sweinfurthii	5	20	4	25	0	0*
Acacia nigrescens	83	7	66	0	16	281
Xanthocercis zambesiaca	23	4	13	0	2	0*
Schotia brachypetala	102	3	83	4	33	0
Acacia albida	16	0	1	0	0	0*
Albizia brevifolia	15	0	7	0	0	0*

* = total number of recruitment class trees

Mortality

Given in Table 2 are the percentages of all trees sampled in May 1991 that had died (death prior to May 1991). For six species (*Xanthocercis zambesiaca*, *Schotia brachypetala*, *Acacia albida*, *A. tortilis*, *A. nigrescens*, *Combretum imberbe* and *Albizia brevifolia*), more than 20% of the specimens sampled were dead. For nine of the 14 species in which dead individuals were identified with elephant damage, more trees had elephant damage than did not have damage. For *Combretum imberbe*, 61.8% of the dead trees had no elephant damage. Of the dead trees from which wood samples were collected three species (*Acacia burkei*, *A. caffra* and *Tarchonanthus trilobus*), previously unrecorded in the Reserve, were identified in the laboratory (Table 2). Wood-borer insect damage following bark removal by elephants was identified in each of these individuals.

The percentages of accessible dead trees recorded in May 1991 with elephant inflicted bark damage are given in Table 3. Also given are the percentages of accessible living trees recorded as debarked in May 1991. For *Acacia tortilis*, *Lonchocarpus capassa*, *Colophospermum mopane* and *Croton megalobotrys*, a larger proportion of accessible dead trees with bark damage was recorded than accessible living trees with bark damage. No differences were found for the remaining species.

Table 2. Comparison between the proportion of trees sampled in May 1991 that were dead and had elephant damage and the proportion of trees sampled that were dead and had no elephant damage.

Species	No. of dead trees with elephant damage	No. of dead trees with no damage	% of trees that were dead and had no elephant damage	% of trees that were dead and had elephant damage
Acacia albida	4	8	14.3	28.6
Xanthocercis zambesiaca	4	9	11.1	25.0
Schotia brachypetala	17	39	10.8	24.7
Acacia nigrescens	64	68	29.8	31.6
Acacia tortilis	11	45	5.4	22.0
Combretum hereroense	6	2	3.0	1.0
Combretum imberbe	98	50	14.2	7.2
Lonchocarpus capassa	5	8	1.9	5.9
Colophospermum mopane	11	16	1.7	2.5
Boscia albitrunca	2	1	3.6	1.8
Croton megalobotrys	4	7	0.0	0.0
Ziziphus mucronata	0	1		
Combretum apiculatum	1	0		
Albizia brevifolia	6	3	25.0	12.5
Acacia burkei	1			
Acacia caffra	1			
Tarchonanthus trilobus	1			

Table 3. Comparison between the proportion of accessible dead trees sampled in the Northern Tuli Game Reserve in May 1991 with bark damage and the proportion of accessible living trees sampled in this Reserve in May 1991 with bark damage. G = Fisher's exact G-test values.

	No. of accss. lvng trees		No. of accss. dead trees		% of accss. dead trees with bark damge	% of access. living trees with bark damge	
Species	Bark damge	No damge	Bark damge	No damge			G
Acacia albida	14	2	8	4	87.5	66.7	1.8
Xanthocercis zambesiaca	17	4	9	4	69.2	81.0	0.6
Schotia brachypetala	64	36	34	17	66.7	64.0	0.1
Acacia nigrescens	34	45	40	64	38.5	43.0	0.4
Acacia tortilis	29	118	44	11	80.0	19.7	63.3^{s}
Combretum hereroense	38	151	1	6	14.3	25.0	0.5
Combretum imberbe	115	421	32	98	24.6	21.5	0.6
Lonchocarpus capassa	67	189	7	5	58.3	26.2	5.2^{s}
Colophospermum mopane	121	496	12	11	52.2	19.6	11.5^{s}
Croton megalobotrys	23	465	4	7	36.4	4.7	10.2^{s}
Albizia brevifolia	1	11	3	6	50.0	9.1	2.1

s = significant difference, $P < 0.05$

Given in Table 4 are comparisons (for the trees sampled at the sites photographed in 1986) between the proportion of debarked trees that died between 1986 and May 1991 and the proportion of undamaged trees that died between 1986 and May 1991. Dead multi-stemmed individuals were only found for *Croton megalobotrys* and *Acacia tortilis*. The percentage of debarked single-stemmed *A. tortilis* trees that died between 1986 and May 1991 exceeds that found for multi-stemmed individuals (Table 4). No difference was found for *Croton megalobotrys*.

Table 4. Comparison between the death of accessible debarked and undamaged trees and between the death of debarked single-stemmed and multi-stemmed trees between 1986 and May 1991 at sites photographed in 1986. G = Fisher's exact G-test values.

Species	No. of access. trees that died: 1986-1991		No. of living, access. trees		1986-May 1991		G
	Bark dam.	No bark dam.	Bark dam.	No bark dam.	% of deb., accss trees that died	% of undam., accss trees that died	
Xanthocercis zambesiaca	2	0	11	4	15.4	0.0	1.2
Schotia brachypetala	4	0	36	24	10.0	0.0	3.9^s
Acacia nigrescens	5	0	26	38	16.1	0.0	8.5^s
Acacia tortilis	30	3	29	101	51.7	22.3	55.3^s
Combretum hereroense	0	2	37	109	0.0	1.8	1.2
Combretum imberbe	6	1	104	325	5.5	0.3	11.6^s
Lonchocarpus capassa	3	0	57	148	5.0	0.0	7.6^s
Colophospermum mopane	1	0	70	400	1.4	0.0	3.8
Croton megalobotrys	2	1	20	444	38.9	0.2	8.7^s
Albizia brevifolia	0	3	1	10	0.0	23.1	0.5

Species	No. of dead, accss. trees with bark damage		No. of livng, accss. trees with bark damage		1986-May 1991		G
	S/stm	M/stm	S/stm	M/stm	% of deb., accss S/stm trees that died	% of deb., accss. M/stm trees that died	
Croton megalobotrys	1	1	6	14	14.3	6.7	0.3
Acacia tortilis	21	9	13	16	61.8	36.0	3.9^s

s = significant difference, P < 0.05

Table 5. Annual mortality rates of large trees with elephant damage for the period 1986 to May 1991.

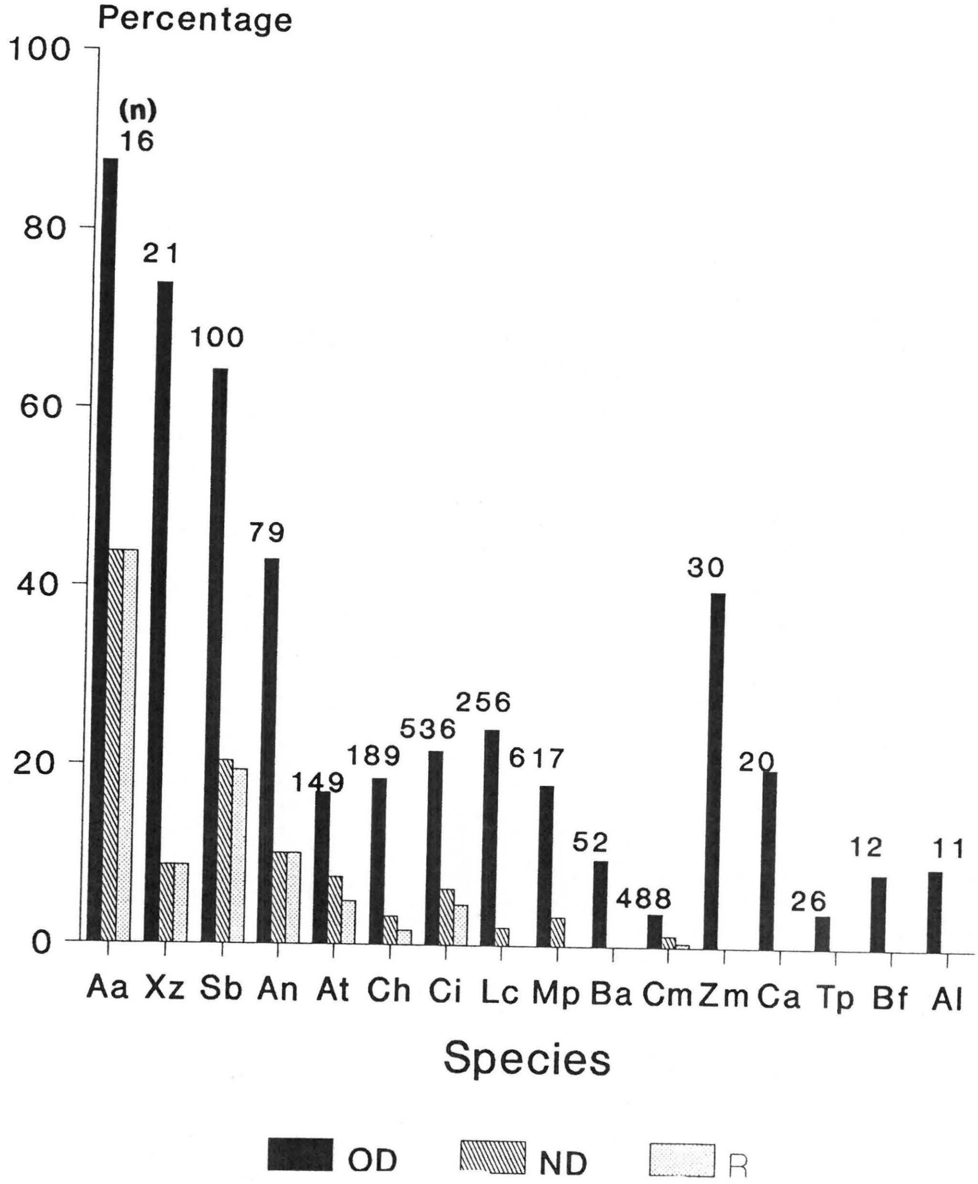
Species	No. of trees with elephant damage that died: 1986-1991	Annual mortality rate (%): 1986-1991	
		Elephant damage	No damage
Xanthocercis zambesiaca	2	3.1	0.0
Schotia brachypetala	4	2.0	0.0
Acacia nigrescens	5	3.2	0.0
Acacia tortilis	31	10.3	0.6
Combretum hereroense	0	0.0	0.3
Combretum imberbe	6	1.1	0.1
Lonchocarpus capassa	3	1.0	0.0
Colophospermum mopane	1	0.3	0.0
Croton megalobotrys	2	1.8	0.0

Of the trees that died between 1986 and May 1991, 84.3% had elephant damage. This is a significantly larger proportion (G = 19.3, df = 1, P < 0.001, Fisher's exact G-test) than that of trees that died prior to 1986 (43%). *Acacia tortilis* had the highest mortality rate (see Table 5) for trees with elephant damage (comprises 57.4% of sample of all dead trees that had elephant damage). Of the trees that died prior to 1986 that had elephant damage, only 6.8% were *A. tortilis*, and 25.2%, 13.6% and 32% were *Combretum imberbe*, *Schotia brachypetala* and *Acacia nigrescens* respectively.

Bark utilization

Twenty-one percent of the accessible living trees sampled in May 1991 had bark damage; 3.3% of the trees had damage in excess of 50% of their trunk circumference. Given in Fig. 6 are the percentages of accessible trees with new damage and old damage (only species with ten or more debarked trees). The species for which the largest percentage of trees had been debarked (both old and new damage) include *Acacia albida*, *Xanthocercis zambesiaca*, *Schotia brachypetala* and *Acacia nigrescens* (Fig. 6).

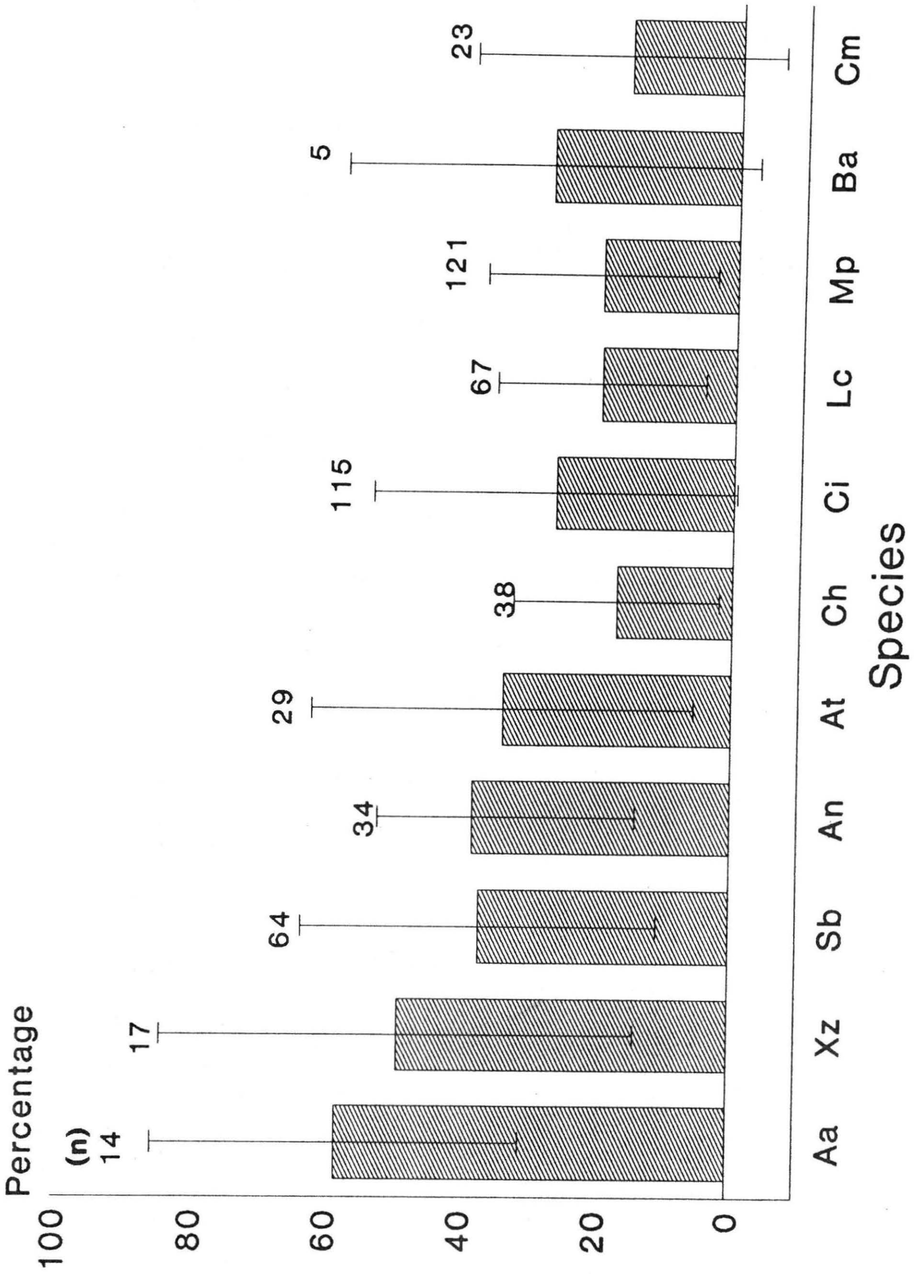
Given in Fig. 7 is the extent of bark utilization per species. The data concerning percentage bark removed per tree, were grouped into two categories of trees, irrespective of species: preferred and non-preferred species classes (see Fig. 8). A comparison between these two data sets revealed that the percentages of bark removed from trees in the preferred species class (28.7 ± 24.9) exceeded ($Z = 3.8$, $n_1 = 144$ and $n_2 = 377$, $P < 0.001$, Mann Whitney *U*-test) that of trees in the non-preferred species class (18.9 ± 16.9). It is evident from Fig. 7 that there is considerable variation between trees of a species with respect to the percentage of bark removed.



SPECIES KEY:

Aa: *Acacia albida*
Xz: *Xanthocercis zambesiaca*
Sb: *Schotia brachypetala*
An: *Acacia nigrescens*
At: *Acacia tortilis*
Ch: *Combretum hereroense*
Ci: *Combretum imberbe*
Lc: *Lonchocarpus capassa*
Mp: *Colophospermum mopane*
Ba: *Boscia albitrunca*
Cm: *Croton megalobotrys*
Zm: *Ziziphus mucronata*
Ca: *Combretum apiculatum*
Tp: *Terminalia pruniodes*
Bf: *Boscia foetida*
Al: *Albizia brevifolia*

Fig. 6. Percentages of accessible trees identified in May 1991 with signs of old (OD) and new (ND) damage in the Northern Tuli Game Reserve. Also indicated are the percentages of accessible trees sampled in May 1991 with signs of repeated utilization (R).



SPECIES KEY:

Aa: *Acacia albida*
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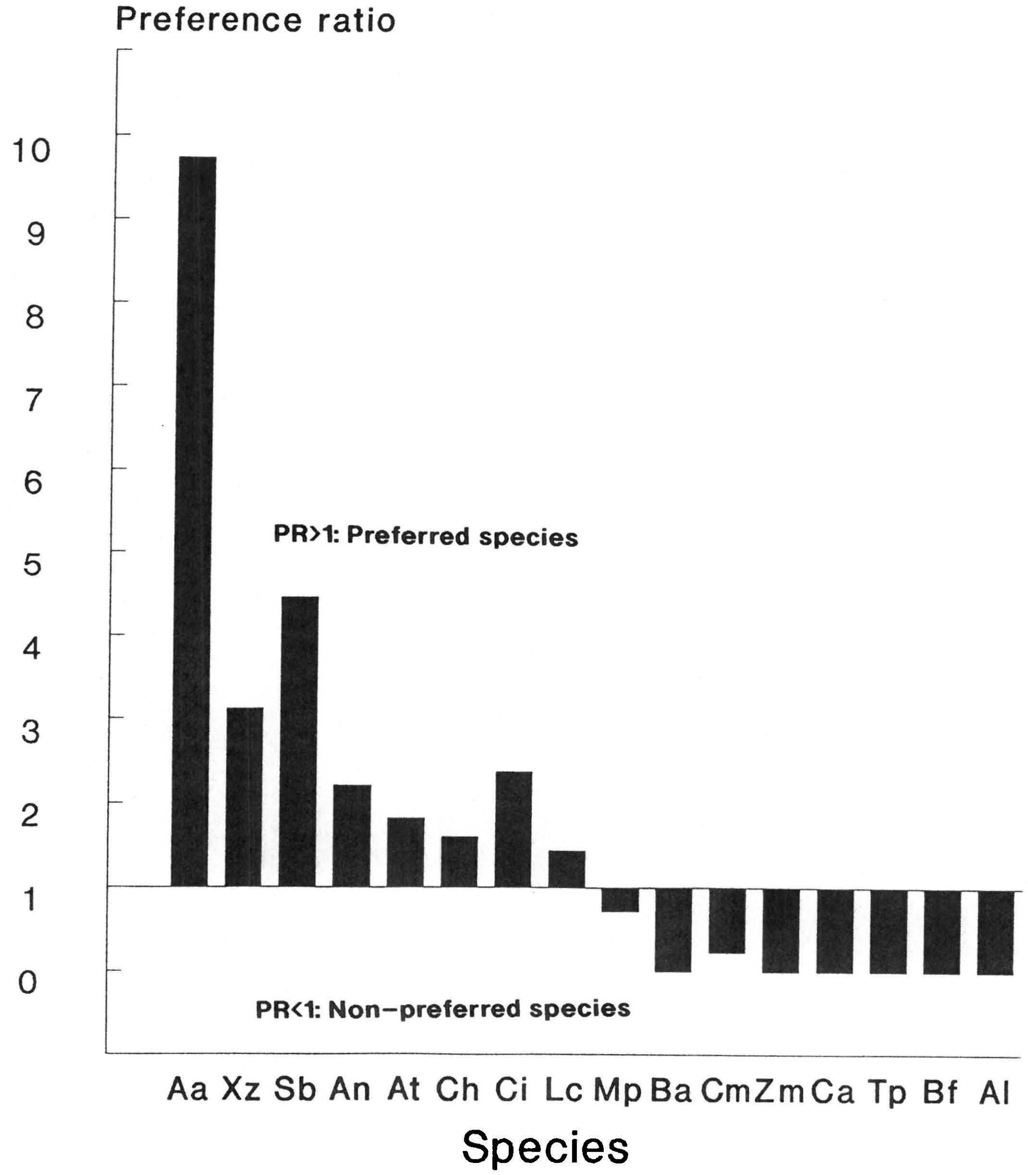
An: *Acacia nigrescens*
At: *Acacia tortilis*
Ch: *Combretum hereroense*
Ci: *Combretum imberbe*
Lc: *Lonchocarpus capassa*
Mp: *Colophospermum mopane*
Ba: *Boscia albitrunca*
Cm: *Croton megalobotrys*

Fig. 7. Mean (± SD) percentage bark removed from trees with bark damage.

The monthly rates of debarking for April/May 1991, September/October 1991 and January/February 1992 was 0.7%, 0.6% and 0.8% respectively.

Preference ratios

Old damage may include damage that has accumulated over many years. To prevent a bias in results, the preference ratios were calculated (Fig. 8) based only on those trees with new damage. Elephants show a preference for the bark of *Combretum imberbe*, *Acacia nigrescens*, *A. tortilis*, *A. albida*, *Schotia brachypetala* and *Xanthocercis zambesiaca*, that of the latter three species being markedly preferred. Relative to its abundance, very few *Croton megalobotrys* trees had been debarked by elephants.



SPECIES KEY:

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Xz: *Xanthocercis zambesiaca*
Sb: *Schotia brachypetala*
An: *Acacia nigrescens*
At: *Acacia tortilis*
Ch: *Combretum hereroense*
Ci: *Combretum imberbe*
Lc: *Lonchocarpus capassa*

Mp: *Colophospermum mopane*
Ba: *Boscia albitrunca*
Cm: *Croton megalobotrys*
Zm: *Ziziphus mucronata*
Ca: *Combretum apiculatum*
Tp: *Terminalia pruniodes*
Bf: *Boscia foetida*
Al: *Albizia brevifolia*

Fig. 8. Preference ratios (PR's) for the bark of large riverine trees sampled in May 1991 in the Northern Tuli Game Reserve.

Schotia brachypetala sites

Given in Table 6 are the results obtained from data collected at two sites in the Reserve, one along the northern and the other along the southern section of the Majale River. A larger proportion of trees were recorded as dead in the southern site than in the northern site. The proportion of accessible living trees in the southern site with bark damage (100%) exceeds the proportion of accessible living trees in the northern site with bark damage (45.8%). The proportion of debarked trees that had wood-borer insect damage in the northern site does not differ from the proportion of debarked trees that had wood-borer insect damage in the southern site.

Table 6. Comparisons between the northern and southern sections of the Majale River, with respect to the number of accessible *Schotia brachypetala* trees that were dead, the proportion of accessible living trees that had bark damage and the proportion of accessible debarked trees that had secondary damage inflicted by wood-borer insects. G = Fisher's exact G-test values.

Site	No. dead	No. living	Living trees with bark damage (%)	Debarked trees with wood-borer insect damage (%)
Southern site	15	10	100.0	80.0
Northern site	1	24	45.8	81.8
G	11.7^{s}		12.1^{s}	0.0

s = significant, $P < 0.05$

Discussion

Utilization of bark

In southern Africa, browse forms an important part of the diet of elephants during the dry season (Anderson & Walker 1974), particularly towards the end of this season (Buechner & Dawkins 1961; Williamson 1975; Guy 1976; Barnes 1982) when the grasses have withered and the trees have shed their leaves. During the present study, however, no difference (G = 0.01%, df = 1, P > 0.05, Fisher's exact G-test) was found between the rate of debarking in September/October 1991 and earlier in the dry season (April/May 1991).

A larger proportion of debarked single-stemmed *Acacia tortilis* trees than debarked multi-stemmed *A. tortilis* trees died (1986-May 1991). It is suggested that multi-stemmed trees have a higher likelihood of long-term survival than single-stemmed trees. This may be attributable to the fact that multi-stemmed individuals have sections of bark located between the stems which are inaccessible to elephants, thus allowing continued translocation of sap between the roots and the leaves.

As found in other studies (Caughley 1976; Short 1981; Barnes 1983; Jachmann & Bell 1985; Lewis 1986; Viljoen

1989), the NTGR elephants show a preference for the bark of certain tree species. Species identified as preferred during the present study include *Xanthocercis zambesiaca*, *Schotia brachypetala*, *Acacia albida*, *A. nigrescens* and *A. tortilis*. Individuals of these species are repeatedly utilized (Fig. 6), the extent of debarking in the preferred species exceeding that of non-preferred species. In particular, *Xanthocercis zambesiaca*, *Schotia brachypetala* and *Acacia albida* (species markedly preferred by elephants), when debarked have had, on average, bark removed from more than 33.3% of the trunk circumference. In contrast, although heavily browsed by elephants in the Kruger National Park (Van Wyk & Fairall 1969), *Croton megalobotrys* rarely showed signs of debarking in the NTGR, and when debarked had on average a relatively small percentage (16.4 ± 22.9) of bark removed.

Mortality

For at least four species (*Acacia tortilis*, *Lonchocarpus capassa*, *Colophospermum mopane* and *Croton megalobotrys*), a proportionately larger number of trees with elephant damage were dying than would be expected if bark damage had no effect on the long-term survival of a tree. These results, however, are based on calculations which include trees that died prior to 1986. Some of these trees had been lying in the field for a long period of time. Owing to the difficulty in identifying signs of elephant damage, elephants were always given the benefit of the doubt. It is, therefore, likely that the death of a larger percentage of trees than that recorded had elephant damage, and that the differences depicted in Table 3 may be much larger, and significant for more species.

To investigate the effect of bark damage on the long-term survival of a tree, the percentages of debarked trees that died between 1986 and May 1991 were compared with the percentages of undamaged trees that died between 1986 and May 1991 (Table 4). Debarked *Schotia brachypetala, Acacia tortilis, A. nigrescens, Combretum imberbe, Lonchocarpus capassa* and *Croton megalobotrys*, trees are likely to have a shorter lifespan than undamaged individuals.

There is considerable variation in the amount of bark removed from individuals of a particular species (Fig. 7). However, wood-borer insects are active even in trees from which only a small amount of bark has been removed (Thomson 1975). This allows rot to enter old scars of damaged stems (Afolayan 1975), which weakens the trunk. The tree eventually falls, toppled by the wind or its own weight (Guy 1981). Of the damaged *Schotia brachypetala* trees sampled at the two Majale River sites (northern and southern sites), 80.5% had secondary damage inflicted by wood-borer insects. Wood-borer insect damage was also observed (general field observations) in the *Acacia albida*, *A. nigrescens* and *A. tortilis* trees, but never in *Croton megalobotrys* trees. As trees with signs of elephant utilization are predisposed to mortality (Table 4), compared to that of the other species found, the relatively high mortalities (1986-May 1991) recorded for debarked *Schotia brachypetala*, *Acacia nigrescens* and, in particular, *A. tortilis* trees is likely to be attributable to the preference elephants have for their bark (debarking sometimes being followed by wood-borer insect damage). A study conducted in the Sengwa Wildlife Research Area, Zimbabwe (Anderson and Walker 1974), showed that damaged *A. tortilis* trees are particularly susceptible to attack from wood-boring insects.

The climate of the region incorporating the Reserve is semi-arid tropical, with rainfall being low and unpredictable (Harrison 1984). The prevailing dry conditions in the NTGR may have a detrimental effect on the long-term survival of trees in the Reserve, particularly those predisposed to mortality by high levels of bark utilization by elephants. However, the large riverine trees may be adapted to the dry conditions. If the dry conditions in the NTGR have predisposed trees to stress, it is likely that this has been the case for a relatively long period of time. Under these dry conditions, elephants may utilize the woody vegetation to a greater extent, thus depleting the large riverine tree component even further.

In the present study, 57.4% of the trees that died between 1986 and May 1991 (and identified with elephant damage) were *A. tortilis*; of the trees that died prior to 1986, only 6.8%. The largest percentage of trees that died from elephant damage prior to 1986 were recorded for *Combretum imberbe*, *Schotia brachypetala* and *Acacia nigrescens* (25.2%, 13.6% and 32% respectively). This may partly be attributable to the difference in the rate of decay between individuals of these species. *Acacia tortilis* has a softer wood than *Combretum imberbe*, *Acacia nigrescens* and *Schotia brachypetala*, all of which are known to have extremely hard woods (Van Wyk 1984). Of the specimens that died prior to 1986, a larger percentage of *Acacia tortilis* trees, compared to that of the other three species, may have decayed prior to the time of sampling.

Based on the observations made by Thomson (1975) in the Chizarira Game Reserve, Zimbabwe, it is likely that secondary damage inflicted by wood-borer insects following bark removal by elephants will affect the longetivity of all damaged *S. brachypetala* trees in the NTGR. In this case, at least 80% of *S. brachypetala* trees in the southern zone and 37.5% of the *S. brachypetala* trees in the northern zone will show an accelerated mortality. This would be the case even if elephant activity were to cease immediately (which is unlikely). With the continued utilization by elephants, the mortality is expected to be somewhat higher.

The relation between the rates of mortality and recruitment is a crucial demographic issue. However, only the total number of recruitment class trees could be determined during this study. Both inside and outside the NTGR, a relatively small number of *Schotia brachypetala* recruitment class trees were found. Owing to variable edaphic factors and climate, there may be a pulse of recruitment to the large tree component. In the long-term, therefore, a relatively high mortality rate is not likely to be threatening. Recruitment class trees, as defined in this study, are individuals with a stem circumference of less than one metre. Some of these individuals are nevertheless large trees, and die as a result of damage inflicted by wood-borer insects. In the short to medium term, based on the mortality of large and recruitment class trees, the relatively large percentage of trees that have and continue to be damaged by elephants and wood-borer insects and the small recruitment class component, there is cause for concern for the large *S. brachypetala* trees in the riverine communities of the NTGR.

Recruitment

For large riverine tree species to survive in the NTGR, it is essential that the rate of recruitment equal or exceed the rate of mortality in the long-term. Due to time limitations, and absence of data from previous studies in this regard, recruitment rates to the large riverine tree component could not be determined during the present study; only total counts.

Over a long period of time, the number of trees in the recruitment class may show considerable variation due to a variable seedling establishment and growth rate (possibly related to changes in climate). It may be argued that, over a relatively long period of time, the recruitment class to large tree ratios calculated during this study provide relatively little, if any, information. However, it is evident from comparisons with the sites sampled outside the NTGR that the recruitment tree class component in the NTGR has been affected by some factor in the Reserve. For *Lonchocarpus capassa*, *Acacia tortilis* and *A. nigrescens*, a significantly smaller number of recruitment class trees were recorded at the eleven sites in the northern zone of the Reserve than were sampled at the three sites outside the Reserve. This is in contrast to the situation inside the Reserve. It is evident from Table 1 that the large riverine tree populations presently found in the Reserve (excluding *Acacia tortilis* and *Croton megalobotrys*), both in the northern zone of the Reserve and for all sites, could not within the near future be replaced by the members of the present recruitment tree class component. In contrast, outside the NTGR, with the exception of *Schotia brachypetala*, the present recruitment trees component is sufficient to replace the present large tree component.

Owing to variable edaphic and climatic conditions, the germination of seeds is not constant. The transition between the various tree size classes in the NTGR is, therefore, likely to be variable. The relatively small number of recruitment class trees sampled in the NTGR may be a reflection of this. The small number of recruitment class trees in the NTGR, compared to that outside, is suggested to be attributed to seedling mortality induced by browsers (elephant, impala, kudu, eland, duiker and steenbok) and/or unfavourable edaphic and climatic conditions, or a combination of these. Unfavourable edaphic and climatic factors may also have profound effects on seedling germination rates. Mortality may also occur once seedlings have reached the recruitment class. Seedlings of species other than *Croton megalobotrys* were noted in the present study to exhibit signs of heavy browser utilization.

Species composition

As early as 1972, Lind (1974) recognized a decline in density and change in species composition of the riverine tree communities of the NTGR. Three species now extinct within the Reserve, which prior to 1986 undoubtedly formed part of the riverine communities sampled, are *Acacia caffra*, *A. burkei* and *Tarchonanthus trilobus*. Only a single tree of each species (each of which showed signs of wood-borer insect damage following bark removal by elephants) was found. Elephants may have been responsible for the possible extinction of these species in the NTGR. If this were the case, their occurrence in the NTGR is likely to have already been rare in 1973 because no mention was made of them in Lind's report (Lind 1974). On the other hand, it may be argued that these specimens were relics at the margins of their species distributions.

Edaphic factors are likely to play an important role in the composition of the riverine communities of the NTGR. As suggested by Dye and Walker (1980), factors such as soil depth, soil permeability and sodium content of soils may be responsible for the separation of stands dominated by *Colophospermum mopane* and stands dominated by *Acacia* trees.

Large riverine tree species other than *Croton megalobotrys* are being removed from the ecosystem as a result of elephant damage and subsequent wood-borer insect activity but are not, as is apparent from the recruitment presently found in the Reserve, being replaced. For *Croton megalobotrys*, a far larger recruitment class than large tree component was recorded (It should be noted (B.R. Page, pers. comm.)* that some *C. megalobotrys* trees die from causes which are apparently unrelated to elephant wood-borer insect damage before they reach the large tree component). *C. megalobotrys* exhibits characteristics of an early succession (pioneer) species. Coupled with a tendency to form monospecific stands, its present status according to Barbour, Burk and Pitts (1987), would be indicative of the emergence of a retrogressive succession pattern within the NTGR riverine tree communities.

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C. megalobotrys is a fast growing, broadleaf, species restricted to alluvial soils along rivers and large streams (Van Wyk 1984). The less frequent occurrence of *C. megalobotrys* in the northern zone of the Reserve, compared to that of the middle and southern zones, may be attributable to edaphic factors such as the depth of the alluvial soils along the rivers (Alexander 1984). It is, however, suggested that the activity of elephants in the NTGR has facilitated the formation of dense thickets of *C. megalobotrys* in the middle and southern zones of the Reserve. Seedlings of slower growing, light dependent species such as *Acacia tortilis* (Smith & Shackleton 1989) and *A. albida* (Feely 1965) may not grow well in the presence of *Croton megalobotrys*. Coupled with its low level of utilization by elephants, *C. megalobotrys* appears to be increasing in numbers in the NTGR. Owing to its less frequent occurrence in the northern zone of the Reserve, it is suggested that this pattern of succession may be at a less advanced stage in this zone than in the middle and southern zones. The higher rate of mortality of *Schotia brachypetala* in the southern zone of the Reserve, in comparison with that in the northern zone, supports this suggestion.

Likely future changes

Apart from their aesthetic qualities, the loss of the large riverine tree communities of the NTGR would lead to a reduction in raptor nesting sites and food sources for small mammals, as well as a loss of a major food source for elephants and other browsers. Debarked trees are particularly susceptible to damage caused by fire (Thomson 1975). Fires in the riverine tree communities of the NTGR would cause severe damage, possibly resulting in the death of many of the moderately debarked trees in the Reserve. Even in the absence of fire, the following processes may occur in the riverine tree communities of the NTGR:

1) the loss of a large number of trees as result of progressive wood-borer insect and fungal damage following debarking, even if no further debarking occurs;

2) relatively high rates of mortality of *Acacia tortilis*, *A. nigrescens* and *Schotia brachypetala* due to the preference shown by elephants for their bark and their susceptibility to secondary damage from wood-borer insects;

3) an increase in the number and density of *Croton megalobotrys* trees in the riverine communities due to its low mortality rate and possibly high level of recruitment in the Reserve.

As the number of trees of currently preferred species decline, elephants will presumably adjust their feeding habits and begin utilizing other species which, during the present study, were less preferred or possibly even avoided. It seems likely that, at current levels of bark utilization by elephants, the riverine vegetation of the NTGR will eventually be composed of *Croton megalobotrys* thickets separated by a few scattered large specimens of other species.

Acknowledgments

We would like to thank His Excellency, Dr. Quett D.J. Masire, President of the Republic of Botswana and the landowners of the Northern Tuli Game Reserve for extending their permission to conduct the project. Our sincere thanks to M.S de Villiers, Dr. H.M. Dott, Prof. J.D. Skinner and Prof. A.E. van Wyk for their valuable comments. Special thanks to Mr. C.V. Styles, Peet van Dyk and Kieren Kanavan for helping with the field work, and Stephanie Dyer for identifying the species of wood samples collected in the field. We would like to express our gratitude towards Prof. J.D. Skinner for financial assistance and the McKenzie and Steyn families for their generous hospitality. Financial support from the University of Pretoria and the Foundation for Research Development is gratefully acknowledged.

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Chapter 4

BARK STRUCTURE AND PREFERENTIAL BARK UTILIZATION BY THE AFRICAN ELEPHANT*

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*Accepted for publication in *IAWA BULLETIN*

BARK STRUCTURE AND PREFERENTIAL BARK UTILIZATION BY THE AFRICAN ELEPHANT

by

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Summary

Bark fracture properties are thought to influence the debarking of selected trees by the African elephant. This hypothesis was tested for large riverine tree species in the Northern Tuli Game Reserve, Botswana. An index of bark breakage strength and pliability of secondary phloem tissue was compiled for 11 common riverine species, and the bark anatomy of the species was investigated to determine relative fibrosity. The majority of species preferred by elephants were found to have strong and pliable barks, associated with a high proportion of fibres. However, not all species have these characteristics, which indicates that factors other than bark fracture properties affect species preference. Bark structure influences the way in pieces of bark are stripped from a tree trunk during debarking. It is hoped that this paper will stimulate further studies on the effects of bark structure on the preferential feeding behaviour of the African elephant.

Key words: African elephant, bark anatomy, debarking, gelatinous fibres, sclereids, mechanical properties.

Introduction

The devastating effects that large numbers of elephant have on their habitat are evident in many parts of eastern and southern Africa (Anderson & Walker 1974). The relatively large size and high mean age of survival enable this species to have a major, often long-term, impact on the ecosystem (Watson & Bell 1968), particularly in areas where the movements of elephant herds are restricted. Elephants are second only to man in their capacity for altering their environment (Skinner & Smithers 1990, and references therein).

In any particular area, elephants show a preference for stripping and ingesting the bark of certain tree species; bark of *Acacia tortilis* and *A. nigrescens* are especially favoured (Skinner & Smithers 1990, and references therein). Elephants loosen the bark with their tusks and then strip it off. Even if only part of the bark is stripped off, debarked trees are susceptible to further damage by fire, insect borers and fungi, and often succumb to their injuries (Thomson 1975).

Little is known about the effects of bark structure and strength on the extent of debarking. In fact, the possible influence of plant fracture properties on animal behaviour is rarely considered (Vincent 1990). Thomson (1975) suggests that the ease with which bark is stripped from a tree may account, in part, for the differences in species preference shown by elephants. Laws et al. (1975) remarked that the mechanical properties of bark, which either facilitate or hinder debarking, may be involved in determining the incidence of debarking of a particular tree species.

The present study was initiated following a suggestion that the breakage strength and pliability of bark plays an important role in the preference shown by elephants for certain tree species in southern Africa (McKenzie, pers. comm.). In this paper we explore the relationship between the intensity of bark damage caused by elephants and aspects of bark anatomy. We test the hypothesis that fibrous barks tend to be tough, pliable, and hence easily stripped from extensive areas of stem, whereas barks in which the sclerenchyma is completely lacking or is comprised of mainly sclereids, are brittle and therefore less likely to be removed in relatively large pieces. This study forms part of a comprehensive project on the association between African elephants and the large riverine trees of the Northern Tuli Game Reserve in Botswana.

Study area

The Northern Tuli Game Reserve (NTGR) is situated in the eastern corner of Botswana, between 21°55'S and 22°15'S, and 28°55'E and 29°15'E, where Botswana, South Africa and Zimbabwe meet. It 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 veterinary control fence. The Reserve, which covers an area of approximately 60 000 ha, is neither gazetted nor proclaimed as a private game reserve, but relies solely on a shared interest in conservation between the landowners of several privately owned farms. From aerial censuses conducted in 1986, 1987 and 1988 (Le Roux 1989), it is evident that the density of elephants within the NTGR is approximately one per square kilometre. The vegetation of the area is broadly classified as *Colophospermum mopane* woodland and scrub woodland (White 1983).

Materials and Methods

Choice of trees

A stratified sample of the riverine tree communities within the NTGR, comprising 16 sites, was taken in May 1991. The sites were located along the main rivers within the reserve and include the Majale, Pitsani, Njaswe, Matabole and Jwala rivers. Two hundred large trees, both living and dead, were sampled at each site. Only large trees were included in the sample as these constitute the most important structural component of the riverine forests. Large trees were defined as trees with a trunk circumference exceeding 1 m when measured just above the basal swelling.

For each living tree sampled, the species and extent of bark damage inflicted by elephants were recorded. Bark damage was defined as the width of bark removed at the height of greatest width damage, expressed as a percentage of the stem circumference at that height:

$$\text{Percentage bark removed (\%BR)} = 100 \cdot A_i/C$$

where:

A_i = the width of a debarked area at tree height x

C = circumference of tree at height x

x = the height at which the greatest area of bark has been removed.

Choice of species

An objective of this study was to distinguish, on the basis of bark damage, preferred woody plants from non-preferred ones. A preferred species is defined as one that is utilized more frequently than indicated by its availability in the environment (Petrides 1975). For this purpose preference ratios were calculated using the following equations, adapted from Petrides (1975):

$$\text{Preference ratio (PR)} = \frac{\text{Percentage utilization } (U_i)}{\text{Percentage availability } (A_i)}$$

where:

$$U_i = 100 \cdot \frac{\text{Number of debarked trees of species i in all sites sampled}}{\text{Number of debarked trees of all species within all sites sampled}}$$

$$A_i = 100 \cdot \frac{\text{Number of available trees of species i within all sites sampled}}{\text{Number of available trees of all species within all sites sampled}}$$

For each tree the time of debarking prior to sampling (weeks, months and/or years) was determined from the appearance of the exposed wood and/or stripped bark and/or signs of regenerative bark growth. From observations made on the response of trees from which we have removed bark (to test bark strength), these criteria were found to be a reliable measure of estimating the relative time of debarking. Preference ratios were calculated based only on bark damage that had occurred weeks and/or months prior to the time of sampling (= recent damage), and only for species for which ten or more trees were sampled.

Bark strength

The fracture properties of bark were tested for 11 NTGR riverine tree species. For each species, bark from six randomly chosen trees, located along the Majale and Jwala rivers, was collected in October 1991 (the end of the dry season). The bark was removed from each tree at breast height, and only from trees with a trunk circumference of between 100 and 200 cm when measured just above the basal swelling. Bark sampled from the various species differed in thickness. For comparative purposes, a standard 1 x 2 x 100 mm axial strip of tissue, removed from the central part the living secondary phloem of a bark sample, was used in the following tests (n = 6 for each species).

To measure breakage strength (stress at which the sample breaks), a homemade wooden clamp was attached to each end of a bark strip, leaving a 10 mm gap between each clamp. The clamps were then pulled apart with a mini hand-wrench. The weight at which a bark strip snapped was read from a 100 kg weight scale and used to establish an index of the breakage strength for the bark of the species sampled.

An index of pliability (toughness) for the bark was based on the number of bends required to break a strip of bark, each strip of bark being clamped as previously described. A bend is defined as a 90° change in the angle between the clamps (initially at an angle of 180° to each other), and the direction of successive bends is alternated.

Bark anatomy

Fresh bark samples, collected as described above, were fixed in FAA (Johansen 1940). Unembedded fixed material was softened with steam and transverse and radial sections cut at 15--20 µm on a sliding microtome. Sections were stained with safranin O and fast green (Johansen 1940), and mounted in entellan. The presence of lignin was determined using phloroglucinol (Jensen 1962). Drawings of transverse sections were made using a projection light microscope. Unless otherwise indicated, descriptive bark anatomy terminology follows Trockenbrodt (1990).

Results

Preference ratios

The number of large riverine trees sampled (both accessible and inaccessible to elephants), and their percentage occurrence within the riverine tree communities of the NTGR, are listed in Table 7. Based on bark damage inflicted by elephants, preference ratios calculated for species with ten or more trees sampled are given in Table 8. The median percentage bark removed from all trees of each species sampled (Table 9) was calculated, and results are plotted in Fig. 9.

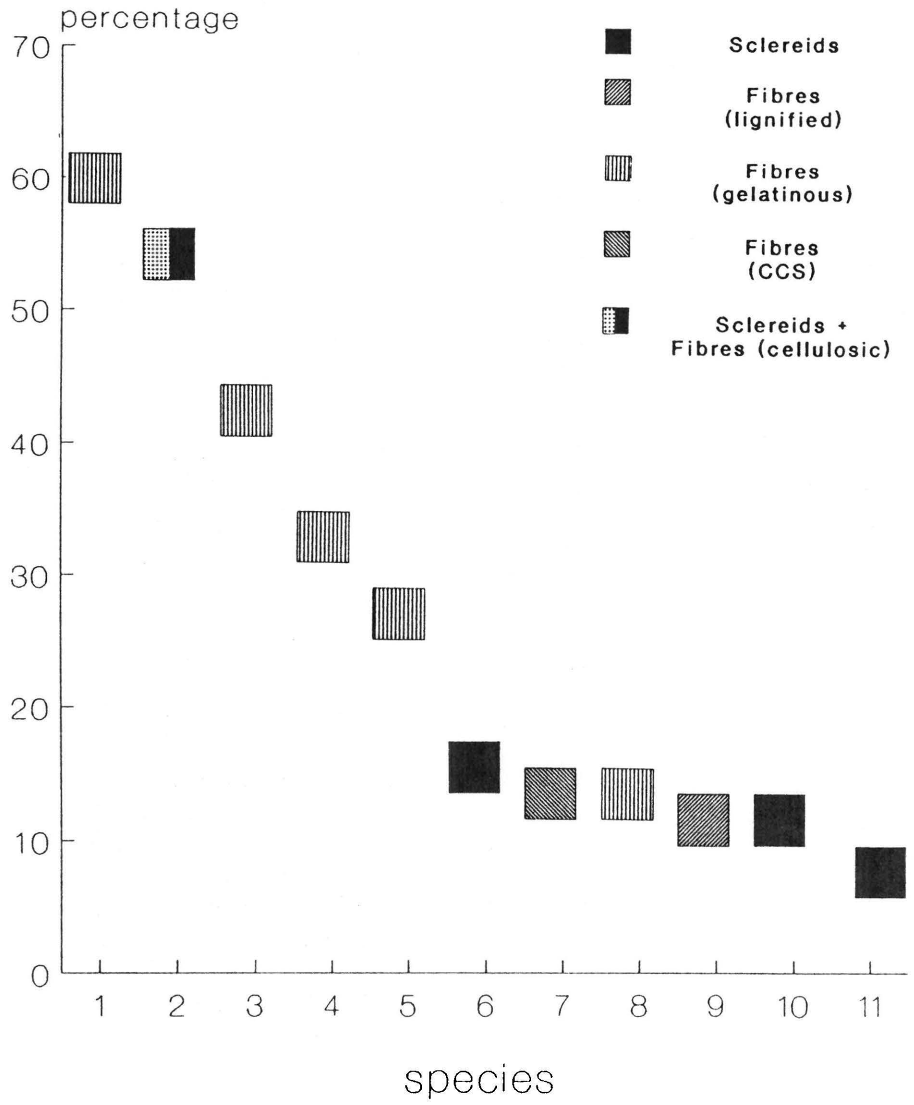
Table 7. Number of large trees sampled (irrespective of their accessibility to elephants) and the percentage occurrence of each species within the riverine tree communities of the Northern Tuli Game Reserve.

Species	No. of trees sampled	Percentage occurrence
Colophospermum mopane	617	22.91
Combretum imberbe	543	20.16
Croton megalobotrys	489	18.16
Lonchocarpus capassa	257	9.54
Combretum hereroense	190	7.06
Acacia tortilis	149	5.53
Schotia brachypetala	102	3.79
Acacia nigrescens	83	3.08
Boscia albitrunca	53	1.97
Combretum apiculatum	37	1.37
Terminalia pruniodes	26	0.97
Xanthocercis zambesiaca	23	0.85
Ziziphus mucronata	21	0.78
Acacia albida	16	0.59
Sterculia rogersii	16	0.59
Albizia brevifolia	15	0.56
Boscia foetida	12	0.45
Spirostachys africana	8	0.30
Cassia abbreviata	6	0.22
Markhamia acuminata	6	0.22
Lannea sweinfurthii	5	0.19
Ficus sycamorus	4	0.15
Berchemia discolor	4	0.15
Sclerocarya birrea	3	0.11
Commiphora glandulosa	3	0.11
Salvadora angustifolia	2	0.07
Hyphaene natalensis	1	0.04
Pappea capensis	1	0.04
Kirkia acuminata	1	0.04

Table 8. Characteristics of debarked species sampled within the Northern Tuli Game Reserve riverine tree communities. Damaged = number of trees with bark damage; Total = number of trees living excluding trees inaccessible to elephants; U_i = percentage utilisation; A_i = percentage availability; PR = preference ratios; * = trees for which bark strength and pliability, as well as bark anatomy, were recorded.

Species	Damaged	Total	U_i	A_i	PR
*Acacia albida	7	16	5.98	0.62	9.65
*Schotia brachypetala	20	100	17.09	3.85	4.44
*Acacia nigrescens	8	79	6.84	3.04	2.25
*Xanthocercis zambesiaca	2	21	1.71	0.81	2.11
*Acacia tortilis	11	147	10.26	5.65	1.82
*Combretum imberbe	33	536	28.21	20.59	1.37
*Colophospermum mopane	20	617	17.09	23.70	0.72
*Combretum hereroense	6	189	4.27	7.26	0.59
*Lonchocarpus capassa	5	256	4.27	9.87	0.43
*Croton megalobotrys	5	488	4.27	18.75	0.23
*Boscia albitrunca	0	52	0.00	2.00	0.00
Ziziphus mucronata	0	20	0.00	0.77	0.00
Combretum apiculatum	0	30	0.00	1.15	0.00
Albizia brevifolia	0	11	0.00	0.42	0.00
Boscia foetida	0	12	0.00	0.46	0.00
Terminalia pruniodes	0	26	0.00	1.00	0.00

PR < 1: species neglected; PR = 1: species neither neglected nor preferred; PR > 1: species preferred.



SPECIES KEY:

1:	*Acacia albida*	7:	*Colophospermum mopane*
2:	*Xanthocercis zambesiaca*	8:	*Lonchocarpus capassa*
3:	*Acacia nigrescens*	9:	*Boscia albitrunca*
4:	*Schotia brachypetala*	10:	*Combretum hereroense*
5:	*Acacia tortilis*	11:	*Croton megalobotrys*
6:	*Combretum imberbe*		

Fig. 9. The median percentage bark removed from all trees of each species sampled, compared to the type of sclerenchyma in the bark.

Table 9. Extent of debarking compared to fracture properties, method of bark removal by elephants, and the predominant type of sclerenchyma in the secondary phloem (extent of debarking and symbols explained below). Numbers preceding species name refer to numbers used in Figure 9.

Species	Extent of debarking	Breakage strength (kg) Av ± SD	Bending strength Av ± SD	Method of debarking	Type of sclerenchyma
1. *Acacia albida*	5	1.14 ± 0.38	4.00 ± 2.50	SS	F(G)
2. *Xanthocercis zambesiaca*	5	<1	1.00 ± 0.00	G	F(C)+S
4. *Schotia brachypetala*	4	3.00 ± 1.41	3.00 ± 1.50	SS	F(G)
3. *Acacia nigrescens*	4	19.25 ± 3.54	60+	LS	F(G)
5. *A. tortilis*	3	27.64 ± 5.51	60+	LS	F(G)
9. *Boscia albitrunca*	3	<1	1.38 ± 0.52	G	F
7. *Colophospermum mopane*	2	13.38 ± 1.92	60+	SS	CCS
8. *Lonchocarpus capassa*	2	6.00 ± 1.31	41.00 ± 5.50	SS	F(G)
10. *Combretum hereroense*	2	1.13 ± 0.35	1.25 ± 0.46	B	S
11. *Croton megalobotrys*	1	<1	1.38 ± 0.52	G	S
6. *Combretum imberbe*	1	<1	1.00 ± 1.50	B	S

Extent of debarking: 1 = slight damage (1--15%); 2 = mild damage (16--25%); 3 = moderate damage (26--35%); 4 = extensive damage (36--45%); 5 = severe damaged (46--99%); where (x--y%) = mean percentage bark removed per species.

Bending strength: Number of 90° bends before breaking of standard bark strip (1 x 2 x 100 mm).

Method of bark removal: B = comes off in squares or blocks; G = tusk placed on bark and groove formed as tree is debarked; SS = removed as short strips; LS = removed as long strips.

Predominant type of sclerenchyma in secondary phloem (excluding dilatation tissue): CCS = lignified chambered crystalliferous strands; F = phloem fibres (lignified); F(C) = phloem fibres, exclusively cellulosic; F(G) = phloem fibres, exclusively or predominantly gelatinous; S = sclereids.

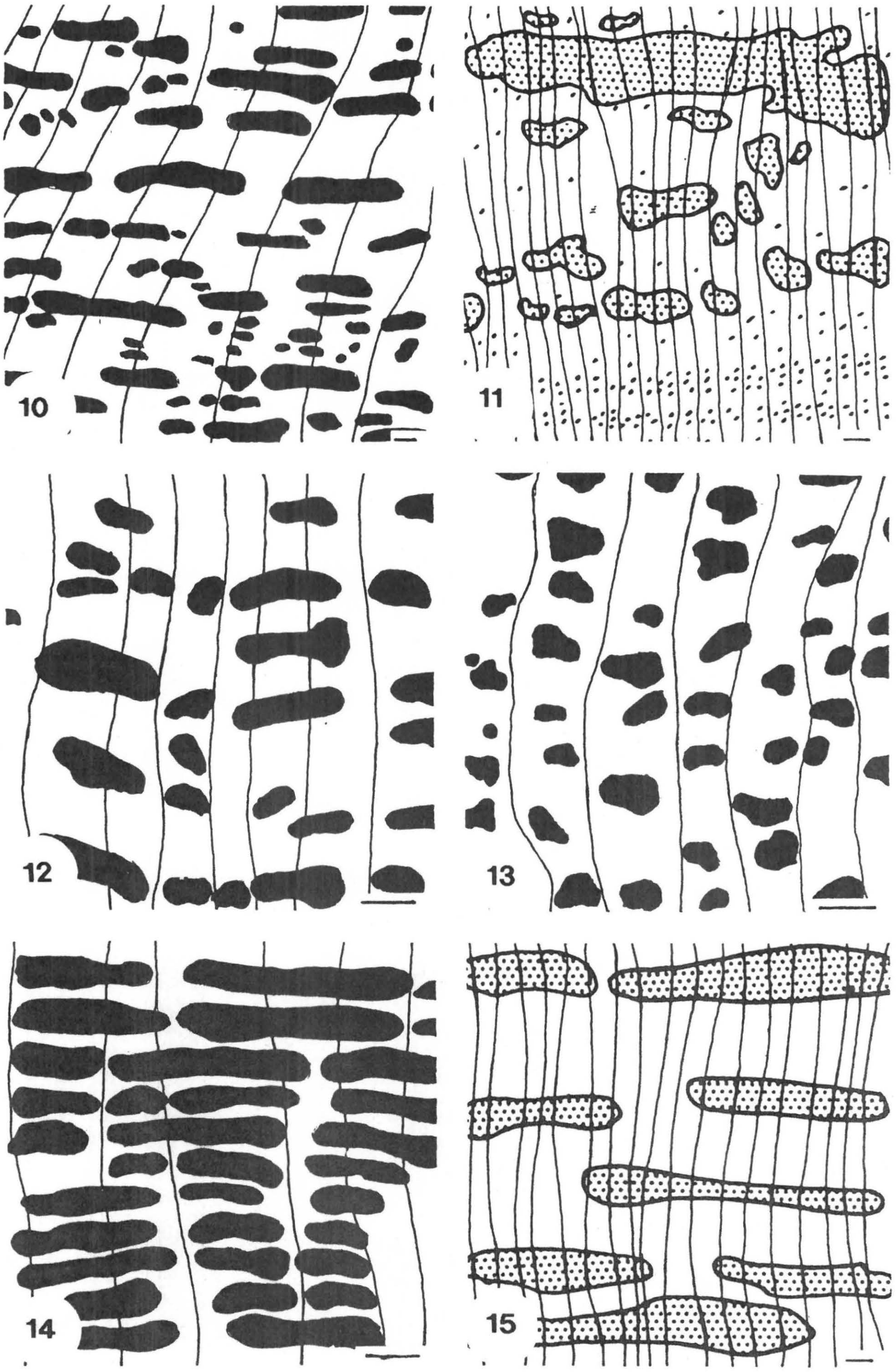
Bark structure

The predominant type of sclerenchyma in the secondary phloem of each investigated species is recorded in Table 9. Sclerenchyma arrangement, as seen in transverse section, is illustrated in Figures 10--21. Because the secondary sclereids that are associated with the dilatation zone are variable in occurrence and degree of development, these cells were not illustrated, nor taken into account for relating sclerenchyma type to bark mechanical properties, except in the case of <u>Xanthocercis zambesiaca</u> , where masses of secondary sclereids form at an early stage.

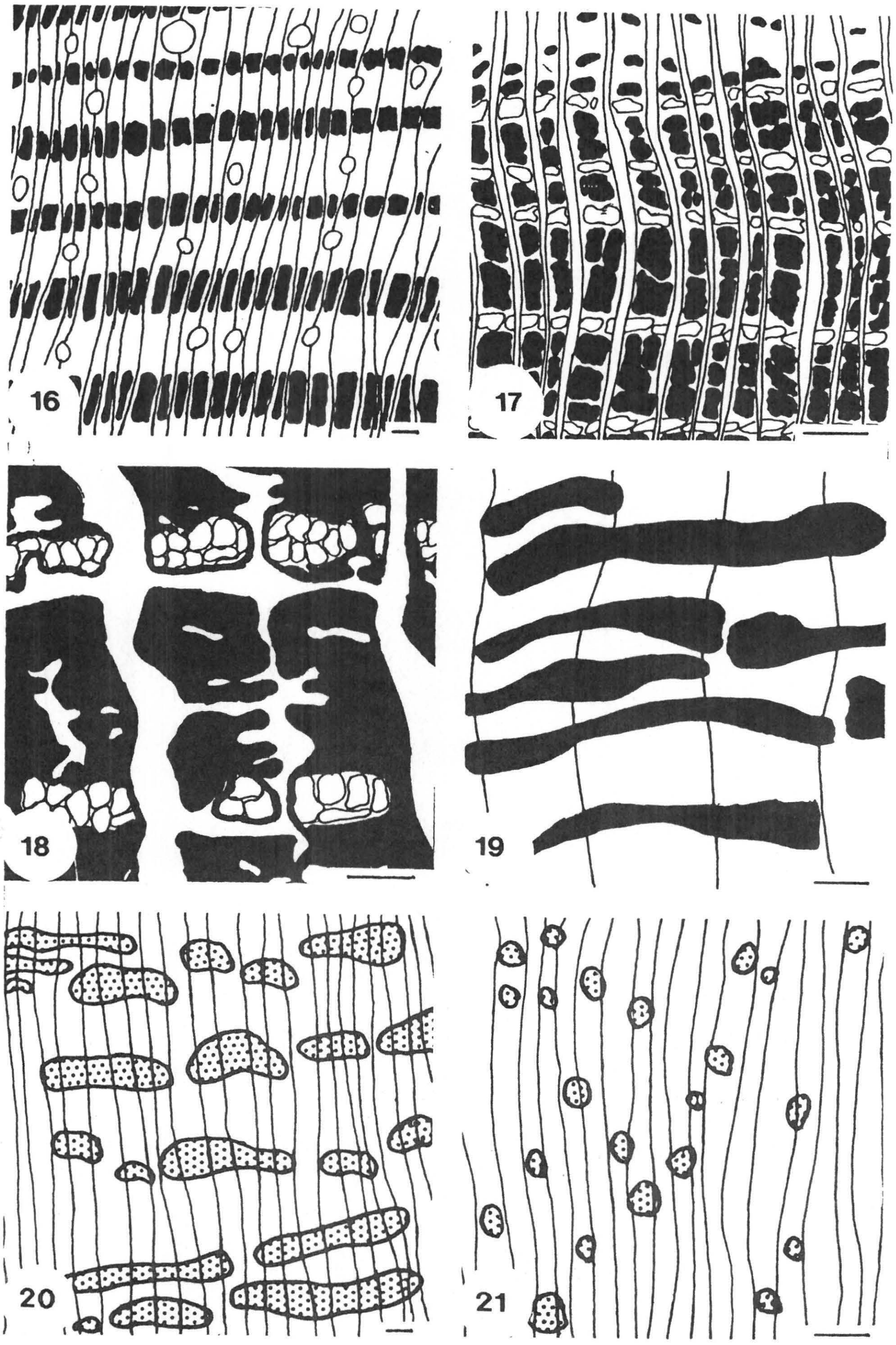
<u>Croton megalobotrys</u> (Fig. 21) is characterized by sclerenchyma consisting of scattered clusters (strands) of thick-walled sclereids, each cluster wreathed by crystalliferous cells. The two species of <u>Combretum</u> (Figs. 15, 20) are also characterised by thick-walled sclereids, though in this case the clusters of sclerenchyma are markedly interspersed by relatively large, thin-walled crystalliferous cells. <u>Xanthocercis zambesiaca</u> (Fig. 11), a species with unusual, non-lignified fibres in the secondary phloem, has abundant secondary sclereids in its dilatation tissue. Because the sclereids in <u>X. zambesiaca</u> form relatively closely to the vascular cambium, and are abundant, these sclereids may significantly affect the fracture properties of the bark (see Table 9).

Robust, heavily lignified phloem fibres with exceptionally thick walls (resembling sclereids in transverse section) are present in *Boscia albitrunca* (Fig. 19). Phloem fibres with an unlignified innermost G-layer (gelatinous fibres) predominate in *Schotia brachypetala* (Fig. 13), *Lonchocarpus capassa* (Fig. 17) and the three species of *Acacia* (Figs. 10, 12, 14), the thickness and degree of lignification of the outer S_1 and S_2 layers of these gelatinous fibres show considerable interspecific variation. These latter two layers are relatively thick and lignified in *S. brachypetala*, *L. capassa* and *Acacia albida*, but thin and inconspicuously lignified in *A. nigrescens* and *A. tortilis*.

Slender fibres with very thin, unlignified walls are present in the secondary phloem of *Xanthocercis zambesiaca*. These unusual fibres are easily overlooked in stained sections and, because of the strong birefringence of their walls, are best observed under polarised optics. They prove to be exceptionally tough and elastic during sectioning.



Figs. 10--15. The arrangement of sclerenchyma as seen in transverse section of the inner bark (before conspicuous dilatation growth). Fibres, or elements considered to be homologous to fibres, shown in black (specific type mentioned under species); sclereids stippled. 10: Acacia albida, lignified gelatinous fibres; 11: Xanthocercis zambesiaca, sclereids and scattered cellulosic fibres; 12: Acacia nigrescens, gelatinous fibres; 13: Schotia brachypetala, lignified gelatinous fibres; 14: Acacia tortilis, gelatinous fibres; 15: Combretum imberbe, sclereids. Scale bars = 100 µm (Figs. 12--14), 200 µm (Figs. 10, 11, & 15).



Figs. 16--21. The arrangement of sclerenchyma as seen in transverse section of the inner bark (before conspicuous dilatation growth). Fibres, or elements considered to be homologous to fibres, shown in black (specific type mentioned under species); sclereids stippled. 16: Colophospermum mopane, lignified chambered crystalliferous strands, alternating with concentric secretory ducts; 17: Lonchocarpus capassa, lignified gelatinous fibres; 18: Lonchocarpus capassa, high magnification showing sclerenchyma interspersed with clusters of secretory ducts; 19: Boscia albitrunca, fibres; 20: Combretum hereroense, sclereids; 21: Croton megalobotrys, sclereids. Scale bars = 10 µm (Fig. 19), 100 µm (Figs. 17, 20 & 21), 200 µm (Figs. 16 & 18).

The sclerenchymatous elements in the bark of Colophospermum mopane (Fig. 16) are arranged in broad concentric zones, alternating with concentric secretory ducts which are associated with zones of parenchymatic secondary phloem tissue, thus imparting to the bark a stratified arrangement in transverse sections. Although probably derived from fibre initials, the sclerenchyma of this species comprises mainly lignified, chambered crystalliferous strands.

Fracture properties

In Table 9, the breakage strength and pliability of bark from the 11 tree species most frequently damaged by elephants are compared to certain bark anatomical features. Note that the barks with the highest breakage strengths also demonstrate the highest bending strengths. Thus, the barks of Acacia nigrescens, A. tortilis, Colophospermum mopane and Lonchocarpus capassa proved to be both strong and tough. In contrast, the bark is particularly weak and brittle in Boscia albitrunca, the two Combretum species, Croton megalobotrys, Xanthocercis zambesiaca, and Acacia albida.

Discussion

In the NTGR, elephants show a preference for the bark of certain tree species, and this is not related to the relative availability of each species. In particular, elephants show a marked preference for the bark of Schotia brachypetala, Acacia albida and Xanthocercis zambesiaca, with percentage occurrences of 3.78%, 0.59% and 0.85% respectively, whereas Croton megalobotrys, a relatively common species within the Reserve with percentage occurrence of 18.15%, remains almost undamaged. It is important to ask whether this preferential utilization is due to intentional selection by the elephant or merely a consequence of the mechanical fracture/removal properties of the barks. Alternatively both factors may play a role. The matter is complicated by observations suggesting that the preferential choice of trees by elephants might change over an extended period (Anderson & Walker 1974).

Studies attempting to explain the preference shown by elephants for certain species have usually concentrated on the chemical composition (taste, smell, nutrition) of plant material. Following the differential destruction of Brachystegia boehmii in the Chizarira Game Reserve, Zimbabwe, Thomson (1975) attempted to establish factors for the elephants' preference for this species above four other species in the area, namely Julbernardia globiflora, Brachystegia glaucescens, Colophospermum mopane and Acacia *albida*. However, detailed chemical analysis for several elements, crude protein and ether extract content, failed to indicate any significant differences. In a study analysing only tree foliage, Jachmann (1989) concluded that the mature foliage selected by elephants was characterised by a high mineral and sugar content. Neglected species were high in total phenols and steroidal saponins, and were often poorly digestible due to high concentrations of lignin. Bark is generally rich in phenolic and various other secondary compounds (Srivastava 1964), and therefore these substances are unlikely to play a significant role in bark selection.

In our study, crystals of calcium oxalate were abundant in most bark samples. Furthermore, secretory ducts/cells, sure to contain a diversity of secondary compounds, are present in many species' barks, e.g. *Colophospermum mopane*, *Lonchocarpus capassa* and the *Acacia* species. However, the preponderance of gelatinous fibres, which have a low lignin content, in several of the heavily utilised barks may improve their digestibility. Elephants might also benefit from the calcium contained in the crystals of calcium oxalate which are so abundant in most barks. In a number of tree species, Laws *et al.* (1975) reported a significant correlation between the extent of debarking and bark calcium content. It has also been suggested that bark removal by elephants is a response to nutritional requirement for a substantial proportion of woody or fibrous material in their diet (Laws *et al.* 1975).

Thomson (1975) speculated that ease of bark removal may play a role in preferential bark utilisation by elephants. Two factors are likely to affect the amount of damage: 1) the activity of the vascular cambium at the time of debarking, and 2) the cellular structure of the particular bark. Regardless of its structural characteristics, bark removal would require less effort during periods of increased cambium activity, for example, at the beginning of tree growth following the dry season, or during the growth flushes that usually accompany good rains. On the other hand, Einspahr et al. (1984) found that dormant season wood/bark adhesion in several North American hardwood trees was positively correlated with percent phloem fibres, as well as secondary phloem toughness and strength. Wood/bark adhesion was negatively correlated with percent sclereids in the bark. However, Thomson (1975) noted that elephant damage in the Chizarira Game Reserve in Zimbabwe mainly takes place from August through November, a period likely to overlap with the start of active tree growth.

Guy (1976) suggested that the increase in debarking in the late dry season was due to increased translocation from the roots to the new leaves. Because the porcupine Hystrix africaeaustralis preferential debarking of certain trees during spring, Yeaton (1988) concluding that this animal prefers tree species capable of translocating sugars to their stems prior to the beginning of the rainy season (for example Dombeya rotundifolia, one of the first savanna tree species to flower in spring). In contrast, (Miquelle & Ballenberghe 1989) suggested the seasonal preference for bark stripping by the moose Alces alces may be merely due to the low availability of grass and browse during certain times of year. The size of the area of bark stripped from individual trees by the grey squirrel, Sciurus carolinensis, has been claimed to be strongly related to phloem volume, but not to sugar concentration (Kenward & Parish 1986).

Buechner and Dawkins (1961) suggest feeding on bark by elephants is concentrated during the period of regrowth when the bark will peel easily. The frequency with which grey squirrels remove bark from trees is largely dictated by the ease with which they can remove it (Hampshire 1985, as quoted in Vincent 1990). In a study on a number of temperate Northern Hemisphere trees, the toughness of the cambium has been found to be reduced by a factor of five or more when the cells are actively dividing (Vincent 1990). However, as this will probably affect all species of trees to more or less the same extent, increased cambium activity on its own is unlikely to explain preferential bark stripping by elephants.

Structurally, bark can be broadly interpreted as consisting of various proportions of soft (parenchymatous) and hard (sclerenchymatous) elements. The basis for the particular mechanical properties of bark is therefore complex, undoubtedly involving engineering principles associated with composite materials (Harris 1980). The most obvious structural variations between mature bark of different species usually involve aspects such as the composition, distribution and amount of sclerenchyma tissue. The most common sclerenchyma cell types are fibres and sclereids (for definitions see Trockenbrodt 1990).

The mechanical properties of bark are virtually unknown (Diener et al. 1968; Murphy & Rishel 1977; Einspahr et al. 1984). In one of the few studies on bark strength, Einspahr et al. (1984) presented evidence suggesting that bark strength is increased by the presence of fibres, but decreased by the presence of sclereids. Murphy and Rishel (1977) also reported that fibrous barks are much stronger in compression than the conglomerate (sclereidal) types. Despite the paucity of quantitative evidence, the toughness and strength of certain fibrous barks are taken advantage of by man, e.g., for binding material (cord)---examples from southern Africa include the bark of several species of Acacia, Brachystegia and Colophospermum mopane (Palmer & Pitman 1972).

Our results on the mechanical properties of fibrous barks show that there are marked differences in strength and toughness between species. Generally, barks with gelatinous fibres and slight wall lignification, as in Acacia nigrescens and A. tortilis, proved to be very strong and tough. The bark of Colophospermum mopane, with concentric zones of abundant crystalliferous strands, but with very thin, lignified secondary cell walls, showed similar mechanical qualities. The gelatinous phloem fibres in the bark of the investigated species are not associated with leaning stems. Tension wood, which occurs in many angiosperm trees at the upper side of leaning stems and branches, is characterised by the presence of gelatinous fibres. Some authors suggest the development of gelatinous fibres is initiated by the large tensile stresses generated in the xylem by gravity (Côté et al. 1969; Boyd 1977 and references therein, but see also Höster & Liese 1966; Chalk 1983). Bark tissue found in straight trunks however, also generates longitudinal tensile stresses as a result of the growth of xylem and phloem at the vascular cambium. Because of the sporadic occurrence of gelatinous fibres in bark, growth tensile stresses are probably not the primary cause of their initiation. Our results suggest that, unlike wood, the presence of gelatinous fibres in the bark of a particular species is consistent, and of potential taxonomic significance (recorded during this study in members of the Mimosaceae, Caesalpiniaceae and Fabaceae only).

In spite of the presence of exclusively cellulosic fibres, the bark of Xanthocercis zambesiaca turned out to be weak and brittle. During the preparation of the bark sections, these fibres proved to be tougher and more resilient than any of the other species investigated, making it impossible to obtain intact transverse sections. The abundant secondary sclereids in this species may affect the mechanical properties of this species.

In the remaining fibrous barks, strength and toughness appear to decline with an increase in the thickness of the lignified portion of the fibre walls. This may explain the relatively brittle bark in *Acacia albida* and *Schotia brachypetala*; both have gelatinous fibres, but with the S_1 and S_2 layers conspicuously lignified. Nanko and Côté (1980) have suggested that the thin secondary walls and large lumina in phloem fibres are features that will generally enable them to collapse and become flexible. The very thick and lignified secondary walls of the fibres in *Boscia albitrunca* (lumina almost absent), probably account for the relatively brittle bark in this species. In the case of wood, however, mechanical strength (hardness) largely depends on the proportion of fibres and the thickness of cell walls, while bending and toughness qualities cannot, at least in some species, be specifically referred to as features of anatomical structure (Wilson & White 1986).

All the investigated barks in which sclereids predominate are, as expected, weak and brittle. For these species (notably species of *Combretum*), elephants tend to remove small pieces of bark from around the circumference of the trunk, so that ring-barking is the principal form of damage. Species often ring-barked in this manner include *C.*

imberbe, *Acacia albida* and *Trichilia emetica* (Anderson & Walker 1974). For tree species with fibrous barks, bark stripping by the elephant often takes the form of ripping long strips of bark from the trunk. In the Sengwa Wildlife Research Area, Anderson and Walker (1974) found this type of debarking to be most pronounced in *Acacia tortilis* (which was markedly preferred by elephants), *A. nigrescens* and *Brachystegia boehmii*.

In contrast to wood (e.g., Jeronimidis 1976, 1980; Boyd 1980; Vincent 1990), there have been few attempts to relate the mechanical properties of mature bark tissue to the morphology of the cell elements. The approach followed in our study allows only generalisations. Vincent (1990) stressed the necessity to use "proper" engineering and materials science methods to measure the fracture properties of plant tissues. The method used here was, however, chosen for its simplicity and served mainly as an index to be used for comparative purposes. "There is a need for more studies on the relationship between fracture properties and anatomical structures in plants. The application and refinement of methodologies previously mainly developed and employed by materials scientists, should open exciting new prospects for interdisciplinary co-operation. Such research will not only be of significance in the field of animal behaviour, but may also help in elucidating some of the evolutionary pressures to which plants are exposed. In the process even engineers may benefit--biological designs have already been successfully transferred to engineering applications (e.g., Mattheck 1989)."

Conclusions

Species with bark that is relatively strong and pliable are preferred by elephants, but the reverse is not necessarily true. For example, Acacia albida, Xanthocercis zambesiaca and Schotia brachypetala, although markedly preferred by elephants, have barks which demonstrate a relatively low pliability and small breakage strength. It appears that, in addition to bark strength, factors such as chemical composition, moisture content and nutritive value of bark affect species choice. There is a tendency for fibrous barks to predominate among the tree species with the highest preference ratios. However, fracture properties (breakage and bending strength) of these barks differ and therefore do not show a clear and consistent pattern. This variation is probably due to specific characteristics of the phloem fibres, notably thickness and degree of lignification of the secondary cell walls, and the presence or absence of an inner gelatinous wall layer.

Bark structure has a definite influence on the way in which pieces of bark break away from the trunk during debarking. Fibrous barks with high breakage and bending strength are removed in relatively long axial strips, resulting in relative easy removal of large quantities of bark from a trunk. Brittle barks, and in particular those where sclereids predominant in the bark sclerenchyma, break away in small pieces, resulting in the damage being localised on the stem. These trees are prone to be ring-barked by the elephant.

Comparative evidence on bark structure is lacking for the vast majority of African trees. It is hoped that this paper will serve as a basis for further studies on the possible influence of bark structure on the preferential feeding behaviour of the African elephant, and its effects on the dynamics of specific plant communities.

Acknowledgments

We would like to thank His Excellency, Dr. Quett D.J. Masire, President of the Republic of Botswana and the landowners of the Northern Tuli Game Reserve for extending their permission to conduct the project. Our sincere thanks to Mr. M.J. Potgieter, who prepared the microscope slides used for this study, and to Miss G.L. Day, who critically read and improved the manuscript. The senior author would like to express his gratitude towards Prof. J.D. Skinner for financial assistance, Dr. A.A. McKenzie for scholarly advice and for suggesting this study, and the McKenzie and Steyn families for their generous hospitality. Financial support from the University of Pretoria and the Foundation for Research Development is gratefully acknowledged.

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Chapter 5

THE RELATIONSHIP BETWEEN BARK CHEMICAL COMPOSITION AND UTILIZATION BY ELEPHANTS

The relationship between bark chemical composition and utilization by elephants

Introduction

It is well known that diet selection by herbivores is strongly influenced by anti-herbivory compounds in plant tissues (Freeland, & Janzen 1974; Feeny 1976; Rhoades & Cates 1976; Swain 1979; Bryant & Kuropat 1980; Zucker 1983; Cooper & Owen-Smith 1985; Provenza *et al.* 1991; Du Toit, Provenza & Nastis 1991). With the exception of a study conducted in the Miombo woodlands of the Kasunga National Park in Malawi (Jachmann 1989), no in-depth investigation of the role of plant secondary compounds in the diet of African elephants has been made.

The study reported here is an attempt to integrate food preferences of elephants and analytical data on the energy content, percentage crude protein and the content of secondary plant compounds in the bark of large riverine tree species in the Northern Tuli Game Reserve (NTGR), Botswana.

Tannins, which are high molecular weight polyphenols, have been implicated as functioning to defend plants against herbivory through their effect on protein digestion (Swain 1977). Tannins may, through their interaction with protein, form tannin-protein complexes which tend to be insoluble

(Mole & Waterman 1987a). Condensed and hydrolyzable tannins, the latter being conventionally divided into gallotannins and ellagitannins, are considered to be the two major structural groups of tannins (Haslam 1981). Condensed tannins seem to attach to the cellulose and fiber-bound proteins of cell walls, thereby defending plants against microbial and fungal attack (Zucker 1983; Cooper & Owen-Smith 1985). Hydrolysable tannins have been suggested to inactivate herbivore digestive enzymes (Zucker 1983). When degraded, hydrolysable tannins may be toxic, leading to intestinal irritation (McLeod 1974).

During this study, information has been collected on total phenolic content, condensed tannin content and the capability of tannins *in vitro* to form complexes with proteins.

Methods

Crude protein and energy content

In June 1991 (early dry season) a section of bark, approximately 5 × 10 cm, was removed from each of five individuals of ten common large riverine tree species in the NTGR and stored in paper bags. The trees from which bark was sampled were randomly chosen along the Jwala and Majale rivers (see Fig. 2, Chapter 2, page 12) and had girths ranging between 100 and 200 cm. On immediate return from the field, approximately three days following collection, the bark material was oven dried at 60°C for 72 to 96 hrs. The bark material was then ground in a Wiley mill (40-mesh) and stored in sealed plastic bags at room temperature until the chemical assays were conducted. Bark samples were analysed for crude protein content using the Kjeldahl procedure (Furman 1962), and energy content using a CP 400 bomb calorimeter (Coalab supplies (Pty) Ltd., Johannesburg).

Secondary plant compounds

Bark material collected from six trees (girths ranging between 100 and 200 cm), randomly chosen along the Jwala and Majale rivers, was stored and dried using the same procedures as mentioned above for bark material assayed for crude protein and energy content. To standardise collection procedures, bark material was collected only from the eastern face of trees. With the exception of *Xanthocercis zambesiaca* and *Schotia brachypetala*, for which individuals that have no bark damage are rare, many of the trees sampled had bark damage inflicted by elephants.

The total phenol content of the bark samples was determined using the Prussian blue redox assay (Price & Butler 1977), as modified by Du Toit* (pers. comm.): 100 mg

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dry milled bark material was added to 5 ml MeOH and after 10 min centrifuged (3000 x g); after 10 min 30 ml H_2O and 3 ml 0.005 M $FeCl_3$ were added to a 0.5 ml aliquot of the extract; followed by the addition of 3 ml 0.008 $K_3Fe(CN)_6$; absorbance was read after 10 min at 720 nm in a spectrophotometer. Commercially available catechin was used as a standard.
The condensed tannin content of the bark samples was determined using the vanillin assay (Terill *et al.* 1990), as modified by Du Toit (pers. comm.): 100 mg dry milled bark material was added to 5 ml MeOH; after centrifuging for 10 min at 3000 x g, two 1 ml aliquots of the sample, representing the sample and the blank, were redissolved in a 5 ml MEOH solution (4 ml HCL, 96 ml MEOH and 2 g Vanillin reagent, excluding the vanillin from the blank); after 10 min in a waterbath (30° C), keeping the samples covered in aluminium foil to prevent light from biasing results, the absorbance was read in a spectrophotometer at 495 nm. Commercially available catechin was used as a standard.

The radial diffusion assay (Hagerman 1987) was selected to investigate the ability of tannins to precipitate proteins, due to its simplicity and absence of interference from low-molecular weight, non-tannin phenolics and water-insoluble compounds. In this method tannins diffuse through a protein-containing gel and a visible, disk-shaped precipitate (ring) develops as the tannin interacts with the protein. A 1% agarose solution (w/v) was prepared in a buffer (60 µM ascorbic acid and 50 mM acetic acid adjusted to a pH 5.0) and allowed to cool to 45°C after reaching boiling point; a protein (0.1% (w/v) Bovine Serum Albumin) solution was then added; small volumes (9.5 ml) were then poured into petri dishes which were allowed to cool and then stored at 4°C until used; five 4 mm diameter wells were bored in each gel; 2-3 (8 µl) aliquots of extract (100 mg dry bark material added to 0, 5 ml 70% acetone, left for 1 hr and centrifuged at 3 000 x g) were added to each well; the petri dishes were then sealed and allowed to incubate for 96 to 120 hrs at 30°C. The diameter of the precipitation rings were then measured; for each ring two diameters at right angles to one another were measured to minimize errors due to non-uniform ring development. An index of the tannin concentration of each bark sample was calculated as the square of the average of the two diameters. A value in excess of 0.16 cm^2 indicated the presence of a protein precipitate.

Results

Crude protein and energy

The crude protein and energy contents (mean ± SD) of the bark samples analysed are given in Table 10. The mean percentage crude protein ranged from 1.90% for *Combretum imberbe* to 14.9% for *Boscia albitrunca*. Little variation was, however, found for energy, ranging from 12.6 $kJ \cdot g^{-1}$ for

Combretum imberbe to 18.7 kJ·g^{-1} for *Colophospermum mopane*. No correlation was found between the preference ratio values (Appendix C) and either the crude protein (Spearman's Coef., r = -0.321, n = 11, P > 0.3) or energy (Spearman's Coef., r = 0.564, n = 11, P > 0.09) content of the barks sampled.

Table 10 Percentage crude protein and energy content (kJ· g^{-1}) of the barks of 10 common large riverine tree species in the Northern Tuli Game Reserve. The species are given in descending order of preference (see Appendix C for preference ratio values).

	Crude protein		Energy	
Species	Mean	SD	Mean	SD
Schotia brachypetala	3.89	0.27	18.25	0.65
Acacia nigrescens	7.59	1.33	17.90	0.95
Xanthocercis zambesiaca	4.67	0.84	17.41	0.33
Acacia tortilis	3.17	0.84	17.34	0.87
Combretum imberbe	1.90	0.29	12.59	1.62
Colophospermum mopane	3.29	0.43	18.69	0.46
Combretum hereroense	2.77	1.10	15.17	2.06
Lonchocarpus capassa	8.15	1.29	15.78	0.79
Croton megalobotrys	6.70	1.78	14.77	0.40
Boscia albitrunca	14.87	2.62	16.95	1.25

Table 11. Levels of total phenols and condensed tannins, expressed as catechin equivalents (mg· g^{-1} dry mass bark), and values obtained from the protein precipitation assay (cm^2). The species are presented in descending order of preference (see Appendix C for preference ratio values).

	Total phenols		Condensed tannins		Biologically active tannins	
Species	Mean	SD	Mean	SD	Mean	SD
Schotia brachypetala	52.78	12.26	34.28	12.61	2.09	0.49
Acacia nigrescens	34.44	38.72	27.27	16.69	8.0	0.29
Xanthocercis zambesiaca	61.12	30.46	62.13	8.86	0.16	0.00
Acacia tortilis	28.64	30.83	26.75	14.72	7.1	0.20
Combretum imberbe	53.03	21.67	34.38	12.36	0.87	0.37
Colophospermum mopane	10.06	12.66	4.49	9.41	0.16	0.39
Combretum hereroense	22.15	3.55	17.49	14.26	1.00	0.27
Lonchocarpus capassa	19.28	4.43	10.82	10.69	0.16	0.00
Croton megalobotrys	8.93	15.49	2.16	4.68	0.16	0.00
Boscia albitrunca	4.98	10.87	1.23	4.11	0.16	0.00

Secondary plant compounds

Given in Table 11 is the total phenolic and condensed tannin content (mean ± SD) of the barks analysed. Also given are the protein precipitation assay values. For all species, considerable between-tree variation for the values obtained for all three assays was found. No correlation was found between the preference ratio values and the means of either the total phenolic, condensed tannin or protein precipitation assays (Table 12).

Table 12. Correlation coefficients and significance levels for correlations between the preference ratio values (see Appendix C) and the mean values obtained from the total phenolic, condensed tannin and protein precipitation assays.

	Correlation coefficient	Level of significance
Total phenolics	0.527	0.114
Condensed tannins	0.176	0.598
Protein precipitation	0.503	0.131

Discussion

Defensive compounds produced by plants depend to a considerable extent upon the environment in which the plants grow (Waring *et al.* 1985). Strong seasonal changes in phenolic compounds of leaves (Feeny 1970; Dement & Mooney 1974; Ernst *et al.* 1991) and twigs (Palo, Sunnerheim & Theander 1985) has been documented. Generally, the phenolic content is highest at the start of the growing season. The lowest concentration of phenols in the leaves of Botswana savanna trees was found for July (Ernst *et al.* 1991). It is, therefore, probable that the levels of secondary compounds in the barks (collected in June) assayed during the present study are low relative to levels expected during other times of the year.

The similar levels of total phenols and condensed tannins found (see Table 11) would appear to indicate that a large percentage of the total phenolic content is condensed tannin and that these are responsible for the largest proportion of proteins precipitated. However, conclusions such as this have been strongly criticised by Mole and Waterman (1987b). It is important to note that these assays are biochemically independent, which means that values obtained for different assays cannot be compared.

Standard procedures for chemical assays, which are essential when assaying for tannins (Mole *et al.* 1989), were, as far was possible, followed during the present study. Nevertheless, considerable between-tree variation, within a species, was found for all three assays. It is likely that slight changes in light concentration or soil composition between areas where trees were sampled may have been responsible for these differences.

There is a danger in using correlative evidence to indicate that bark utilization is affected by tannins, because the concentration and types of tannins are often correlated with other factors known to be important to herbivores (Bernays, Driver & Bilgener 1989). For example, Ernst *et al.* (1991) found a strong correlation between high concentrations of nitrogen, phosphorous and potassium and high concentrations of phenolics. No correlations were, however, found during the present study and, therefore, it would appear that the preferential utilization of bark by elephants in the NTGR is not explained by secondary plant metabolites.

In a non-ruminant, where microbial fermentation takes place in the colon and caecum, condensed tannins that partly reduce the availability of structural carbohydrates may be less important than for ruminants (Jachmann 1989). It is also likely that, due to the fact that the trees sampled in the NTGR are indigenous, elephants may have evolved some defence against the allelochemicals in the bark of these species. Such defense may include bile constituents, known to interfere with the potential of tannins to precipitate proteins (Martin & Martin 1984; Mole & Waterman 1985) and/or specialized tannin-binding proteins in the saliva (Austin *et al.* 1989).

No relationship was found between the preferential utilization of the barks of large riverine trees in the NTGR by elephants and the percentage crude protein in these barks. Jachmann (1989) also found that, in general, food selection (leaves) was unrelated to protein content due to the fact that protein is probably available in sufficient amounts throughout the year. Jachmann (1989) showed that the mature foliage selected by elephants in the Miombo woodlands of Kasunga National Park was characterized by high sugar content (Jachmann 1989). The energy content of bark also showed no relationship to the preferential utilization of bark by elephants. This can most likely be attributed to the low variation in energy content of these barks.

In conclusion, the protein, energy and secondary plant metabolite content in the barks of the large riverine tree species of the NTGR do not, as single entities, explain the preferential utilization of bark by elephants in the Reserve. It is suggested that preference is attributable to other factors, such as the mineral content and fracture properties of bark, possibly in combination with the bark components analysed in this study.

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Chapter 6

GENERAL DISCUSSION

The findings of the present study pertaining to the main objectives proposed at the start of this study will be discussed separately for each objective.

Objective 1. *To determine the extent to which the species composition of the riverine tree communities in the NTGR, with respect to large trees, has changed in the recent past, and to assess the nature of these changes.*

Since the early 1970s a decline in density and change in the large riverine tree species composition of the NTGR has been noted (Lind 1974). During the present study, the remains of three individuals, representative of three large tree species (*Acacia caffra, A. burkei* and *Tarchonanthus trilobus*), were found in the riverine communities investigated. These individuals died prior to 1986 and each had signs of debarking and secondary damage inflicted by wood-borer insects. Elephants may have been responsible for the possible extinction of these species in the NTGR. If this were the case, their occurrence in the NTGR is likely to have already been rare in 1973 as no mention was made of them in Lind's report (Lind 1974). On the other hand, it may be argued that these specimens were relics at the margins of their species distributions.

Based on the dominance of certain large tree species at the sites inside and outside the NTGR, three vegetation zones were identified which lie parallel to the Limpopo River. It should be noted that these sites represent different zones in the drainage basin: upper, middle, lower. The tree communities in the northern, middle and southern zones are dominated by *Combretum imberbe* and/or *Colophospermum mopane*, *Croton megalobotrys*, and *C. megalobotrys* and *Acacia tortilis* respectively.

Edaphic factors are likely to have played an important role in the separation of these stands. Dye and Walker (1980), in a study conducted in Zimbabwe, attributed the separation of stands dominated by *Colophospermum mopane* and *Acacia* trees to factors such as soil depth, sodium content and permeability. The less frequent occurrence of *Croton megalobotrys* in the northern zone of the Reserve, compared to its occurrence in the middle and southern zones, may partly be attributable to edaphic factors. With the exception of the mention of its restricted distribution, only occurring on alluvial soils along rivers (Van Wyk 1984), no detailed studies on the ecology of *C. megalobotrys* have been reported in the literature. It is suggested that the present dominance of *C. megalobotrys* in the middle and southern zones of the NTGR has been facilitated by a high incidence of mortality of other large trees in the riverine communities. As elephant utilization does predispose trees to an accelerated mortality (Chapter 3, page 48), the high level of utilization of both young and mature trees by elephants is suggested to have given *C. megalobotrys* a competitive advantage over species more heavily utilized by elephants.

Factors which have facilitated the dominance of *C. megalobotrys* in the riverine tree communities of the NTGR include the following:

1) *C. megalobotrys* is fast growing, broadleaf species (Van Wyk 1984) which may prevent the establishment and growth of light-dependent species such as *Acacia albida* (Feely 1965) and *A. tortilis* (Smith & Shackleton 1989).

2) By comparison with that of other species considered in the present study, *C. megalobotrys* has a low large tree mortality rate (partly attributable to a low level of bark utilization by elephants, possibly coupled with the absence of wood-borer insect activity) and a large recruitment tree class component.

3) The seed anatomy of *C. megalobotrys* may afford it an immediate advantage over other species at the time of germination; splitting of the seed reveals the presence of an embryo with already developed leaves (not recorded for any other African tree species).

C. megalobotrys exhibits characteristics of a pioneer species. Its dominant status in the middle and southern zones of the NTGR, coupled with a tendency to form monospecific stands, may be indicative of the emergence of a retrogressive succession pattern in the riverine tree communities in these regions. Some individuals of this species die from causes which are apparently unrelated to elephant or wood-borer insect damage before they reach the large tree component (B.R. Page, pers. comm.)*. The dominance of large *C. megalobotrys* trees in the riverine communities of the NTGR is, however, likely to increase. This argument is based on the relatively large recruitment class component recorded and saplings observed during this study, the relatively low incidence of debarking and relatively low rate of mortality of this species and the likelihood of a decline in the large tree populations of the remaining species (as will be discussed later). It is suggested that the NTGR riverine tree communities may eventually be composed of *C. megalobotrys* thickets separated by only a few scattered large trees of other species.

In summary, this part of the study revealed a likelihood of a decline in the species richness of the riverine communities of the NTGR. This is represented by a possible loss of some species and an increase in the dominance of a single species. Owing to the relatively short

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period during which these could be determined (1986-1991), no detailed changes could be assessed in this study. However, these results form a basis for future studies.

Objective 2. *To determine the relative importance of elephants as agents of large tree mortality in the riverine tree communities of the NTGR.*

Woody plant material is the result of many years' of growth and is not easily replaced by the individual plant (Barnes 1982). By felling, pushing over or uprooting trees (as well as by the removal of the trunk bark) elephants may exert a major influence on woodlands (Cumming 1982). The removal of bark not only affects the carbohydrate supply link between the roots and leaves (Crawley 1983), but also exposes the tree to wood-borer beetle and fungal attack which often results in the death of the tree (Vesey-Fitzgerald 1973; Afolayan 1975; Thomson 1975).

Twenty-one percent of the trees sampled in the NTGR in May 1991 had bark damage inflicted by elephants. Species for which elephants had a preference included *Acacia nigrescens*, *A. tortilis*, *A. albida*, *Schotia brachypetala* and *Xanthocercis zambesiaca*, the latter three species being particularly favoured. The majority (80.5%) of debarked *Schotia brachypetala* trees at the Majale River sites had secondary damage inflicted by wood-borer insects following bark removal by elephants. The *Acacia* species also appeared, from general observations made in the field, to have a high incidence of wood-borer insect damage.

Thomson (1975), from observations made in *Brachystegia boehmii* woodland in the Chizarira Game Reserve, Zimbabwe, suggested that the majority of trees that are debarked by elephants, and subsequently damaged by wood-borer insects and exposed to fungal attack, are likely to die. It is likely that the longetivity of all debarked *Schotia brachypetala* trees in the NTGR with secondary damage caused by wood-borer insects following bark removal by elephants will be reduced. In this case, at least 80% of *S. brachypetala* trees in the southern zone and 37.5% of the *S. brachypetala* trees in the northern zone will show an accelerated mortality. This would be the case even if elephant activity were to cease immediately, which is unlikely. With the continued utilization by elephants, the mortality is expected to be somewhat higher.

An important issue to consider is the relationship between the rates of mortality and recruitment. With the exception of *Croton megalobotrys* and *Acacia tortilis*, relatively few recruitment class trees were recorded during this study. Owing to variable climatic and edaphic factors, the transition between the various tree size classes is likely to be stochastic. Therefore, in the long term, the mortality rate recorded in this study may not necessarily be threatening. In the short to medium term, however, the relatively high rate of mortality of the large *Schotia brachypetala* trees, largely attributable to elephant and wood-borer insect damage, is a cause for concern. This argument is based on the following: the likelihood of death of trees which have already been and continue to be damaged by elephants and wood-borer insects; the relatively high mortality rate of the large individuals and the relatively small number of recruitment class trees found. It should also be noted that not all recruitment class trees reach the large tree class. Some of the larger individuals in this tree component were identified with damage inflicted by elephants and wood-borer insects.

The majority of trees that died prior to 1986, between 1986 and May 1991 (as is evident from Fig. 6, Chapter 3, page 42) and between May 1991 and February 1992 (see Appendix D) had elephant damage (trees uprooted, debarked (sometimes followed by damaged inflicted by wood-borer insects) and/or ring-barked). A comparison was made between the proportion of debarked trees and undamaged trees that died between 1986 and May 1991. It is evident that for *Schotia brachypetala*, *Acacia tortilis*, *A. nigrescens*, *Combretum imberbe*, *Lonchocarpus capassa* and *Croton megalobotrys*, elephant damage is associated with an increased likelihood of death. Based on the comparisons mentioned above, the relatively high mortality rates (1986-

May 1991) recorded for debarked *Schotia brachypetala, Acacia nigrescens* and in particular *A. tortilis* trees are associated with a relatively high preference by elephants and a high incidence of secondary damage caused by wood-borer insects.

The climate of the region incorporating the Reserve is semi-arid tropical, with the rainfall being low and unpredictable (Harrison 1984). The prevailing dry conditions in the NTGR may have a detrimental effect on the long-term survival of trees in the Reserve, particularly those predisposed to mortality by high levels of bark utilization by elephants. Furthermore, under these dry conditions elephants may be expected to utilize the woody vegetation to a greater extent, thus depleting the large riverine tree component even further. However, the climate of the region incorporating the Reserve is semi-arid tropical, with the rainfall being low and unpredictable (Harrison 1984). It is, therefore, likely that these trees are adapted to the dry conditions. If the dry conditions do result in stress to the tree, owing to the dry climate of the region, it is likely that this has been the case for a relatively long period of time".

In summary, the relatively high mortality rates recorded for at least three species are suggested in part to be attributable to the activity of elephants, in particular the removal of bark. At the present levels of damage to trees, continued mortality is likely.

Objective 3. *To determine the present level of recruitment to the large tree component of the riverine communities in the NTGR.*

It is important to note that the mortality of large riverine trees, due to elephant damage and/or other factors (edaphic, climatic, disease) may not necessarily be a problem. Indeed, by thinning out a mature closed canopy of trees elephants may encourage the regeneration and recruitment of species such as *Acacia tortilis* which do not grow well in the shade (Mwalyosi 1990). However, for the continued long-term survival of trees in the NTGR, it is essential that the rate of recruitment to the large tree component exceeds the rate of mortality. Time limitation, as well as the absence of such data from previous studies, did not permit the assessment of recruitment rates to the large tree component in the riverine communities of the NTGR. However, determination of the present recruitment tree class component inside and outside the NTGR provided some information regarding possible processes occurring in these communities.

With the exception of *Acacia tortilis* and *Croton megalobotrys*, relatively few recruitment class trees were recorded for the large riverine tree species in the NTGR. The recruitment to the large tree component may vary (attributable to a variable seedling establishment and growth rate due to variable edaphic and/or climatic conditions) over time. It may, therefore, be argued that over a relatively long period of time the recruitment components provide relatively little, if any, information concerning the rate of change of the large tree component in the NTGR. It is, however, evident, from comparisons with the sites sampled outside the NTGR, that the level of recruitment to the large riverine tree component in the NTGR has been affected by some factor in the Reserve. For *Schotia brachypetala*, both inside and outside the Reserve, relatively few recruitment class trees were recorded. At the three sites sampled outside the NTGR, larger recruitment tree class components were recorded for *Lonchocarpus capassa*, *Acacia tortilis* and *A. nigrescens*, than were recorded at the eleven sites in the northern zone of the Reserve.

The germination of seeds is not constant, owing to variable edaphic and climatic conditions. As a result, the transition between the various tree size classes in the NTGR is also likely to be variable. The relatively low number of recruitment class trees sampled in the NTGR may be a reflection of this. The low number of recruitment class trees in the NTGR, compared to that outside, is suggested to be attributed to seedling mortality induced by browsers (elephant, impala, kudu, eland, duiker and steenbok) and/or unfavourable edaphic and climatic conditions, or a combination of these. Unfavourable edaphic and climatic factors may also have profound effects on seedling germination rates. Mortality may also occur once seedlings have reached the recruitment class. Seedlings of species other than *Croton megalobotrys* were noted in the present study to exhibit signs of heavy browser utilization.

In summary, with the exception of two species, a relatively low level, and for some species absence, of a recruitment tree class component in the riverine communities of the NTGR was recorded. It is suggested that the processes giving rise to this phenomenon should be studied in detail (eg., exclusion experiments to assess the impact of browsers). If these are found to be factors limiting transition of trees from the seedling to recruitment tree class, and from the recruitment to large tree class, then these may require management intervention.

Objective 4. *To investigate the relationship between the preferential utilization of bark by elephants and the fracture properties of the barks of large riverine tree species in the NTGR.*

Studies attempting to explain the preference shown by elephants for certain species have usually concentrated on the chemical composition (taste, smell, nutrition) of plant material. No attempts have been made to explain preferences by elephants for the bark of certain tree species in terms of their fracture properties. However, Thomson (1975) briefly mentioned this as a factor that may affect the preferential utilization of bark by elephants. The hypothesis that bark fracture properties influence the debarking of selected trees by elephants in the NTGR was tested during the present study. An index of bark breakage strength and pliability of secondary phloem tissue was compiled for 11 common riverine species, and the bark anatomy of the species was investigated to determine relative fibrosity.

Structurally, bark can be broadly interpreted as consisting of various proportions of soft (parenchymatous) and hard (sclerenchymatous) elements. The basis for the particular mechanical properties of bark is therefore complex, undoubtedly involving engineering principles associated with composite materials (Harris 1980). The most obvious structural variations between mature bark of different species usually involve aspects such as the composition, distribution and amount of sclerenchyma tissue. The most common sclerenchyma cell types are fibres and sclereids (for definitions see Trockenbrodt 1990).

The results on the mechanical properties of fibrous barks derived in the present study show that there are marked differences in strength and toughness between species. Generally, barks with gelatinous fibres and slight wall lignification, as in *Acacia nigrescens* and *A. tortilis* (preferred species), proved to be very strong and tough. The bark of *Colophospermum mopane* (a non-preferred species in the NTGR) with concentric zones of abundant crystalliferous strands (but with very thin, lignified secondary cell walls), showed similar mechanical qualities. In spite of the presence of exclusively cellulosic fibres, the bark of *Xanthocercis zambesiaca*, a markedly preferred species in the NTGR, turned out to be weak and brittle. The abundant secondary sclereids in this species may affect the mechanical properties of the bark of this species. In the remaining fibrous barks, strength and toughness appear to decline with an increase in the thickness of the lignified portion of the fibre walls. This may explain the relatively brittle bark in *Acacia albida* and *Schotia brachypetala*. The very thick and lignified secondary walls of the fibres in *Boscia albitrunca* (lumina almost absent), probably account for the relatively brittle bark in this species.

All the investigated barks in which sclereids predominate (all of which are non-preferred by elephants in the NTGR) are, as expected, weak and brittle. For these species (notably species of *Combretum*), elephants tend to remove small pieces of bark from around the circumference of the trunk, so that ring-barking is the principal form of damage. For tree species with fibrous barks, debarking by elephants often takes the form of ripping long strips of bark from the trunk. In the Sengwa Wildlife Research Area, Anderson and Walker (1974) found this type of debarking to be most pronounced in *Acacia tortilis, A. nigrescens* and *Brachystegia boehmii*.

In summary, species with bark that is relatively strong and pliable are preferred by elephants, but the reverse is not necessarily true. For example, *Acacia albida, Xanthocercis zambesiaca* and *Schotia brachypetala*, although they have barks which demonstrate a relatively low pliability and small breakage strength, are markedly preferred by elephants. It appears that, in addition to bark strength, factors such as chemical composition, moisture content and nutritive value of bark affect species choice.

Objective 5. *To investigate the relationship between the preferential utilization of bark by elephants and the content of crude protein, energy and secondary plant metabolites in the barks of large riverine tree species in the NTGR.*

Thomson (1975), for example, attempted to establish factors determining the preference of elephants for *Brachystegia boehmii* in the Chizarira Game Reserve, Zimbabwe, above four other species in the area (*Julbernadia globiflora, Brachystegia glaucescens, Colophospermum mopane* and *Acacia albida*). Detailed chemical analyses for several elements, ether extract and crude protein content failed to indicate any significant differences. Jachmann (1989) found mature foliage selected by elephants to be high in mineral and sugar content, whereas neglected species were high in total phenols and steroidal saponins. During the present study no correlations were found between the preferential utilization of bark by elephants and the content of crude protein, energy and secondary plant metabolites in the barks of large riverine tree species in the NTGR.

It seems unlikely, as stated by Ishwaran (1983), that any single factor would explain the species preference shown by elephants. It is suggested that the preferential utilization of bark by elephants in the NTGR may be explained by a combination of factors which possibly include factors investigated during the present study, particularly the fracture properties of bark.

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SUMMARY

The aim of this study was to determine the extent to which elephants have been responsible for changes in the species composition of the riverine tree communities in the Northern Tuli Game Reserve (NTGR), Botswana. In particular, the importance of elephants as agents of large riverine tree (girth measured just above basal swelling in excess of 1 m) mortality and the extent of bark damage to these trees inflicted by elephants was assessed.

Two-hundred trees were sampled at a total of sixteen sites located along the main rivers in the Reserve. For comparative purposes, the species composition and recruitment (trees with a girth of less than 1 m and height of greater than 1 m) of the large riverine tree component was determined at three sites outside the NTGR.

Species for which elephants showed a preference include *Acacia albida*, *Xanthocercis zambesiaca*, *Schotia brachypetala*, *Acacia tortilis* and *A. nigrescens*, the former three of which were markedly preferred. Species which have a bark that is relatively strong and pliable, such as *Acacia tortilis* and *A. nigrescens*, are preferred by elephants. The reverse is, however, not necessarily true: *Acacia albida*, *Xanthocercis zambesiaca* and *Schotia brachypetala*, the bark of which is markedly preferred by elephants, have bark which exhibits a relatively low pliability and breakage strength.

The percentage crude protein, energy content, total phenolic content and condensed tannin content of the bark of 10 common species in the NTGR do not, as single entities, appear to relate to the preferential utilization of bark by elephants. It is suggested that, in addition to bark strength, factors such as bark nutritive value may affect species choice.

Of the trees that died between 1986 and May 1991, 84.3% had elephant damage. The removal of bark by elephants, which is often followed by wood-borer insect damage, does predispose certain tree species in the NTGR to mortality. The relatively higher mortality rates recorded for *Acacia tortilis*, *A. nigrescens* and *Schotia brachypetala* are likely to be attributable to the preferences elephants have for their bark. Of the trees that died prior to 1986, 43% had elephant damage (a significantly smaller percentage than that for the period 1986 to May 1991). However, this percentage is likely to be much higher when one considers the length of time some of these trees had been lying in the field.

A small recruitment class component was found during the present study. In the long term, mortality of the large riverine trees is not necessarily threatening. In the short to medium term, however, based on the small recruitment class component, the relatively high mortality rates and continued damage by elephants and wood-borer insects of the large riverine trees, and damage to the relatively larger individuals in the recruitment class component by elephants and wood-borer insects, there is cause for concern for the large riverine trees of the NTGR.

Based on the species dominance at each site, three riverine vegetation zones were identified in the Reserve. The riverine tree communities in the northern, middle and southern zones are dominated by *Combretum imberbe* and/or *Colophospermum mopane*, *Croton megalobotrys*, and *C. megalobotrys* and *Acacia tortilis* respectively. With the exception of the absence of *Croton megalobotrys* outside the NTGR, little difference in large tree species composition between the sites inside and outside the Reserve was found.

C. megalobotrys is a fast growing, broadleaf species with a relatively low mortality rate, which is likely to be attributable to its low level of bark utilization by elephants. Large tree species other than *C. megalobotrys* are being removed from the ecosystem as a result of elephant damage and subsequent wood-borer insect activity. There appears to be a retrogressive succession pattern in the riverine tree communities of the NTGR towards monospecific stands of *Croton megalobotrys*, which is likely to be at a more advanced stage in the southern and middle zones of the Reserve than in the northern zone.

OPSOMMING

Die doel van hierdie studie was om te bepaal tot watter mate olifante verantwoordelik is vir veranderinge in die spesiessamestelling van die rivierboomgemeenskappe in die "Northern Tuli Game Reserve" (NTGR), Botswana. In besonder is die belangrikheid van olifante as agente van grootboom (gedefineer as bome met 'n stamomtrek, gemeet net bokant die basale swelling, van groter as 1 m) sterftes bepaal, sowel as die mate van basbeskadiging aan hierdie groot rivierbome toegedien deur olifante.

'n Totaal van twee honderd bome, in elk van sestien tereine geleë langs die hoof riviere in die reservaat, is ondersoek. Vir vergelykende doeleindes, is die spesiessamestelling en rekrutering (gedefineer as bome met n' stamomtrek van minder as 1 m en hoogte van meer as 1 m) van die groot rivierboom komponent vir drie tereine buite die reservaat bepaal.

Olifante het 'n voorkeur vir *Acacia albida*, *Xanthocercis zambesiaca*, *Schotia brachypetala*, *Acacia tortilis* en *A. nigrescens*, waarvan die eerste drie 'n hoë voorkeur geniet. Spesies wat 'n relatiewe sterk en buigsame bas besit, soos *Acacia tortilis* en *A. nigrescens*, word deur olifante verkies. Die teenoorgestelde is egter nie noodwendig waar nie: die bas van *Acacia albida*, *Xanthocercis zambesiaca* en *Schotia brachypetala*, bas waarvoor olifante 'n

groot voorkeur het, toon 'n relatiewe lae buigsaamheid en breeksterkte. Die persentasie ru protein, energie inhoud, totale fenool inhoud en gekondenseerde tanien inhoud van die bas van 10 algemene spesies in die NTGR blyk nie, as enkel bestandele, om 'n verwantskap te hê met die voorkeur van olifante nie. Dit word voorgestel dat, behalwe bassterkte, faktore soos bas voedingswaarde ook spesies se voorkeur mag bepaal.

Van die bome wat gedurende die periode 1986 tot Mei 1991 dood is, het 84.3% olifantskade getoon. Die verwydering van bas deur olifante, wat gewoonlik opvegolg word deur hout-boorder insek aktiwiteit, maak bome wel vatbaar vir die dood. Die relatiewe hoër mortaliteitstempos wat aangeteken is vir *Acacia tortilis*, *A. nigrescens* en *Schotia brachypetala* kan waarskynlik toegeskryf word aan die voorkeur van hierdie spesies deur olifante. Van die bome wat voor 1986 dood is, het 43% olifant skade getoon ('n hoër persentasie as die wat aangeteken is vir die bome wat tussen 1986 en Mei 1991 dood is). Hierdie persentasie is waarskeinlik hoër, as in ag geneem word dat van die bome al vir 'n redelik lang tydperk in die veld lê.

'n relatiewe klein rekruteringskomponent vir die grootboom spesies is waargeneem in die NTGR. Dus, oor die langtermein, is die mortaliteit van die groot rivierbome nie noodwendig 'n probleem nie. In die kort tot medium termein, egter, is daar rede vir kommer. Hierdie stelling is gebaseer op die klein rekruteringskomponent, die relatiewe hoë mortaliteitstempos en voortdurende skade aangerig deur olifante en hout-boorder insekte aan die groot bome, en skade aan die relatiewe groetr bome van die rekruteringsklas aangerig deur olifante en hout-boorder insekte.

Gebaseer op die spesiesdominansie by elke terein, is drie rivierplantegroei sones in die NTGR geïdentifiseer. Die rivierboomgemeenskappe in die noordelike, sentrale en suidelike zones is onderskeidelik oorheers deur *Combretum imberbe* en/of *Colophospermum mopane*, *Croton megalobotrys*, en *C. megalobotrys* en *Acacia tortilis*. Met betrekking tot die spesiessamestelling van die grootboomgemeenskappe is daar, behalwe vir die afwesigheid van *C. megalobotrys* buite die reservaat, min verskil tussen die tereine wat binne en buite die reservaat ondersoek is.

C. megalobotrys is 'n viniggroeiende, breërblaar spesies wat 'n relatiewe lae mortaliteitstempo. Die laasgenoemde kan waarskynlik toegeskryf word aan die lae vlak van basbenutting deur olifante. Met die uitsondering van *C. megalobotrys*, word grootboom spesies verwyder uit die ekosisteem as gevolg van olifantskade en die daaropvolgende hout-boorder insek skade. Daar is oënskynlik 'n agteruitgaande suksessie in die rivierboomgemeenskappe van die NTGR na 'n enkelspesiegemeeskap bestaande uit *Croton megalobotrys*, 'n suksessiepatroon wat waarskynlik in 'n meer gevorderde stadium in die suidelike en sentrale sones as in die noordelike sone van die NTGR is.

APPENDICES

Appendix A

Sample size of trees in the northern (N), middle (M) and southern (S) strata of the Northern Tuli Game Reserve, as well as outside (O) the Reserve.

	Sample size					Sample size			
	N	M	S	O	Species	N	M	S	O
Acacia albida	1	5	10	0	*Boscia foetida*	0	10	2	0
Xanthocercis zambesiaca	13	6	4	2	*Ficus sycamorus*	1	1	2	0
Schotia brachypetala	83	18	1	33	*Berchemia discolor*	1	3	0	0
Acacia nigrescens	66	17	0	16	*Albizia brevifolia*	7	8	0	0
Acacia tortilis	22	14	113	19	*Hyphaene natalensis*	1	0	0	0
Combretum hereroense	177	13	0	64	*Peltophorum africana*	0	0	0	3
Combretum imberbe	479	37	27	95	*Sclerocarya birrea*	3	0	0	5
Lonchocarpus capassa	199	33	25	62	*Cassia abbreviata*	4	2	0	0
Colophospermum mopane	597	20	0	294	*Sterculia rogersii*	6	10	0	0
Boscia albitrunca	37	16	0	0	*Pappea capensis*	1	0	0	0
Croton megalobotrys	33	303	153	0	*Lannea sweinfurthii*	4	1	0	0
Ziziphus mucronata	21	0	0	1	*Spirostachys africana*	7	1	0	0
Combretum apiculatum	27	10	0	4	*Commiphora glandulosa*	0	3	0	0
Terminalia pruniodes	24	2	0	1	*Kirkia acuminata*	0	1	0	0
Salvadora angustifolia	0	0	2	0	*Markhamia acuminata*	5	1	0	1

Appendix B

Number of recruitment class trees outside and in the northern zone of the Northern Tuli Game Reserve (NTGR).

Site	Ci	Lc	An	At
Outside				
BM1	9	23	8	220
BM2	20	34	3	30
BM3	57	18	34	44
NTGR				
A	19	6	2	6
C10	74	5	0	0
C20	0	0	0	1
D	5	1	0	37
E	5	11	0	3
F	59	5	0	11
G	1	3	1	9
H	53	3	1	4
I	17	7	2	1
J	80	5	0	1
K10	1	2	0	113
K20	0	0	0	544
M	90	13	0	14
X	6	5	0	31
Y	17	1	0	2
Z	7	3	0	8

Ci=*Combretum imberbe*; Lc=*Lonchocarpus capassa*; An=*Acacia nigrescens*; At= *Acacia tortilis*

Appendix C

Characteristics of debarked species sampled within the Northern Tuli Game Reserve riverine tree communities. Damaged = number of trees with bark damage; Total = number of trees living excluding trees inaccessible to elephants; U_i = percentage utilisation; A_i = percentage availability; PR = preference ratios.

Species	Damaged	Total	U_i	A_i	PR*
Acacia albida	7	16	5.98	0.61	9.73
Schotia brachypetala	20	100	17.09	3.84	4.45
Acacia nigrescens	8	81	6.84	3.11	2.20
Xanthocercis zambesiaca	17	21	1.71	0.81	2.12
Acacia tortilis	11	147	10.26	5.65	1.82
Combretum imberbe	33	536	28.21	20.59	1.37
Colophospermum mopane	20	617	17.09	23.70	0.72
Combretum hereroense	6	189	4.27	7.26	0.59
Lonchocarpus capassa	5	257	4.27	9.87	0.43
Croton megalobotrys	5	488	4.27	18.75	0.23
Boscia albitrunca	0	52	0.00	2.00	0.00
Ziziphus mucronata	0	20	0.00	1.15	0.00
Combretum apiculatum	0	30	0.00	1.15	0.00
Albizia brevifolia	0	11	0.00	0.42	0.00
Boscia foetida	0	12	0.00	0.46	0.00
Terminalia pruniodes	0	26	0.00	1.00	0.00

*

$$PR = \frac{\text{Percentage utilization (U)}}{\text{Percentage availability (A)}}$$

PR < 1: species neglected; PR = 1: species neither neglected nor preferred; PR > 1: species preferred.

Appendix D

Mortality of large riverine trees in the Northern Tuli Game Reserve between October 1991 and February 1992.

Date	Species	Cause of mortality	Site
Oct 1991	1	Wood-borer insect activity subsequent to debarking	K1
	1	Wood-borer insect activity subsequent to debarking	K1
Feb 1992	2	Wood-borer insect activity subsequent to debarking	C2
	3	Uprooted by elephants	F
	4	Wood-borer insect activity subsequent to debarking	G
	5	Uprooted by elephants	M
	6	Unknown	G
	7	Rot due to wood-borer insect activity/ no signs of elephant damage found	F

Species Key: 1 = *Acacia tortilis*; 2 = *Xanthocercis zambesiaca*; 3 = *Sterculia rogersii*; 4 = *Schotia brachypetala*; 5 = *Combretum imberbe*; 6 = *Colophospermum mopane*; 7 = *Sclerocarya birrea*