FACTORS INFLUENCING THE IMPACT OF ELEPHANTS ON WOODY VEGETATION IN PRIVATE PROTECTED AREAS 'N SOUTH AFRICA'S LOWVELD

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This dissertation is submitted in partial fulfillment of the requirements for the degree of Master of Science. I declare that this research report is my own unaided work. It has not been submitted previously for any degree or examination at this or any university.

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ABSTRACT

This study of the impact of elephants, *Loxodonta africana* (Blumenbach), in private reserves in South Africa's lowveld region aimed to determine the sizes and species of woody plants most often affected by elephants and the proportion and severity of elephant impact on the marula tree *Sclerocarya birrea*. The study was conducted in three parts: vegetation quadrats in areas where elephants had been foraging, direct observation of the feeding behaviour of hand-raised elephants, and transects to sample *S. birrea* across the study areas. To distinguish preferences, the frequency of elephant impact on each species was compared with the frequency with which it was encountered by the elephants. In the vegetation quadrats, I found that uprooting and leaf stripping were infrequent in all sizes of stems. Main stem breakage affected stems less than 30 cm in diameter whereas branch breakage and bark stripping increased with increasing size. Favoured species were *Combretum collinum, Acacia gerrardii, Albizia harveyi, Sclerocarya birrea, Dalbergia melanoxylon*, and *Pterocarpus rotundifolius*. Notable among neglected species were *Acacia tortilis, Terminalia prunioides*, and *Terminalia sericea* which are favoured food items for elephants elsewhere. Other common species which were not selected by elephants were *Acacia exuvialis, Cassine transvaalensis, Ehretia amoena, Euclea natalensis* and *Securinega virosa*. Behavioural observation revealed that hand-raised elephants favoured eating *Sclerocarya birrea, Combretum apiculatum*, and *Acacia nigrescens*. The elephants stripped bark from *A. nigrescens* and *S. birrea*. Assessment of marula trees revealed that elephant impact killed fewer than 2% of stems during the preceding season. Fewer than 24% of trees had current season breakage or bark removal. Main stem breakage was found in stems smaller than 40 cm in diameter. Ring barking was concentrated on the larger size classes, while the smaller size classes escaped any detectable form of elephant impact.

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CHAPTER 1. INTRODUCTION

1.1 Background

The relationship between elephants and trees has become known as the "elephant problem" in many African conservation areas. Increasing densities of elephants are often blamed for decreasing woodlands but the exact dynamics of this relationship have evaded ecologists and managers for many years.

As early as 1963, fears were voiced that elephant numbers were becoming artificially high in national parks and that increases in population size threatened to "drastically alter whole biotic communities within those areas" (Corfield 1973). Poaching reversed this trend in many countries where ivory hunting went unchecked, but with the ban on trade in ivory and recent improvements in law enforcement, the problem of high elephant density is resurfacing throughout the continent.

High elephant density combined with unusually low rainfall in the drought of 1970-1971 in Tsavo National Park in Kenya caused the death of almost one half of the park's 14 000 elephants (Corfield 1973). Improved understanding of elephant impact on the environment is necessary in order to prevent such die-offs and, wherever possible, to anticipate and prevent environmental damage inflicted by heavy elephant pressure by maintaining elephant numbers at a level which the local vegetation can tolerate. In Kenya, historical records and recent long-term scientific studies provide evidence that natural cycling between woodland and grassland occurs as a result of the combined impacts of elephants and fire (Dublin 1992). A model of the interactions of fire, elephants, and woodlands from data recorded in Zambia predicted similar cycling (Caughley 1976) but has not been proven. If such cycles exist, periodicity is on the order of 20 to 200 years which may be unacceptable recovery times from the point of view of a land-owner or park manager who does not want to see the landscape altered. Keeping the landscape static is a disruption of cycling, but human settlements and industrialized or cultivated areas which obstruct natural migration pathways have already disrupted the system. For these reasons and others, management decisions must be undertaken to prevent loss of woodland. Defining the elephant "carrying capacity" is very subjective and controversy has arisen over the scientific basis for elephant quotas prescribed for protected areas.

In Kruger National Park, the ceiling for the elephant population was fixed at 7 000 - 8 000 individuals for the 2 000 000 ha reserve. The excess was culled annually. As elephant numbers underwent drastic decline in other parts of the continent and questions arose about the humaneness of culling elephants, the continued culling of the Kruger elephants came under scrutiny (Walker 1991).

As an alternative to culling, elephant pressure can be alleviated by introducing or restoring elephants to other protected areas. The importance of elephants as a tourist attraction makes them a very valuable commodity (Moore 1991). As legislation made it possible for private landowners to purchase elephants and improved technology facilitated movement of live animals, more and more private ranches expressed interest in keeping elephants (Mulder 1991, Anderson 1991). In many cases, guidelines for stocking rates do not exist, or do not take into account the natural rate of increase of herds, and the elephants may have an undesirable effect on the land (De Villiers *et al.* 1991). Private landowners are now beginning to see the consequences of introducing elephants onto their land: many owners report a drastic decline of large trees in certain sections of their properties. Others are pleased with the decrease of woody vegetation brought about by the heavy browsing and uprooting done by the herds because it improves visibility for game viewing.

1.1.1 Elephant Feeding Ecology

Elephants are selective foragers at the landscape, habitat, species, and plant levels. The diet comprises mainly grasses, herbs, shrubs, and trees (Barnes 1983) but the proportion of each in the diet changes seasonally and spatially. In northwestern Uganda, grass levels as high as 94% of the droppings and 80-90% of overall stomach content were reported, but in woodland and bushland, levels around 30-50% are more typical (Laws *et al.* 1975). Trees and shrubs which elephants preferentially feed upon include members of the genera *Acacia, Azima, Balanites, Baphia,* some *Brachystegia, Combretum, Colophospermum, Cordia, Dalbergia, Grewia, Maerua, Pandera, Terminalia* and *Uapaca,* whereas *Boscia, Burkea, Capparis, Diospyros, Melia* and *Protea* spp. are rarely eaten (Vesey-Fitzgerald 1973, Laws *et al.* 1975, Owen-Smith 1988). Hypotheses for elephant food choice include nutritional content (either for energy, protein, fibre, or minerals) and mechanical properties which render the plant easy to eat.

Food selection is known to shift seasonally and nutritional intake also undergoes variation. In Uganda, the year round average intake for an elephant was 8.4% protein, 1.5% lipid, 43.5% carbohydrate, 35.7% fibre, and 11.0% inorganic ash (dry weight). These levels varied with rainfall, with protein changing the most significantly; from 12% after rains to 5% during the dry season (McCullagh 1969 in Laws *et al.* 1975).

Food is a significant factor governing movements and distribution of elephants in semi-arid zones and food availability is determined largely by the spatial and temporal pattern of rainfall (Leuthold and Sale 1973). Elephants congregate near permanent water supplies in the dry season, and disperse during and after rain (Leuthold and Sale 1973, Jachmann and Croes 1991). Within an area, emphasis on browsing rather than grazing is most extreme during the dry season (Anderson and Walker 1974, Jachmann and Croes 1991, Dublin 1992). Human modifications of the environment can intensify use of particular areas by disrupting traditional elephant pathways and preventing elephants from making large scale movements in response to resource supply.

Elephants typically pluck entire plants or bundles of vegetation, remove bark, heavily browse young saplings (Laws *et al.* 1975) or push over entire trees. Some studies show that elephants have the greatest impact upon younger age classes of trees by increasing seedling mortality and inhibiting seedling growth (Barnes 1983, Jachmann and Croes 1991, Dublin 1992, Tchamba 1995) while others (Croze 1974) report no bias in size class eaten. Vulnerability of seedlings, high nutrition and low fibre, and possibly low concentrations of secondary compounds may increase their susceptibility to being eaten (Barnes 1983). The possible benefit of elephant as combatants of bush encroachment has been suggested by DuToit (1991).

Elephants do not affect the vegetation equally: adult and subadult male elephants typically have a greater impact on woody vegetation than juveniles and calves (Guy 1976). Some studies have shown a dichotomy in tree pushing between adult male and female: males pushed 54 trees and females 17 trees in 365 hours of observation ($\chi^2 = 19.64$, $p < 0.001$) in Sengwa Valley, Zimbabwe (Guy 1976). The number of trees pushed per day is extremely variable from place to place; from 0.15 trees per hour of observation in Sengwa Valley (Guy 1976) to 0.02 per hour in the Serengeti National Park (Croze 1974).

Elephant utilization of vegetation has been quantified by dietary, behavioural or vegetation based research. Feeding behaviour and physiological studies have employed examination of faecal matter or stomach contents, observing bite size and rate, and vegetation-based methods have included examining trees for broken branches, missing bark, tusk marks or other sign (De Villiers *et al.* 1991, Barnes 1979, Laws *et al.* 1975).

1.1.2 Plant Responses to Elephant Utilization

Owing to their mass, their dietary needs, and their habit of uprooting trees, breaking branches and stripping bark, elephants are capable of altering trees more noticeably than any other vertebrate browser. Trees which are affected by elephants may be weakened to the point that the ability to withstand drought, insect borers, fungi, or fire is compromised (Vesey-Fitzgerald 1973, Thomson 1975).

Trees which have compensatory growth or coppice may respond positively to browsing with a net increase in primary production (Laws *et al.* 1975). Woody plants which have a spreading canopy and multiple stems (shrubs) are more resilient to breakage by elephants than woody plants with branches low to the ground and with one or two stems (Vesey-Fitzgerald 1973).

Trees typically initiate seasonal growth on standing biomass or by resprouting from below ground storage. Timing of herbivory on leaves has a strong influence on the tree's response (Owen-Smith 1988), as consumption of early growth may reduce growth potential for the rest of the season by removing the tissues necessary for capturing more photosynthetic energy and fueling growth.

Elephant use of browse is related to grass availability and therefore the rate at which trees are depleted is strongly dependent upon any events which alter grass availability (Dublin 1992). Megaherbivore populations are slow to respond to environmental changes. Their large body size and long gestation times buffer population sizes against rapid fluctuation (Owen-Smith 1988). When resources become depleted via exploitation competition, or environmental stress, consumers are prone to starvation. But when alternative resources are available, population collapse can be delayed or avoided (Owen-Smith, in prep.). Elephants are capable of switching to alternative food items, so tree loss is unlikely to have an immediate reaction in elephant numbers. The alternative food is likely to be of lower quality, requiring higher intake to sustain the same level of nutrition, but the consumer, in this case elephant, can still maintain high population numbers.

Elephant pressure on trees increases during drier, colder periods due to poorer quality of grasses. It is likely to decrease during the growing season when fresh green grass growth is available. Anything which leads to destruction of the grass layer will cause increased elephant reliance on the woody layer. High intensity grazing by other herbivores or fire may instigate such a shift in diet (Dublin 1992). Obstructing elephant migration routes will also increase pressure on trees by preventing elephant movement following rainfall (Croze *et al.* 1981).

Differential mortality among tree species used by elephants may reflect differences in resource needs of the elephants. For example, in southern Tanzania, elephants make use of *Acacia albida*'s shade, fruits and leaves during the dry season when resources are in short supply and feed on *Commiphora ugogensis* throughout the year but do not rely upon the latter for shade during the dry season (Barnes 1983). Since elephants affect trees so differently, it is erroneous to extend impact data from one species to another.

Tree loss is undesirable from many points of view. Reasons include aesthetic, economic and ecological importance (Barnes 1983, Laws *et al.* 1975). Trees provide shade, fruits, browse, and fallen leaves for herbivorous and detritivorous organisms, and play an essential role in the flow of nutrients within the system (Barnes 1983). In some cases, absolute size and species composition of woodlands can change when elephant pressure is intense (Pellew 1983), but elephants are nonetheless an essential part of their ecosystem (DuToit 1991). Feeding preference for certain species can cause a net decline of those species while permitting expansion of less palatable species (Laws *et al.* 1975). The unbrowsed trees may be unpalatable to all browsers thereby decreasing the overall browse available to ungulates and depressing the heterogeneity of the area (Moolman and Cowling 1994). Alternatively, elephants can eat some plants which are relatively unpalatable to other mammals (Viljoen 1991). Furthermore, elephants prevent thicket formation, open up paths to choice food spots and create waterholes (Viljoen 1991). Elephant browsing can maintain low-growing shrubs and stimulate coppicing at a height accessible to smaller sized browsing animals (Guy 1981, Viljoen 1991). Elephants are also credited with contributing to energy and mineral cycles by pushing over trees, preventing spread of veld fires by creating wide paths, forming pans by wallowing, and enhancing seed germination in dung (DuToit 1991, Viljoen 1991).

1.1.3 Previous Studies of Elephant Impact on Woody Vegetation

Studies of vegetation impact by elephants have been conducted at numerous sites throughout Africa, but the findings seem to be highly site-specific.

An assessment of 328 live baobab trees *Adansonia digitata* in Ruaha National Park, Tanzania revealed that 219 (68%) had been ring-barked (Barnes 1980). Although it is impossible to link tree decline with elephant impact without direct evidence, only 10 trees were found in the 0-24 year age-class which is the largest age class in a stable or increasing population. The damage to the baobabs was incurred mostly during the dry season, when elephants were most reliant on baobabs as a food source. During a five year period when rainfall remained constant but elephant density increased due to immigration, the density of *Acacia albida* trees decreased by 72% in one catchment area and 84% in another (Barnes 1985). From an aesthetic point of view, this loss is also significant, as the shady riverine groves of *A. albida* were once a tourist attraction. *Commiphora ugogensis* trees were believed to have suffered a 95% decrease in density over 15 years (Barnes 1985).

In the Chobe National Park and surroundings, the occurrence of affected plants and biomass removal from the canopy were independent of elephant density (Ben-Shahar 1993). Stem diameter was significantly correlated with degree of biomass removal from each species. Co-occurrence of new and old elephant feeding scars on the same trees revealed repeated usage by elephants.

1.1.4 Analyzing Utilization Preferences

Herbivores may eat or not eat plants for several reasons. Among these are metabolic considerations (nutrients and secondary metabolites), physical deterrents (thorns or spines), environmental conditions affecting either plant or animal (soil nutrient and light availability), or previous defoliation (Owen-Smith and Cooper 1987b), and accessibility.

Scientists typically describe herbivore preferences for plant species using one of several expressions which relate the frequency with which the animal feeds on the species to its availability. Preferred foods are those which are proportionately more frequent in the diet than in the available environment (Petrides 1975). For reasons discussed in Owen-Smith and Cooper (1987a), many commonly used expressions of food preferences are ambiguous, have difficult to calculate confidence limits, and are subject to the interpretation of the investigator. Preference ratings describe preference for a food species by dividing the percentage of the species which has been fed upon to its relative abundance in the environment (Petrides 1975). Preference ratings > 1 indicate preferred or favoured items whereas ratings <1 are interpretted as neglected or avoided items. Where feeding behaviour is recorded and a specific measure of local vegetation composition is available, site-based acceptance may better describe species "favoured" by the animal (Owen-Smith and Cooper 1987a) because it is limited to values between 0 and 1 and has a less arbitrary, though still subjective, delineation between preferred and non-preferred items.

1.1.5 Valuable Trees

In addition to their ecological importance, trees can be essential to the aesthetic appearance of an area. Park management in the Serengeti National Park regarded conservation of the *Acacia tortilis* woodland as high priority, in part because of its attractiveness to tourists (Pellew 1983). *Acacia albida* trees in Ruaha National park were valued shade trees (Barnes 1985). Managers in the eastern lowveld regard the marula tree, *Sclerocarya birrea,* as a crucial element of the scenery and are hesitant to acquire more elephants if elephants jeopardize the abundance of these trees (L. Sussens, pers. comm.).

The marula tree is a member of the Anacardiaceae family, which includes mangos, cashews, pistachios, and other economically important trees (Von Teichman *et al.* 1986). It is found throughout the eastern low altitude regions of southern Africa and is among the most highly valued of indigenous trees (Coates Palgrave 1977). Its leaves and bark are used for medicinal purposes (Shone 1979 in Von Teichman *et al.* 1986), the oil of its seeds has cosmetic uses, and various plant parts are used in religious ceremonies by Tonga, Tsonga and Venda peoples (Coates Palgrave 1977). The marula tree's edible fruit can be consumed directly, processed into juice or jam, or fermented into various alcoholic beverages (pers. obs.).

In spite of its popularity, the tree is harvested for fuel wood on communal lands in Mpumalanga and Northern Provinces (pers. obs.). The tree has been declared a protected tree in South Africa (Coates Palgrave 1977) and many local authorities have prohibited cutting of live trees (pers. obs.). Trees which have economic value warrant conservation for financial reasons. Marula trees are a desired and valuable resource and it is important to establish whether conservation of the species is compatible with conservation of elephants.

1.2 Project Motivation

Measurements of the type and extent of woodland alteration are necessary in order to accurately document elephant depletion of woody vegetation. Recently introduced elephant herds in private wildlife reserves in the eastern lowveld of South Africa provided the opportunity to examine elephant impact on woody vegetation in somewhat controlled conditions; the elephant population size was known, and remained constant throughout the study period.

1.3 Objectives

1 To determine which species of woody plants are prone to elephant impact.
2 To determine which sizes of woody plants are most susceptible to elephant impact.
3 To document elephant impact on the smallest size classes of woody plants.
4 To determine the proportion of marula trees *Sclerocarya birrea* which have been affected by elephants.
5 To determine the rate at which marula trees have been affected by elephants.

1.4 Hypotheses

1 Locally occurring woody plant genera likely to be severely impacted will include *Acacia, Balanites, Combretum, Dalbergia, Grewia, Sclerocarya* and *Terminalia* species.
2 Species which are known to be preferred browse elsewhere (listed in Hypothesis 1) will experience heavy impact in small size classes. Species which only experience bark removal will be utilized only in the larger size classes.
3 Elephant use of marula trees, *S. birrea*, is related to proximity to road and presence of fruit.

1.5 Terms and Abbreviations

The term "impact" will be used to describe all forms of biomass loss or alteration. Impact includes loss to leaf plucking, breakage, ring-barking, bark stripping, and tusk gouging. Utilization will refer specifically to consumption while damage will refer to pushing or destroying without any evidence of being eaten.

BB	Branch breakage
BS	Bark stripping
cm	centimetre
et al.	*et alii*
ha	hectare
in prep.	in preparation
km	kilometre
LS	Leaf stripping
m	metre
MSB	Main stem breakage
pers. obs.	personal observation
pers. comm.	personal communication
RB	Ring-barking
TG	Tusk gouging
unpubl.	unpublished
UPROOT	Tree broken at or below ground level

1.6 Study Areas

The study was conducted on three properties in the eastern lowveld of the Mpumalanga and Northern Provinces of South Africa (Figure 1.1). The three study areas were less than 30km apart. The properties are approximately 20-30km west of the eastern border to the Kruger National Park, between the Phalaborwa and Orpen gates. The region is characterized by flat to undulating topography. Most precipitation occurs during the summer months of October, November, January, and February (Agricultural Research Council, unpubl. data).

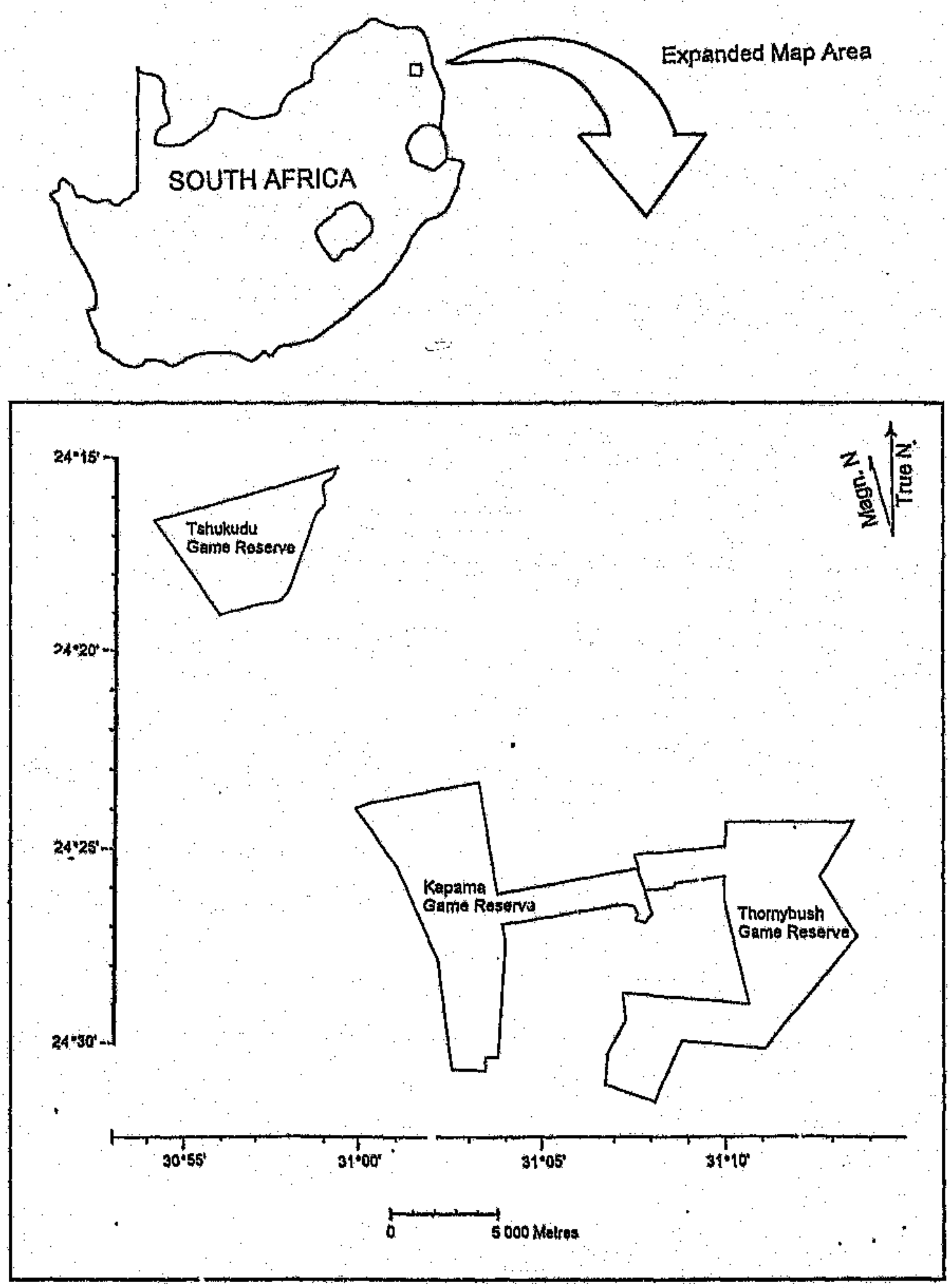

Figure 1.1 Map of study areas.

Research on wild elephants was conducted between August and December 1996 on the Kapama and Thornybush Private Game Reserves. Both properties have fenced perimeters; elephants did not migrate outside of the game reserve and population density did not fluctuate during the course of my study. On both properties, the elephants were said to spend more time in certain areas, but during this study, they traversed the entire space available to them.

Research on two hand-reared elephants took place between August and December 1996 on Tshukudu Private Game Reserve. The subjects were both nine year old elephants which were purchased as two-year old calves and were habituated to humans.

1.6.1 Kapama

Kapama Wildlife Reserve is situated at 24°22'S and 31°04'E, 500 m above mean sea level. Mean annual rainfall between July 1983 and June 1996 was 511 mm (SD = 177 mm, max = 950 mm during 1995-96, min = 240 mm during 1991-92) (Agricultural Research Council, unpubl. data).

Kapama had 21 elephants on approximately 7 000 hectares (overall density = 0.30 elephants per km^2). Eighteen were subadults and three were youngsters (two less than one year old). All were purchased from the Kruger National Park. At first, six youngsters were released on Kapama in 1992 and were initially very agitated, moving rapidly through the bush and were rarely seen by visitors. With the addition of older cows and a bull in 1994, the herd became calmer and settled in the northern portion of the reserve.

When asked about specific concerns about the elephants' behaviour, Kapama managers were concerned about a decline in the number of big trees on the property.

1.6.2 Thornybush

Thornybush Private Game Reserve is located at 24°22'S and 31°11'E, 500 m above mean sea level. Mean annual rainfall between July 1992 and June 1996 was 593mm (SD = 299 mm, max = 985 mm during 1995-96, min = 336 mm during 1993-94)(Agricultural Research Council, unpubl. data).

Thornybush had a total of 21 elephants on 7 500 ha (overall density = 0.28 elephants per km²) which typically stayed in two separate herds plus two roaming males. A herd of nine animals was purchased in 1993 from Mabula Game Lodge. The herd was well settled and could be approached by vehicle. A second group of 11 animals was purchased in 1994 from Kruger National Park. This herd was initially relatively unpredictable in both ranging behaviour and reaction to people and vehicles, but at the time of this study was easily observed from a vehicle. Though both herds had dominant females which led, the herds were relatively young with all animals less than 25 years of age. The two bulls on the property were also not fully mature.

Thornybush management personnel expressed concern about elephants killing large trees.

1.6.3 Tshukudu

Tshukudu Game Reserve is located at 24°15'S and 30°55'E, 500 m above mean sea level. Mean annual rainfall between July 1989 and June 1996 was 414mm (SD = 147 mm, max = 666 mm during 1995-96, min = 179 mm during 1991-92) (Agricultural Research Council, unpubl. data).

Tshukudu had no wild elephants on the property. Two elephants were purchased as orphans from a cull from Kruger National Park in February 1990. The male and female were estimated to have been born in 1988. Initially the animals were kept in a boma, but at the time of the study were only confined by the property's perimeter fence and an exclosure around the main lodge. When purchased, the elephants were aggressive towards all people. After repeated contact, they became accustomed to the company of one Tshukudu employee to the point that they followed him wherever he went. With age, the two became more independent, but both still recognized the employee, and the female was particularly dependent on human attention, seeking out human company and physical contact. During this study, the elephants foraged freely but were occasionally given feed cubes by the landowners. The two also ate small amounts of discarded vegetable refuse which was dumped in the bushes outside the main lodge.

When asked if the elephants were causing any problems, the land owners said that they were causing noticeable damage by breaking trees. The owners expressed concern about the marula trees which they said the elephants were knocking over. Because the elephants were accustomed to interaction with people and seemed to seek out human attention, they stayed close to the lodge during the day and may have been causing a disproportionate amount of damage in the vicinity of the lodge.

1.7 Overview of Methods

1.7.1 Quadrats on Elephant Paths

In the first part of the study, I assessed vegetation quadrats in areas which elephants had just passed through in order to measure elephant impact on woody plants. By examining all woody plant stems in the vicinity of fresh elephant impact, I was able to address questions about the habitat and vegetation, the type and extent of impact, and differences in impact on each species and size of woody plant.

1.7.2 Hand-Raised Elephant Observation

The second part of the study was devoted to behavioural observation of two hand-raised elephants. By pairing the vegetation-based research with direct observation of elephants at close range I was also able to identify and quantify their intake of the smallest size classes of woody plants more precisely than is possible by following elephants at a distance. Elephants which were accustomed to human beings and could be approached on foot allowed the opportunity to obtain information on the exact woody plant intake, especially of plant species or sizes which would be difficult to identify from a distance.

1.7.3 Survey of a Valuable Tree Species

A detailed survey of elephant impact on a single tree species was a logical accompaniment to the vegetation and behavioural studies. At many elephant areas in the region, land owners and managers were concerned about the loss of large trees due to pushing or bark removal by elephants (M. Peel, pers. comm.). In my study areas, managers were most frequently concerned about the destruction of large trees, and the marula tree specifically. The marula tree *Sclerocarya birrea*, a species valued by humans, is also favoured by elephants. Localized elephant use of marulas could give an inaccurate impression of the overall extent of damage to the population on each property, so a survey was designed to sample the subpopulation at each area. In areas which have had elephants for several years, it is impossible to pinpoint the time scale of elephant impact, but Kapama, Thornybush and Tshukudu only recently obtained elephants, so the rate of damage could be established.

CHAPTER 2. IMPACT OF ELEPHANTS ON VEGETATION ALONG FEEDING PATHWAYS

2.1 Introduction

Between 03 September 1996 and 28 November 1996, vegetation quadrats on elephant foraging paths were surveyed on Kapama, Thornybush, and Tshukudu Game Reserves. In all, 13 052 individual woody stems were enumerated, measured and assessed for elephant impact.

Elephants affected woody vegetation by uprooting stems, breaking main stems or branches, and stripping bark or leaves. These types of impact were examined for patterns in sizes and species of woody plant stems commonly affected. The degree to which elephants used different species was analyzed by comparing the incidence of impact to the overall abundance of the plant. Many of the species which are known to be used by elephants elsewhere in Africa (section 1.3) coincided with species with high incidences of impact at my study areas, but some species were surprisingly under-utilized in comparison to other studies.

2.2 Materials and Methods

Wild elephant herds at Kapama and Thornybush Game Reserves were located by looking for fresh elephant spoor from a vehicle. Only tracks or dung which were believed to be less than 12 hours old were followed, thereby limiting the scope of the study to elephant impact during the late night and early morning hours. From the point at which elephant tracks were intercepted, the tracks were followed towards the animals. If the animals were visible or audible from the road, the tracks were not followed until the animals had moved out of sight and out of hearing range so as to minimize risk of injury to researchers and to prevent disturbing the animals and altering their behaviour.

During a preliminary observation period prior to the start of data collection, it was determined that direct observation of feeding behaviour of wild elephant herds was not possible; even herds which could be approached closely could not be seen clearly, nor followed directly owing to the dense vegetation in the area. However, trees freshly broken by elephants were easily found. Although the path of a single animal could not be followed, patches of impact were easily located. In most cases, sites of impact were close enough together that an elephant at one site could have had access to all the vegetation in between the two sites; so although the exact path was not known this sufficed as a measure of vegetation available to the foraging elephant(s). By connecting the two nearest neighbouring sites of impact, a path was inferred to allow assessment of plants in the vicinity of the elephant(s) and, of those, which were eaten or broken.

Sample quadrats of 5 m radius at sequential points along the putative feeding pathway were assessed. I spaced quadrats 15 m apart to reduce autocorrelation between the sampling sites. The line connecting the visible areas of elephant use was constructed by placing the 0 m mark of a measuring tape at the first sign (broken branches or broken tree visible from road) and laying the tape along the tracks, dung and broken vegetation. The quadrats were then centred at the 10 m mark, and then the 25 m, the 40 m, and the 55 m mark, and so on until (a) the sign was no longer traceable; or (b) five sequential quadrats were assessed. The centre point of the 5 m circle was at the appropriate metre mark on the tape. Quadrats were surveyed shortly after the elephants moved through, so fresh sign was obvious: broken branches still had living leaves and exposed stems were still wet.

For the first nine weeks, each game reserve was visited once per week, and during the last three weeks (10-12) only Kapama and Thornybush were visited. During 33 field days devoted to this part of the survey, 243 5 m circle quadrats were surveyed on 56 independent feeding paths. Owing to inclement weather, time constraints, difficulty in finding elephant spoor, the number of quadrats varied from 4 to 15 per day.

Fresh breakage and gouges in the immediate vicinity of other damage were assumed to also be caused by elephants. Old damage was recorded in a separate category and is likely to include some damage inflicted by other animals so is not included in this report.

All live or just-killed woody plants with at least half of the main stem base inside the quadrat were included. If multi-stemmed shrubs were partially in, only the stems with bases inside the quadrat were included. The survey was based on number of stems, rather than the number of distinct individuals, so no attempt was made to distinguish multiple trees from multi-stemmed individuals. All woody plants within the quadrat were identified to species level, measured and classified. The circumference of the main stem above the basal swelling was measured to the nearest centimetre. Plants smaller than 2 cm in circumference were classified as 2 cm. The height of each tree was visually estimated to the nearest 0.5 m.

Biomass loss due to elephants was categorized into five categories: 1) uprooting, 2) main stem breaking, 3) branch breaking, 4) bark stripping, and 5) leaf stripping (after Ishwaran 1983, McDonald 1992, Wackernagel 1992). The height of impact point (if any) was estimated to the nearest 0.5 m. Where entire branches or stems were broken off, the circumference and height of these breakage points were recorded. The proportion of the overall plant which was removed was visually estimated (after Anderson and Walker 1974). Breakage was categorized as branch breakage (BB) when the stem had forked into two or more branches. Proportion was visually estimated as the fraction of biomass which had been removed, judging from the size of the break in relation to the remaining branches at the break point. If all above-ground biomass was removed, breakage was categorized as 100%. However, trees capable of coppicing or initiating growth from below-ground biomass were not necessarily killed by total main stem breakage.

Basal cover and stem diameter were calculated from the stem circumference measured in the field. Woody plants are grouped into size classes by the stem diameter above the basal swelling for the purpose of discussion. Stems with a diameter of 2 cm or less (0-2 cm class) will be referred to as "seedlings".

Elephant preferences for each species cannot be assessed without taking availability into account. Site-based acceptance frequencies (Owen-Smith and Cooper 1987a) were calculated for each species using the following equation:

$$= \frac{\text{Number of vegetation quadrats in which the species was eaten or damaged by elephants}}{\text{Number of vegetation quadrats in which the species was present}}$$

Acceptance frequencies can range from 0 to 1. The maximum possible acceptance frequency (corresponding to a species which is eaten or damaged in 100% of quadrats) is 1.0. The mean acceptance ratio for each species was calculated by pooling the number of quadrats with impact from all three game reserves and dividing it by the pooled number of quadrats in which the species was present on all three game reserves. Data were analyzed using the number of quadrats in which the species was present rather than the number of stems to reduce autocorrelation.

χ^2 tests (Zar 1996) were used to test for significant differences between site-based acceptance frequencies for each woody plant species at each property.

Taxonomy follows Coates-Palgrave 1983 and Van Wyk 1984.

2.3 Results

2.3.1 Local Vegetation

During the survey, 80 distinct species were found, representing 51 genera and 25 families (See Appendix A for scientific names, common names, families and authors). Five additional species were identified to genus level. Eighty-six stems could not be identified to genus or species level (0.66% of total stems in sample). In most cases, these unidentifiable plants were leafless and flowerless so specimens were not taken. However, these represented such a small percentage of the total sample that they are unlikely to have significantly influenced the results.

2.3.2 Community Structure

The mean stem density for the three properties combined was one stem per 1.46m^2, or 6 839 stems · km^{-2}. Basal cover on all three properties was less than 0.2% (Table 2.1). Tshukudu had the lowest stem density but the highest basal cover due to large, but relatively few, stems . Stem densities ranged from 7670 ha^{-1} at Kapama, to 4145 ha^{-1} at Tshukudu. Stem basal cover ranged from 10.57 m^2 ha^{-1} at Thornybush to 16.69 m^2 ha^{-1} at Tshukudu.

Table 2.1. Number and density of woody plant stems at each study area.

	Kapama	Thornybush	Tshukudu
Quadrats	104	93	46
Independent paths	22	24	10
Area sampled (m^2)	8168	7304	3612
Total stems	6265	5290	1497
Basal cover (m^2)	10.80	7.72	6.03
% of ground covered with stems	0.13%	0.11%	0.17%
Stems per hectare	7670	7243	4145
Coverage per hectare (m^2 ha^{-1})	13.22	10.57	16.69

At all three study areas, the smallest size classes were best represented, and bigger trees were less common (Table 2.2). See Appendix 2 for size class percentages for each species.

Table 2.2. Size class distribution of woody plants on each property.

Diameter (cm)	Kapama	%	Thornybush	%	Tshukudu	%
<2	3558	57%	3394	64%	952	64%
2-5	1495	24%	1089	21%	381	25%
5-10	899	14%	593	11%	94	6%
10-20	291	5%	194	4%	36	2%
20-30	15	0%	14	0%	11	1%
30-40	5	0%	3	0%	8	1%
40-60	2	0%	2	0%	9	1%
60+	0	0%	1	0%	6	0%
Total stems	6265		5290		1497	

When data from all three properties were pooled, *Sclerocarya birrea* was dominant by total basal cover, followed by *Acacia gerrardii, Acacia nigrescens, Combretum collinum, Combretum apiculatum, Dalbergia melanoxylon*, and *Pterocarpus rotundifolius* (Table 2.3).

Table 2.3. Dominant 25 woody plant species according to pooled basal cover at Kapama, Thornybush and Tshukudu Game Reserves.

Woody species	Sum of area	% of woody cover
Sclerocarya birrea	2.68	10.94%
Acacia gerrardii	2.46	10.05%
Acacia nigrescens	2.38	9.70%
Combretum collinum	2.10	8.55%
Combretum apiculatum	1.80	7.33%
Dalbergia melanoxylon	1.28	5.22%
Pterocarpus rotundifolius	1.26	5.14%
Combretum hereroense	0.93	3.78%
Albizia harveyi	0.87	3.54%
Lannea schweinfurthii	0.77	3.12%
Terminalia sericea	0.65	2.67%
Ormocarpum trichocarpum	0.60	2.45%
Combretum imberbe	0.52	2.13%
Dichrostachys cinerea	0.52	2.12%
Strychnos madagascariensis	0.40	1.65%
Acacia tortilis	0.38	1.55%
Peltophorum africanum	0.37	1.49%
Maytenus heterophylla	0.36	1.48%
Commiphora mollis	0.35	1.43%
Grewia monticola	0.34	1.37%
Bolusanthus speciosus	0.33	1.36%
Acacia exuvialis	0.31	1.25%
Combretum zeyheri	0.28	1.13%
Lonchocarpus capassa	0.26	1.05%
Euclea divinorum	0.26	1.04%

When examined by total number of stems rather than by basal cover, species with smaller stems ranked higher (Table 2.4). However, 17 of the 25 most common species by number of stems were also among the 25 dominant species according to basal cover, so there was substantial overlap. Species which were dominant by number of stems but not by area were *Cassine transvaalensis, Cissus cornifolia, Ehretia amoena, Grewia bicolor, Grewia flavescens, Grewia hexamita, Grewia villosa,* and *Securinega virosa*. Conversely, species which were dominant by area but not by stem numbers were *Acacia tortilis, Bolusanthus speciosus, Combretum imberbe, Commiphora mollis, Lannea schweinfurthii, Lonchocarpus capassa, Peltophorum africanum*, and *Sclerocarya birrea*. *Grewia flavescens* had the most stems, followed by *Dalbergia melanoxylon* and *Grewia monticola*.

Table 2.4. Dominant 25 woody plant species according to pooled number of stems at Kapama, Thornybush and Tshukudu Game Reserves.

Woody species	Total stems	% of all stems
Grewia flavescens	878	6.73%
Dalbergia melanoxylon	762	5.84%
Grewia monticola	762	5.84%
Strychnos madagascariensis	689	5.28%
Combretum apiculatum	625	4.79%
Combretum collinum	595	4.56%
Ormocarpum trichocarpum	586	4.49%
Pterocarpus rotundifolius	576	4.41%
Ehretia amoena	539	4.13%
Acacia gerrardii	530	4.06%
Combretum hereroense	501	3.84%
Acacia exuvialis	495	3.79%
Grewia bicolor	446	3.42%
Acacia nigrescens	414	3.17%
Albizia harveyi	390	2.99%
Securinega virosa	387	2.97%
Dichrostachys cinerea	379	2.90%
Maytenus heterophylla	349	2.67%
Euclea divinorum	325	2.49%
Cissus cornifolia	299	2.29%
Combretum zeyheri	240	1.84%
Grewia hexamita	174	1.33%
Terminalia sericea	169	1.29%
Grewia villosa	141	1.08%
Cassine transvaalensis	114	0.87%

Kapama Game Rese·ve ·· is dominated by *Combretum collinum* and *Acacia gerrardii* (Table 2.5). *Acacia exuvialis, Acacia tortilis, Bolusanthus speciosus, Combretum imberbe, Euclea divinorum,* and *Grewia monticola* were less common than in the other areas. *Balanites maughamii* was common at Kapama but not found elsewhere.

Table 2.5. Woody species abundance by overall basal cover at Kapama Game Reserve ,ncludes only species which contributed >1% of overall basal cover.

Rank	Species	Total stem area (m^2) of 8168 m^2	% of ground covered by species	% of total woody plant cover
1	*Combretum collinum*	1.71	0.02%	15.79%
2	*Acacia gerrardii*	0.98	0.01%	9.09%
3	*Pterocarpus rotundifolius*	0.98	0.01%	9.03%
4	*Combretum apiculatum*	0.89	0.01%	8.22%
5	*Dalbergia melanoxylon*	0.67	0.01%	6.23%
6	*Albizia harveyi*	0.64	0.01%	5.96%
7	*Terminalia sericea*	0.45	0.01%	4.15%
8	*Lannea schweinfurthii*	0.44	0.01%	4.12%
9	*Strychnos madagascariensis*	0.40	0.00%	3.75%
10	*Combretum hereroense*	0.35	0.00%	3.28%
11	*Ormocarpum trichocarpum*	0.35	0.00%	3.26%
12	*Acacia nigrescens*	0.30	0.00%	2.78%
13	*Combretum zeyheri*	0.27	0.00%	2.49%
14	*Lonchocarpus capassa*	0.25	0.00%	2.31%
15	*Dichrostachys cinerea*	0.21	0.00%	1.92%
16	*Commiphora mollis*	0.19	0.00%	1.79%
17	*Sclerocarya birrea*	0.19	0.00%	1.73%
18	*Peltophorum africanum*	0.19	0.00%	1.73%
19	*Balanites maughamii*	0.14	0.00%	1.32%
20	*Maytenus heterophylla*	0.12	0.00%	1.08%
	TOTAL	10.80	0.13%	

Thornybush was dominated by *Acacia* savanna. *Acacia tortilis, Combretum imberbe, Com zeyheri, Commiphora mollis, Lannea schweinfurthii, Lonchocarpus capassa*, and *Strychnos madagascariensis* were less common than in the overall rankings (Table 2.6). *Diospyros mespiliformis* and *Ziziphus mucronata* were more common at Thornybush than at the other two areas.

Table 2.6. Woody species abundance by overall basal cover at Thornybush Game Reserve. Includes only species which contributed >1% of overall basal cover.

Rank	Species	Total stem area (m^2) of 7304 m^2	% of ground covered by species	% of total woody plant cover
1	*Acacia gerrardii*	1.34	0.02%	17.39%
2	*Acacia nigrescens*	0.72	0.01%	9.38%
3	*Dalbergia melanoxylon*	0.61	0.01%	7.88%
4	*Combretum apiculatum*	0.51	0.01%	6.56%
5	*Combretum hereroense*	0.48	0.01%	6.25%
6	*Sclerocarya birrea*	0.41	0.01%	5.29%
7	*Combretum collinum*	0.34	0.00%	4.38%
8	*Bolusanthus speciosus*	0.30	0.00%	3.89%
9	*Pterocarpus rotundifolius*	0.29	0.00%	3.71%
10	*Dichrostachys cinerea*	0.25	0.00%	3.25%
11	*Maytenus heterophylla*	0.24	0.00%	3.16%
12	*Ormocarpum trichocarpum*	0.24	0.00%	3.15%
13	*Albizia harveyi*	0.21	0.00%	2.69%
14	*Terminalia sericea*	0.21	0.00%	2.66%
15	*Euclea divinorum*	0.20	0.00%	2.56%
16	*Peltophorum africanum*	0.18	0.00%	2.28%
17	*Grewia monticola*	0.17	0.00%	2.22%
18	*Acacia exuvialis*	0.17	0.00%	2.19%
19	*Diospyros mespiliformis*	0.16	0.00%	2.01%
20	*Ziziphus mucronata*	0.14	0.00%	1.78%
21	*Grewia flavescens*	0.09	0.00%	1.20%
	TOTAL	7.72	0.11%	

Tshukudu was dominated by a smaller subset of woody plants than the other two reserves. Its dominant species, *Sclerocarya birrea*, covered almost twice the overall basal cover of any species on the other two sites (34.64% in comparison to 15.79% at Kapama and 17.39% at Thornybush). The second most common species at Tshukudu, *Acacia nigrescens*, also covered more area than the most dominant species elsewhere. *Cordia* spp. were common at Tshukudu but not at Kapama or Thornybush.

Table 2.7. Woody species abundance by overall basal cover at Tshukudu Game Reserve. Includes only species which contributed >1% of overall basal cover.

Rank	Species	Total stem area (m^2) of 3612 m^2	% of ground covered by species	% of total woody plant cover
1	*Sclerocarya birrea*	2.09	0.06%	34.64%
2	*Acacia nigrescens*	1.36	0.04%	22.48%
3	*Combretum imberbe*	0.47	0.01%	7.82%
4	*Combretum apiculatum*	0.40	0.01%	6.70%
5	*Acacia tortilis*	0.38	0.01%	6.30%
6	*Lannea schweinfurthii*	0.29	0.01%	4.79%
7	*Acacia gerrardii*	0.14	0.00%	2.32%
8	*Acacia exuvialis*	0.12	0.00%	2.07%
9	*Commiphora mollis*	0.11	0.00%	1.89%
10	*Combretum hereroense*	0.09	0.00%	1.46%
11	*Grewia monticola*	0.08	0.00%	1.39%
12	*Cordia* sp.	0.07	0.00%	1.10%
13	*Dichrostachys cinerea*	0.06	0.00%	1.01%
	TOTAL	6.03	0.07%	

2.3.2 Elephant Impact on Different Size Classes

Uprooting

Fewer than 1% of all stems were uprooted (Table 2.8) and less than 0.5% of all stems in any size class. Three stems in the smallest size class (0-2 cm) were uprooted, two in the 2-5 cm class, six in the 5-10 cm class, and one in the 20 cm class. No stems greater than 20 cm diameter were uprooted.

Main Stem Breakage

Main stem breakage affected 66 stems (0.51%) and was confined to stems less than 30 cm in diameter (Table 2.8). The 10-20 cm and 20-30 cm size classes experienced the highest percentages of main stem breakage, with 4% and 10% of the stems broken respectively. The smallest three size classes had main stem breakage, but the abundance of stems in these classes maintained the overall percentages at less than 1%.

Branch Breakage

By far the most common form of elephant impact was branch breakage, which was apparent on 222 of 13 052 stems (1.7%, Table 2.8). Incidence of branch breakage steadily increased as the size of the stem increased: climbing from less than 1% in the <2 cm class, to 15% in the 40-50 cm class, to almost half of all stems in the >50 cm class.

Bark Stripping

Bark was stripped from five stems in the present survey (<0.04% of all stems, Table 2.8). Bark stripping was found only on stems greater than 10 cm diameter.

Leaf Stripping

Sixty-three stems had leaves stripped from them (0.48%, Table 2.8). The number of stems with leaf stripping decreased with diameter, but was proportional to the number of stems in each class.

Table 2.8. Number and percentage of stems in each size class affected by uprooting, MSB (main stem breakage), BB (branch breakage), BS (bark stripping), or LS (leaf stripping) at Kapama, Thornybush and Tshukudu.

Diameter (cm)	Total stems	Stems uprooted	% uprooted	Stems with MSB	% with MSB	Stems with BB	% with BB	Stems with BS	% with BS	Stems with LS	% with LS
0-2	7904	3	0.04%	12	0.15%	11	0.14%	0	0.00%	38	0.48%
2-5	2965	2	0.07%	13	0.44%	62	2.09%	0	0.00%	11	0.37%
5-10	1586	6	0.38%	15	0.95%	91	5.74%	0	0.00%	8	0.50%
10-20	521	1	0.19%	22	4.22%	47	9.02%	3	0.58%	4	0.77%
20-30	40	0	0.00%	4	10.00%	4	10.00%	1	2.50%	1	2.50%
30-40	16	0	0.00%	0	0.00%	2	12.50%	0	0.00%	0	0.00%
40-50	13	0	0.00%	0	0.00%	2	15.38%	0	0.00%	1	7.69%
50+	7	0	0.00%	0	0.00%	3	42.86%	1	14.29%	0	0.00%
TOTAL	13052	12	0.09%	66	0.51%	222	1.70%	5	0.04%	63	0.48%

2.3.3 Elephant Impact At the Species Level

Uprooting

The 12 stems which were uprooted were from five species, affecting no more than 2.5% of stems in any one species (Table 2.9). *Albizia harveyi* had six stems uprooted.

Table 2.9. Woody plant species uprooted by elephants at Kapama, Thornybush and Tshukudu.

Species	Total Stems	Stems uprooted	% of stems uprooted
Lannea schweinfurthii	40	1	2.50%
Albizia harveyi	390	6	1.54%
Ormocarpum trichocarpum	586	2	0.34%
Strychnos madagascariensis	689	1	0.15%
UNKNOWN	86	2	2.33%
TOTAL	13052	12	0.09%

Main Stem Breakage

Sixty-six stems from 19 species were broken at the main stem (Table 2.10). One species, *Rhus gueinzii*, suffered main stem breakage in one of three stems. *Acacia gerrardii* had the greatest number of stems broken, with 23 of its 530 stems broken (4.3%).

Table 2.10. Woody plant species with fresh main stem breakage at Kapama, Thornybush and Tshukudu.

Species	Total Stems	Stems with main stem breakage	% of stems with main stem breakage
Rhus gueinzii	3	1	33.33%
Lannea discolor	13	1	7.69%
Acacia gerrardii	530	23	4.34%
Commiphora mollis	108	2	1.85%
Lonchocarpus capassa	74	1	1.35%
Terminalia sericea	169	2	1.18%
Grewia monticola	762	9	1.18%
Albizia harveyi	390	4	1.03%
Combretum collinum	595	6	1.01%
Ziziphus mucronata	110	1	0.91%
Mundulea sericea	114	1	0.88%
Dalbergia melanoxylon	762	5	0.66%
Pterocarpus rotundifolius	576	3	0.52%
Ormocarpum trichocarpum	586	2	0.34%
Dichrostachys cinerea	379	1	0.26%
Acacia nigrescens	414	1	0.24%
Grewia bicolor	446	1	0.22%
Combretum hereroense	501	1	0.20%
Combretum apiculatum	625	1	0.16%
TOTAL	13052	66	0.51%

Branch Breakage

Branches were broken on 31 of the 80 species found in the survey (Table 2.11). A total of 222 stems had fresh branch breakage (1.7%). *Ximenia caffra* had the highest percentage of branch breakage, with two of five stems affected. Branch breakage affected almost all common species: 19 of the 30 most common species (by basal cover or by abundance) had branch breakage. Among common species, *S. birrea, D. melanoxylon,* and *C. collinum* had branch breakage on >5% of stems. *Albizia harveyi, A. gerrardii, D. cinerea, P. rotundifolius, O. trichocarpum, M. heterophylla, A. nigrescens, C. zeyheri* and *G. monticola* were the common species with branch breakage on 1-5% of stems. *Euclea divinorum, T. sericea, C. apiculatum, C. hereroense, C. cornifolia, S. madagascariensis, G. bicolor,* and *G. flavescens* were common species with branch breakage on fewer than 1% of stems.

Table 2.11. Woody plant species with branch breakage at Kapama, Thornybush and Tshukudu.

Species	**Total stems**	**Number of stems with branch breakage**	**% of stems with broken branches**
Ximenia caffra	5	2	40.00%
Sclerocarya birrea	34	6	17.65%
Schotia brachypetala	13	1	7.69%
Rhus pentheri	14	1	7.14%
Combretum imberbe	16	1	6.25%
Dalbergia melanoxylon	762	44	5.77%
Combretum collinum	595	32	5.38%
Diospyros mespiliformis	21	1	4.76%
Albizia harveyi	390	18	4.62%
Acacia gerrardii	530	22	4.15%
Commiphora mollis	108	4	3.70%
Dichrostachys cinerea	379	12	3.17%
Grewia hexamita	174	5	2.87%
Pterocarpus rotundifolius	576	15	2.60%
Ormocarpum trichocarpum	586	14	2.39%
Peltophorum africanum	43	1	2.33%
Commiphora glandulosa	92	2	2.17%
Maytenus heterophylla	349	7	2.01%
Ziziphus mucronata	110	2	1.82%
Acacia nigrescens	414	6	1.45%
Combretum zeyheri	240	3	1.25%
Cordia monoica	81	1	1.23%
Grewia monticola	762	9	1.18%
Euclea divinorum	325	2	0.62%
Terminalia sericea	169	1	0.59%
Combretum apiculatum	625	3	0.48%
Combretum hereroense	501	2	0.40%
Cissus cornifolia	299	1	0.33%
Strychnos madagascariensis	689	2	0.29%
Grewia bicolor	446	1	0.22%
Grewia flavescens	878	1	0.11%
TOTAL	13052	222	1.70%

Bark Stripping

Only five stems had fresh ring-barking or bark stripping in the vegetation quadrats. Three of the stems were *Lannea discolor* (three of 13, 23%), one was *Acacia nigrescens* (one of 414, 0.2%), and one was *Dalbergia melanoxylon* (one of 762, 0.1%).

Leaf Stripping

Sixty-three stems (0.48% of the 13 052 total stems) of 15 species had leaves stripped from them by elephants (Table 2.12). More than half of the stems found with leaf stripping were *Albizia harveyi*, affecting 8.7% of the sample of 390 stems. The less common *C. glandulosa* had three of 92 stems (3.3%) stripped and *L. schweinfurthii* had one of 40 stems leaf stripped (2.5%). Including *A. harveyi*, 12 of the most common species had leaf stripping: *M. heterophylla*, *C. zeyheri*, *C. collinum*, *G. hexamita*, *D. melanoxylon*, *D. cinerea*, *A. nigrescens*, *P. rotundifolius*, *O. trichocarpum*, *C. apiculatum*, and *G. monticola*.

Table 2.12. Woody plant species with leaf stripping on Kapama, Thornybush and Tshukudu.

Species	Total stems	Number of stems with leaf stripping	% of stems with leaf stripping
Albizia harveyi	390	34	8.72%
Commiphora glandulosa	92	3	3.26%
Lannea schweinfurthii	40	1	2.50%
Maytenus heterophylla	349	6	1.72%
Bolusanthus speciosus	73	1	1.37%
Combretum zeyheri	240	3	1.25%
Combretum collinum	595	4	0.67%
Grewia hexamita	174	1	0.57%
Dalbergia melanoxylon	762	4	0.52%
Dichrostachys cinerea	379	1	0.26%
Acacia nigrescens	414	1	0.24%
Pterocarpus rotundifolius	576	1	0.17%
Ormocarpum trichocarpum	586	1	0.17%
Combretum apiculatum	625	1	0.16%
Grewia monticola	762	1	0.13%
TOTAL	13052	63	0.48%

2.3.4 Species Most Prone to Impact

Rhus gueinzii and *Ximenia caffra* each had elephant impact in one of two quadrats where they occurred (SA=0.5, Table 2.13). Forty-eight species had no elephant impact whatsoever.

Only one species had acceptance frequencies at individual game reserves which were significantly different from the pooled acceptance frequencies: *Maytenus heterophylla* (χ^2 =6.95, df = 2, p =0.05). *M. heterophylla* was accepted in the only quadrat where it was found at Tshukudu (SA=1.00), and in two of 23 quadrats at Kapama (SA=0.08) and three of 29 quadrats at Thornybush (SA=0.10), respectively (See Appendix 4 for acceptance frequencies at each study area).

Table 2.13. Pooled acceptance frequencies and rankings for woody plant species from Kapama, Thornybush and Tshukudu.

Rank	Species	Quadrats with species	Quadrats with new impact on species	Acceptance
1	*Rhus gueinzii*	2	1	0.50
1	*Ximenia caffra*	2	1	0.50
3	*Combretum collinum*	56	27	0.48
4	*Acacia gerrardii*	104	37	0.36
5	*Rhus pentheri*	3	1	0.33
6	*Lannea discolor*	7	2	0.29
7	*Albizia harveyii*	75	20	0.27
8	*Sclerocarya birrea*	24	6	0.25
9	*Dalbergia melanoxylon*	92	21	0.23
10	*Pterocarpus rotundifolius*	48	10	0.21
11	*Combretum imberbe*	5	1	0.20
11	*Schotia brachypetala*	5	1	0.20
13	*Grewia hexamita*	21	4	0.19
14	*Strychnos madagascariensis*	22	3	0.14
15	*Commiphora mollis*	38	5	0.13
16	*Commiphora glandulosa*	16	2	0.13
17	*Maytenus heterophylla*	53	6	0.11
18	*Ormocarpum trichocarpum*	80	9	0.11
19	*Combretum zeyheri*	19	2	0.11
20	*Grewia monticola*	96	10	0.10
21	*Acacia nigrescens*	88	9	0.10
22	*Cordia monoica*	10	1	0.10
22	*Lannea schweinfurthii*	20	2	0.10
24	*Dichrostachys cinerea*	84	8	0.10
25	*Diospyros mespiliformis*	11	1	0.09
26	*Terminalia sericea*	27	2	0.07
27	*Peltophorum africanum*	14	1	0.07
28	*Lonchocarpus capassa*	16	1	0.06
29	*Ziziphus mucronata*	51	3	0.06
30	*Bolusanthus speciosus*	18	1	0.06
31	*Combretum apiculatum*	87	4	0.05
32	*Combretum hereroense*	72	3	0.04
33	*Grewia bicolor*	53	2	0.04
34	*Mundulea sericea*	28	1	0.04
35	*Euclea divinorum*	61	2	0.03
36	*Cissus cornifolia*	39	1	0.03
37	*Grewia flavescens*	66	1	0.02
	UNKNOWN	33	1	0.03
38	*Acacia exuvialis*	67	0	0
38	*Acacia karroo*	1		0
38	*Acacia nilotica*	4		0
38	*Acacia* sp.	1	0	0

Rank	Species	Quadrats with species	Quadrats with new impact on species	Acceptance
38	*Acacia tortilis*	11	0	0
38	*Balanites maughamii*	8	0	0
38	*Berchemia zeyheri*	14	0	0
38	*Bridelia cathartica*	1	0	0
38	*Canthium* sp.	5	0	0
38	*Carissa edulis*	5	0	0
38	*Cassia senepetersiana*	1	0	0
38	*Cassine aethiopica*	3	0	0
38	*Cassine transvaalensis*	20	0	0
38	*Combretum molle*	2	0	0
38	*Commiphora africana*	1	0	0
38	*Commiphora neglecta*	6	0	0
38	*Cordia* sp.	1	0	0
38	*Croton menyhartii*	1	0	0
38	*Dombeya rotundifolia*	7	0	0
38	*Ehretia amoena*	45	0	0
38	*Ehretia rigida*	7	0	0
38	*Erythrina lysistemon*	1	0	0
38	*Euclea natalensis*	20	0	0
38	*Euclea racemosa*	2	0	0
38	*Euphorbia* sp.	1	0	0
38	*Gardenia volkensii*	13	0	0
38	*Gossypium herbacium*	1	0	0
38	*Grewia villosa*	8	0	0
38	*Hippocratea* sp.	3	0	0
38	*Maerua angolensis*	1	0	0
38	*Maerua* sp.	1	0	0
38	*Manilkara mochisia*	5	0	0
38	*Maytenus senegalensis*	4	0	0
38	*Nuxia oppositifolia*	1	0	0
38	*Olea europaea*	1	0	0
38	*Ozoroa paniculosa*	1	0	0
38	*Ozoroa* sp.	1	0	0
38	*Ozoroa sphaerocarpa*	1	0	0
38	*Pappea capensis*	4	0	0
38	*Pavetta catophylla*	1	0	0
38	*Pavetta* sp.	2	0	0
38	*Protasparagus* sp.	15	0	0
38	*Rhus dentata*	1	0	0
38	*Rhus rehmanniana*	6	0	0
38	*Rhus* sp.	5	0	0
38	*Securinega virosa*	51	0	0
38	*Spirostachys africana*	3	0	0
38	*Terminalia prunioides*	3	0	0

2.4 Discussion

2.4.1 Relationship Between Impact Type and Stem Size

Stem size obviously has some bearing on the susceptibility of woody plants to elephant impact. Stems smaller than 30 cm diameter were susceptible to main stem breakage but this type of breakage was most prevalent in the intermediate diameter classes (10-30 cm) and not in smaller stems. Stems larger than 30 cm in diameter showed no main stem breakage by elephants.

The percentage of stems with broken branches increased with increasing stem diameter. One explanation for this is that branching is a function of stem girth; as trees grow in basal diameter, they also grow more branches which provides more opportunity for breakage. A second explanation is that these older trees display more accumulated damage than the younger ones, but this is unlikely since only fresh breakage was included. Barnes (1979) and Weyerhaeuser (1985) agreed that elephant damage to baobabs, *Adansonia digitata,* increased with size but noted that the likelihood of tree death decreased. Weyerhaeuser (1985) reported that the mean size of killed trees was much smaller than the mean size of the overall population. Baobab trees accumulated damage over time but gained resilience with increasing size.

Bark stripping was extremely uncommon and was limited to trees with stems greater than 10 cm diameter. Elephants were observed stripping bark from trees and the force used to push the tusk into the bark of the tree appeared substantial enough to push over small plants (pers. obs.). Furthermore, smaller plants have less bark available, so may have been ignored by elephants.

In a vegetation impact study on Asian elephants, *Elephas maximus,* Ishwaran (1983) reported peak frequencies in bark peeling in trees between 4 and 64 cm in diameter, whereas bark stripping in my study was found only on trees greater than

10 cm in diameter. Anderson and Walker (1974) also found that African elephants damaged bark of larger trees primarily.

Croze (1974) found that elephant feeding on trees in the Serengeti was a function of abundance: feeding on each size class was proportional to the abundance of that size class in the environment, with the exception of seedlings which may be hidden or inaccessible. At Kapama, Thornybush, and Tshukudu, certain types of feeding (e.g. possibly leaf stripping) were a function of abundance. Branch breaking, on the other hand, was directly proportional to diameter, but inversely proportional to abundance. Similarly, Pellew (1983) reported that elephants in the Seronera woodlands of the Serengeti fed disproportionately upon the larger size-classes and the small-to-medium size mature canopy trees.

The most numerous size class in my study areas was the 0-2 cm diameter group. Percentage of trees with main stem breakage reached a maximum in the 20-30 cm diameter class. Herlocker (quoted in Pellew 1983) hypothesized that when the greatest tree density was in the 30-70 cm group, elephant impact was greatest in the diameter range of 15-50 cm, with a peak at 30 cm.

Many authors have explicitly or implicitly linked the decrease of certain tree species to elephant destruction of certain sizes. Leuthold (1977) attributed the decrease of the Lake Manyara populations of *A. tortilis* and *Commiphora* species to destruction of mature trees and removal of recruitment-age trees. He simultaneously reported an abundance of regeneration potential seedlings, implying that elephants have some role in preventing replenishment of mature trees. Ruess and Halter (1990) reported that elephants contributed to high mortality rates of mature *A. tortilis* trees and that despite an abundance of young trees, the trees failed to grow beyond 3-4m high. Their investigation indicated that giraffe browsing, not elephant browsing, was responsible for the failure of trees to reach canopy height. The data from the present study indicate that the smallest stems were relatively free from elephant impact. The 0-2 cm size class experienced uprooting, main stem breakage, branch breakage and leaf stripping, but on fewer than 1% of stems in each impact type.

Pellew (1983) reported that stems less than 1 m in height were largely ignored by elephants in the Serengeti. In contrast, Van Wyk and Fairall (1969) came to the conclusion that in the Kruger Park, shrubs (stems less than 1.75 m high) were utilised more frequently than trees, except in areas where shrub concentration had been diminished due to fire or other factors. In the current survey, small stems were not ignored, but they were not heavily browsed nor broken.

The severity of elephant impact on each size class was species specific along the Linyanti riparian zone (Wackernagel 1992). Mortality rates were highest among the 2-20 cm diameter stems of *Dichrostachys cinerea*, the 20-50 cm specimens of *Lonchocarpus capassa*, *Peltophorum africanum* and *Terminalia sericea*, and in the 4-50 cm diameter specimens of *Terminalia prunioides*.

Evidence from the vegetation quadrats that trees in excess of 30 cm diameter are unlikely to be broken at the main stem leads to the logical conclusion that trees may reach a threshold size, beyond which they are too big to be pushed over or broken at the main stem. Similarly, Pellew (1983) reported that large trees were too big to be pushed over, but pointed out that they could still be ring-barked. In contrast, Wackernagel (1992) found that tree felling was most common in the two largest classes in his study: 81% of all trees felled were in the 20-50 cm diameter range, while the remaining 19% of felled trees were in the largest size class (greater than 50 cm diameter). Faster decay times for small trees, and inconspicuousness of small fallen trees may have biased these data (Owen-Smith, pers. comm.). Another explanation is that some of these larger trees fell because of senescence or other non-elephant cause and were mistakenly attributed to elephants.

2.4.2 Relationship Between Impact Type and Species

The types of elephant impact I found reflected palatability to a degree. Leaf stripping was primarily restricted to palatable, thorn-less species. Main stem breakage was most common in species known to be preferred by elephants. Branch breaking included a mixture of palatable and non-palatable species; some probably broken and eaten, others broken unintentionally or for non-feeding purposes.

Bark stripping affected only five stems of three palatable species which is too small a sample to draw conclusions. There was no evidence of non-feeding related tusk marking, as hypothesized by Eisenberg and Lockhart (1972, as cited in Ishwaran 1983) who questioned whether tusking might be used for marking paths and tracks. The vegetation quadrats in the present study were on feeding pathways so even if African elephants do mark pathways across areas where they do not feed they would not have been found in this study.

In the present study, very little ring-barking occurred and no tree species appeared to be a particular target for bark removal. Wackernagel (1992) reported that ring-barking was prevalent in *Acacia erioloba, A. nigrescens, D. mespiliformis* and most canopy tree species. This disparity may be explained by one or all of three reasons: 1) the different vegetation and environmental factors of the areas; 2) the time factor (immediate vs. accumulated damage); and 3) the fact that my surveys were conducted after an extremely wet year and elephants were not as reliant on woody vegetation as they may be in harsher environments or time periods.

2.4.3 Species Susceptibility

Distinguishing between preferred and non-preferred species is subjective. For species with adequate sample sizes and similar acceptance frequencies at all three sites, I believe acceptance frequencies above 0.20 denote highly preferred species. The highest frequencies (0.50) in my survey were for two species which were found in only two quadrats which is too small to be tested with acceptance frequencies.

However, I would designate *Combretum collinum, Acacia gerrardii, Albizia harveyi, Sclerocarya birrea, Dalbergia melanoxylon,* and *Pterocarpus rotundifolius* as highly preferred species because all scored acceptance frequencies above 0.20 and were found in a substantial number of quadrats. Notable among the species neglected by elephants (with acceptance frequencies of 0) were *Acacia exuvialis, A. tortilis, Cassine transvaalensis, Ehretia amoena, Euclea natalensis,* and *Securinega virosa,* all of which were among the most common species, but appear to be rarely or never eaten by elephants at Kapama, Thornybush and Tshukudu. In addition, *Ormocarpum trichocarpum, Strychnos madagascariensis* and *Ziziphus mucronata* were all major substituents of the woody plant layer, but were rarely utilized by elephants. Stem size may confound the conclusions from species preferences since some species may have been prone to elephant impact simply by having a predominance of stems in the size classes favoured by elephants. For example, lack of use of *Acacia tortilis* could be attributed to the dearth of stems smaller than 5 cm in diameter. *Sclerocarya birrea* may have have shown much greater usage by elephants than *Acacia nigrescens* owing to the abundance of large individuals of the former.

Acacia species

Of the six *Acacia* species found in this study, only *A. gerrardii* was highly preferred (SA = 0.36). *Acacia nigrescens* was also eaten occasionally, but *A. exuvialis, A. karoo, A. nilotica* and *A. tortilis* were free of elephant impact. This low preference is surprising since *Acacia* spp. are often among the first to undergo visible decline in areas with high elephant densities

Acacia gerrardii was among the most common and the most accepted of all species in the present study. The species had elephant impact in 37 of 104 quadrats (SA = 0.36). Impact was limited to branch breaking and main stem breakage. In the nearby Kruger National Park, *A. gerrardii* was occasionally subject to heavy elephant browsing (Van Wyk and Fairall 1969).

At Kapama, Thornybush and Tshukudu, elephants broke main stems and branches and leaf stripped *Acacia nigrescens*, but it was not highly preferred (SA = 0.10). Elsewhere in southern Africa, *A. nigrescens* is heavily used by elephants. In the Linyanti River area of northern Botswana, *A. nigrescens* was frequently bark stripped and uprooted (Wackernagel 1992). Anderson and Walker (1974) recorded bark stripping in 77.8% of *A. nigrescens* stems in the Sengwa research area. In the Kruger National Park, *Acacia nigrescens* was frequently completely uprooted or destroyed (Van Wyk and Fairall 1969).

Acacia nilotica was present at all study areas, but was not affected by elephants. Van Wyk and Fairall (1969) reported only infrequent heavy elephant impact on *A. nilotica* in the Kruger Park.

Elephants had no impact on the 33 *Acacia tortilis* stems encountered in my survey. *Acacia tortilis* is the primary species of concern in the Seronera woodland in the Serengeti National Park, Tanzania (Croze 1974, Ruess and Halter 1990, Pellew 1983). Douglas-Hamilton (1972, in Leuthold 1977) and Vesey-Fitzgerald (1973) documented serious bark stripping of *A. tortilis*. Along the Letaba River in the Kruger National Park, *A. tortilis* suffered branch breakage on greater than 50% of all stems in both small (<6 cm circumference) and larger stems (6-128 cm circumference) and a high incidence of bark peeling. Overall, 84% of *A. tortilis* stems had some type of damage (McDonald 1992).

Balanites spp.

Balanites maughamii was the only member of the genus found in the study areas. It was restricted to Kapama Game Reserve and was never eaten or broken by elephants. This contrasts with the heavy elephant usage of congener *Balanites aegyptiaca* in Zimbabwe (Guy 1981).

Combretum spp.

Of the six *Combretum* species found in the survey, two were preferred, three were eaten but not preferred, and one was completely untouched. *Combretum collinum* had the highest acceptance frequency (0.48) of all the common species, with elephant impact in 27 of 56 quadrats. *Combretum imberbe* was the second most preferred of the *Combretu*ʳ cies with an acceptance frequency of 0.20, but was relatively uncommon. *Combretum zeyheri, C. apiculatum,* and *C. hereroense* had impact, but at very low levels. *C. molle* was only found in two quadrats and had no elephant impact. Other studies have found differential preference among the *Combretum* species. In Sengwa, Anderson and Walker (1974) found that although *Combretum elaeagnoides* and *C. mossambicense* were co-dominant in the *Baikiaea-Baphia* vegetation communities, the former was elephant damaged on 86% of stems and the latter only 5.8%. Van Wyk and Fairall (1969) reported that *C. apiculatum, C. hereroense, C. imberbe* and *C. zeyheri* in the Kruger Park frequently had elephant breakage.

Anderson and Walker (1974) reported ring barking in 81.9% of stems of *Combretum imberbe*. Moroka (1984 in McDonald 1992) reported bark stripping of *C. imberbe* in 43% of trees in Chobe in Botswana, and McDonald reported 66% in Kruger Park ripa.ian habitat. *Combretum imberbe* was never ring barked in my vegetation quadrats (n = 16) nor in direct behavioural observations of the hand-raised elephants (Chapter 3). Anderson and Walker's and McDonald's studies were conducted in riverine vegetation. Possibly *C. imberbe* is more accessible or more susceptible to elephants in the riparian zone than in the higher parts of the catena I studied.

Dalbergia melanoxylon

Dalbergia melanoxylon was one of the species with the greatest frequency of impact; the species had impact in 21 of 92 quadrats, representing an overall acceptance ratio of 0.23. It was subject to every recorded form of elephant impact except uprooting. Elephants broke branches on stems of *D. melanoxylon* more than any other species; 44 of its 763 stems showed branch breakage. Five stems were broken at the main stem, four were leaf stripped, and one was bark stripped. This substantial degree of usage of the species is in agreement with findings elsewhere. Anderson and Walker (1974) found *D. melanoxylon* and *Combretum* spp. to be the most heavily damaged trees (55-88% old elephant damage) in *Colophospermum mopane-Combretum-Acacia* communities. In the Kruger National Park, Van Wyk and Fairall (1969) reported that *D. melanoxylon* regularly experienced severe damage and was often uprooted. I may not have found uprooting of *D. melanoxylon* if this impact is relatively rare or if it only happens during particularly dry periods.

Dichrostachys cinerea

Despite being a very common species in the survey, *Dichrostachys cinerea* had a low acceptance ratio (0.10). It experienced only a small amount of branch breakage (3.2% of its stems), main stem breakage (0.3%) and leaf stripping (0.3%). In most of the quadrats at Kapama, Thornybush and Tshukudu, *D. cinerea* was present only as small-stemmed shrubs, less than 3m in height, with few stems in the size classes most heavily used by elephants, which could preclude its appearance as a favoured species. In the Kruger National Park, *D. cinerea* is a significant component of the elephant's diet in some places (Van Wyk and Fairall 1969), but the quality and quantity of alternative food at my study areas may be related to the apparent lack of reliance on this species.

Diospyros mespiliformis

McDonald (1992) found that *Diospyros mespiliformis* suffered the most extensive elephant impact in his study area and concluded that it must be a favourite food item of elephants. My data indicate the opposite. In only one instance was *D. mespiliformis* broken and the broken pieces were found lying on the ground, not eaten. The discrepancy could be due to harsher environmental conditions during McDonald's study period or variation in habitat use between riverine areas (McDonald 1992) and toplands (my sites).

***Grewia* spp.**

Grewia bicolor, G. flavescens, G. hexamita, and G. monticola were all used by elephants during my study at acceptance levels of <0.20. Only *G. villosa* showed no impact in the vegetation quadrats (but it was a component of the hand-raised elephants' diet, Chapter 3). Van Wyk and Fairall (1969) also found heavy utilization of *Grewia bicolor, G. hexamita*, and *G. monticola* in all places where the species occurred in the Kruger Park. In the Sengwa Wildlife Research Area, *G. flavescens* was uprooted by elephants so frequently that its overall abundance decreased (Anderson and Walker 1974, Cumming 1981). In the present study, *G. flavescens* was virtually ignored by elephants which broke only one of 878 stems.

Lonchocarpus capassa

In my study, *L. capassa* never suffered bark damage and had only one of 74 stems affected in any way (branch breakage). McDonald (1992), Moroka (1984), and Anderson and Walker (1974) all reported damage in *L. capassa*. Anderson and Walker (1974) found bark damage in 78.6% of *L. capassa* stems.

Pterocarpus rotundifolius

Pterocarpus rotundifolius is known to be used by elephants (VanWyk and Fairall 1969) and was likewise favoured by the Kapama, Tshukudu and Thornybush elephants. *Pterocarpus rotundifolius* had the tenth highest acceptance frequency (0.21). Three of 576 of *P. rotundifolius* stems were broken at the main stem, and 15 had fresh branch breakage. In almost all cases, the elephants chewed the bark off of the broken branches, then dropped the branches without eating the leaves or the wood.

Sclerocarya birrea

Sclerocarya birrea had a high incidence of branch breakage (17.7% of stems) and the eighth highest acceptance ratio (0.25). Elephants did not uproot it, break it at the main stem, or strip its bark in any of the 24 vegetation quadrats where it occurred. In a study of elephant impact in *Sclerocarya birrea, Anogeissus leiocarpus* and *Lannea humilis* woodland in Waza National Park, Cameroon, 86% of *Sclerocarya birrea* trees were not browsed, 14% were damaged (less than 75% of tree removed) and none was seriously damaged (75-100% of tree removed or uprooted entirely) (Tchamba 1995). Van Wyk and Fairall (1969) reported elephant use of *S. birrea (caffra)* especially in the southern region of the Kruger Park. Owen-Smith (1988) wrote the extent of elephant bark damage and felling of *S. birrea* in the

Kruger Park was a source of concern to park managers. Data from the vegetation quadrats confirm that *S. birrea* is favoured browsing for elephants (see Chapter 4 for comprehensive *S. birrea* survey).

Securinega virosa

Securinega virosa was a very common species in my study but never experienced elephant impact and is apparently neglected by elephants. Tchamba (1995) came to the same conclusion in his study site in Waza, Cameroon, where *S. virosa* comprised 8% of the woody vegetation but had no elephant use. Guy (1976) reported that elephants showed strong negative selection for *S. virosa*. In areas of intense elephant use and regular fires, *S. virosa* was one of the species to increase in number at the cost of the more palatable and more fire-susceptible *A. tortilis* (Guy 1981).

Terminalia spp.

Compared to the degree of utilization elsewhere, *T. sericea* had a very low acceptance frequency in the present study. Wackernagel (1992) and Anderson and Walker (1974) reported high levels of elephant use on *Terminalia sericea*, describing it as the most favoured tree species in the *Combretum-Terminalia* savanna, but this was not the case in my study. Anderson and Walker (1974) also reported that although *T. sericea* was once the dominant species by stem area, a combination of elephant utilization and fire damage led to a severe decline in *T. sericea* population numbers. Of 169 stems found in my quadrats, two had main stem breakage, and one had branch breakage: less than 1.7% of the total. In the three instances where *T. sericea* was broken it was not eaten. *Terminalia prunioides* was relatively uncommon. Elephants did not have any impact on it in any of the three quadrats where it was found (but hand-raised elephants did eat it, Chapter 3).

CHAPTER 3. ELEPHANT FEEDING BEHAVIOUR

3.1 Introduction

Most assessments of large mammal-plant interactions are done using one of two separate methods: vegetation surveys or behavioural observation. Past studies of elephant impact encountered the problem that data taken without direct observation overlooked seedling mortality because little or no sign remained (Croze 1974). Behavioural observations of wild herds are limited in their accuracy by constraints on approachability and visibility, so small plants are often unintentionally overlooked and food items eaten infrequently by the subject animal are omitted. Close-up observation allows more accurate recording of exact food intake (Dublin 1992). In order to get a better estimate of the impact of elephants on woody vegetation in lowveld reserves, the vegetation surveys (Chapter 2) were complemented by direct behavioural observation of two hand-raised nine year old elephants. The following pages discuss the importance of woody plants in the elephants' diet, preferences for different woody species and the rate of seedling consumption.

3.2 Materials and Methods

One male and one female hand-raised elephant at Tshukudu Game Reserve could be approached to within an arm's reach, but were usually followed at a distance of approximately 10 m. By recording their activities I could directly record impact on woody plants of any size. In order to estimate vegetation composition, and to permit comparison with the wild herds, I repeated the vegetation quadrats used on the wild elephant paths (section 2.2) at sites where I directly observed and recorded the hand-raised elephants feeding.

Continuous focal animal observation techniques were employed (Altmann 1974) for consecutive ten minute periods between 08:00 and 13:00 one day per week. On a few occasions, the elephants stopped foraging when tourists approached, so these ten minute periods were removed from the data, leading to discontinuous observations. On the first and last observation days (3/9/96 and 16/11/96), a field assistant was not available so only one elephant was observed.

During the observation periods, every feeding event was manually recorded on data sheets. A trained assistant followed one elephant while I followed the other. The two elephants were observed at the same time whenever possible. The elephants usually foraged together, rarely more than 100 m apart.

Each bite or trunkful of vegetation was termed a "feeding event". Each item the animals ate was identified and each feeding event was categorized according to how the elephant handled the food item. Handling methods were trunk full of vegetation, trunk full loosened by kicking plant with foot, or bitten directly with mouth.

When the elephants removed bark from trees with their tusks, the number of tusk gouges was recorded. Tusk gouging was recorded and analyzed separately from feeding events because the bark which was removed was not always consumed.

Woody plants were identified to species whenever possible. When it was not possible to identify plant species as the elephants foraged, a sample was taken for later identification. Grasses and sedges were not identified to species level. Feeding on grasses or sedges was recorded as a single category in order to compare grass intake with browse intake. Feeding on other items (dung, dirt, dead wood) was noted, but was not included in the analyses.

Vegetation quadrats were sampled using the 5 m circle method described in section 2.2. The quadrat sites were chosen as the midpoint, i.e. the 5 minute mark, of ten minute observation periods. If no woody plants were consumed during a ten minute interval, no quadrat was done. During the initial observation periods, my assistant and I tried to do vegetation quadrats immediately after the corresponding behavioural observation period. However, this gave the elephants sufficient time to move away and sometimes they could not be found again. In order to be more observations. On the first and last observation days (3/9/96 and 16/11/96), a field assistant was not available so only one elephant was observed.

During the observation periods, every feeding event was manually recorded on data sheets. A trained assistant followed one elephant while I followed the other. The two elephants were observed at the same time whenever possible. The elephants usually foraged together, rarely more than 100 m apart.

Each bite or trunkful of vegetation was termed a "feeding event". Each item the animals ate was identified and each feeding event was categorized according to how the elephant handled the food item. Handling methods were trunk full of vegetation, trunk full loosened by kicking plant with foot, or bitten directly with mouth.

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To assess differences in hand-raised elephant selection of food species, I used a selection index (SI) to compare feeding events on a species to the frequency of its occurrence in the area. Site-based acceptance frequencies (as used to analyze the vegetation quadrats in section 2.3) were not appropriate since plant species use was based on the number of feeding events by the elephant rather than on the number of plant stems affected. Instead the preferences of the female and male were calculated as a ratio of the contribution of a plant species to the diet (proportion of all feeding events) to the frequency of occurrence of that species in the area (proportion of 46 quadrats):

$$SI = \frac{\text{proportion of all feeding events on each woody species}}{\text{occurrence of the woody species in 46 quadrats}}$$

The proportion of all feeding events on each woody species is simply the number of feeding events on the woody species divided by the total number of feeding events during observation periods (female = 3296 events, male = 3751 events). The number of woody stems was not independent due to the patchy nature of species distribution so woody species occurrence was the proportion of quadrats in which the species was present rather than the proportion of total stems. Species which were present in all 46 quadrats had a frequency of occurrence of 1.0, while species present in half the quadrats had a frequency of occurrence of 0.5. For example, the female fed on *Grewia monticola* 330 times and it was found in 23 quadrats. This yields a ratio of 0.10/0.5 for an SI of 0.20. The male fed on *G. monticola* 225 times, yielding a ratio of 0.06/0.5 for an SI of 0.12. The mean SI is therefore (0.20+0.12)/2 = 0.16. The χ^2 test (Zar 1996) was used to test for significant differences between the selection index value for each woody species for the male and the female.

3.3 Results

3.3.1 Feeding Behaviour

The hand-raised elephants were observed one morning per week for 10 weeks, resulting in a total of 10 observation days. The female elephant was observed for 1730 minutes and the male for 1760 minutes. During this time, the female took 3296 mouthfuls of vegetation and the male took 3751 mouthfuls; together, 7047 feeding events were recorded (Table 3.1). The most common handling method was trunk fulls (76% of all feeding events), followed by trunk fulls with kick (16%). Leaf stripping and mouth biting contributed fewer than 10% of all feeding events.

Table 3.1. Incidences of each handling method by two hand-raised elephants during 10 observation days.

Handling method	Number of occurrences	Percentage of all feeding events
Trunk fulls	5335	75.7%
Trunk fulls with kick	1119	15.9%
Leaf stripping	488	6.9%
Mouth bites	105	1.5%
Total feeding events	7047	

The animals ate 31 known species of woody plants. Ten feeding events were on species which could not be identified. In addition to woody plants, the elephants ate grass, alfalfa, weeds, creeping vines, underground tubers, sticks and wood, dirt, rocks, elephant dung, and one parasitic orchid *(Plicosepalus amplexicalus)* from the branch of an *Acacia nigrescens*. Grass and alfalfa consumption accounted for 53% to 95% of daily feeding activities (see Figure 3.1).

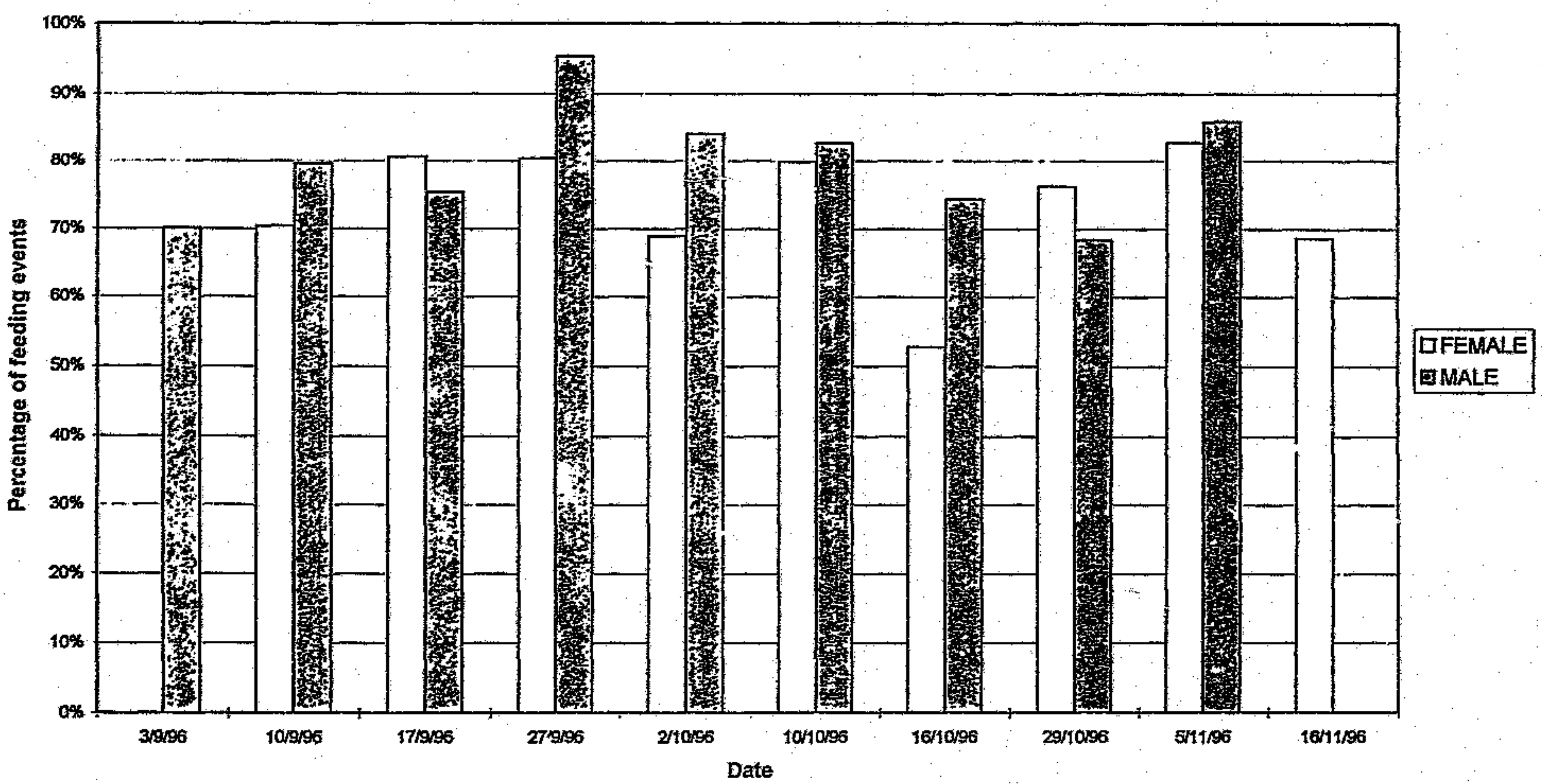

Figure 3.1. Importance of grass in the diet of two hand-raised elephants.

Woody plants accounted for 775 feeding events by the female (23.5% of feeding events) and 743 feeding events by the male (19.8%). For the purpose of elucidating feeding differences among woody plant species, all non-woody plants were excluded from the following analyses.

3.3.2 Favoured Woody Species

The female and the male elephant ate *Sclerocarya birrea* more frequently than any other woody species (Female: 155 of 775 feeding events, Male: 267 of 743 feeding events, Figure 3.2), followed closely by the *Grewia* spp.: *G. bicolor, G. monticola,* and a third unknown *Grewia* which was either *bicolor, monticola* or a hybrid of the two (J. Rushworth, pers. comm.). The next most frequently eaten woody species were *Acacia nigrescens, Combretum apiculatum, Maytenus heterophylla, Combretum imberbe, Cassine transvaalensis, Albizia harveyi, Cissus cornifolia,* and *Dichrostachys cinerea.*

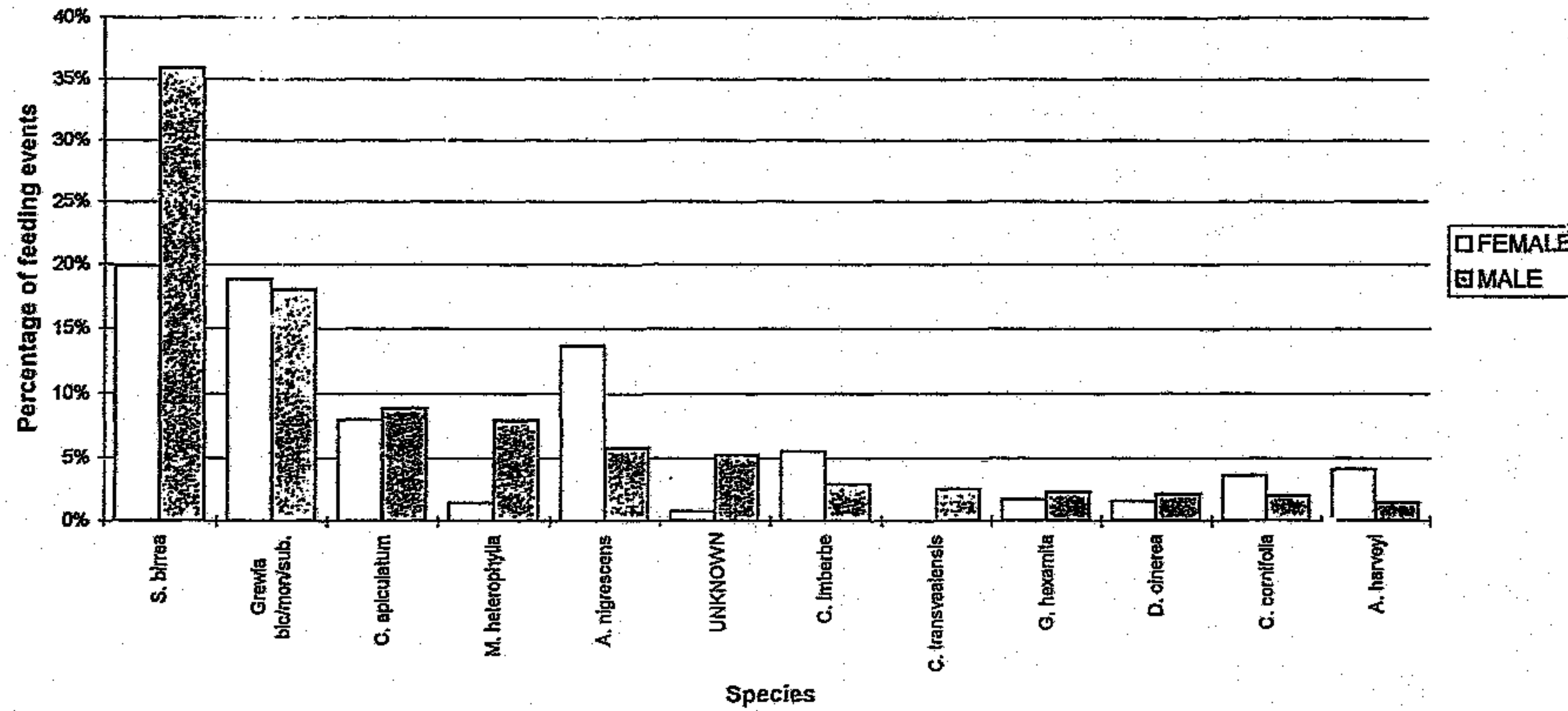

Figure 3.2. Importance of woody species in the diet of two hand-raised elephants.

Selection indices were not calculated for woody species which occurred in fewer than five vegetation quadrats. Mean selection index values ranged from 0 to 1.07 (Table 3.2). There were no significant differences in the female and male selection index values for any species (χ^2 test, all χ^2<2.09, df = 1).

Table 3.2. Relative abundance in the woody plant layer, contribution to hand-raised elephant diet, and selection index (SI) for each woody plant species at Tshukudu. Note: N/A is reported for species which were eaten in behavioural observations but never occurred in vegetation quadrats.

Species	Quadrats	Plant occurrence	Female diet	Male diet	Mean SI
Acacia exuvialis	16	35%	<1%	1%	0.02
Acacia gerrardii	4	9%			-
Acacia nigrescens	22	48%	14%	6%	0.20
Acacia nilotica	1	2%			-
Acacia senegal	0	0%	1%		-
Acacia tortilis	11	24%	3%		0.07
Albizia harveyi	3	7%	4%	1%	-
Cassine transvaalensis	0	0%		3%	-
Cissus cornifolia	11	24%	4%	2%	0.12
Combretum apiculatum	14	30%	8%	9%	0.28
Combretum collinum	1	2%		<1%	-
Combretum hereroense	1	2%			-
Combretum imberbe	1	2%	6%	3%	-
Commiphora glandulosa	4	9%	2%		-
Commiphora mollis	5	11%	1%		0.05
Cordia monoica	1	2%			-
Cordia sp.	1	2%			-
Dalbergia melanoxylon	1	2%			-
Dichrostachys cinerea	17	37%	2%	2%	0.05
Ehretia amoena	1	2%			-
Euphorbia sp.	1	2%			-
Gossypium herbacium	1	2%			-
Grewia bicolor	9	20%	6%	7%	0.33
Grewia flavescens	11	24%	3%		0.06
Grewia hexamita	1	2%	2%	2%	-
Grewia monticola	23	50%	10%	6%	0.16
Grewia sp.	0	0%	3%	6%	-
Grewia villosa	8	17%	1%	<1%	0.04
Lannea schweinfurthii	6	13%	1%	<1%	0.06
Lonchocarpus capassa	1	2%	1%		-
Maerua parvifolia	0	0%	<1%	1%	-
Maerua sp.	1	2%	1%	<1%	-

Species	Quadrats	Plant occurrence	Female diet	Male diet	Mean SI
Manilkara mochisia	1	2%			-
Maytenus heterophylla	1	2%	1%	8%	-
Ormocarpum trichocarpum	3	7%	<1%	<1%	-
Ozoroa paniculosa	0	0%	1%	<1%	-
Peltophorum africanum	1	2%	<1%		-
Protasparagus sp.	1	2%			-
Sclerocarya birrea	12	26%	20%	36%	1.07
Securinega virosa	2	4%			-
Sterculia rogersii	0	0%	1%	<1%	-
Terminalia prunioides	2	4%	4%		-
UNKNOWN	6	13%	1%	5%	0.23
Ximenia caffra	1	2%			-
Ziziphus mucronata	4	9%			-
TOTAL	46				

3.3.3 Impact on Seedlings

Ten seedlings (stems smaller than 2 cm diameter) were eaten during the 3490 minutes of observation. Four seedlings were eaten before the species could be identified. The remaining six seedlings comprised one seedling each of *A. nigrescens* and *D. cinerea*, and four seedlings of *M. heterophylla*. Total seedling consumption amounted to fewer than 0.14% of all feeding events.

From data I obtained from the vegetation quadrats at Tshukudu (Table 2.7), seedlings accounted for 64% of the vegetation in the area. The ratio of the incidence of feeding events on seedlings (0.14%) to the relative frequency of seedlings (64%) is 0.0022.

3.3.4 Bark Removal

The female elephant removed bark from trees with her tusks 54 times and the male removed bark with his tusks 39 times during the course of the study. Six woody plant species were subject to tusk gouging (Table 3.3). Bark was removed and eaten from *A. nigrescens, A. tortilis, G. monticola, S. birrea,* and *S. brachypetala.* Bark removed from *L. schweinfurthii* was not eaten. Tusk gouging was somewhat episodic: all tusk gouges on *A. nigrescens, A. tortilis, G. monticola,* and *S. brachypetala* were on single trees. *Sclerocarya birrea* was tusk gouged on numerous occasions and on numerous individual trees. A maximum of 32 tusk gouges on one *S. birrea* tree were observed.

Table 3.3. Incidence of bark removal from trees by two hand-raised elephants.

Species	Number of tusk gouges	% of all tusk gouges
Acacia nigrescens	31	33%
Acacia tortilis	2	2%
Grewia monticola	2	2%
Lannea schweinfurthii	1	1%
Sclerocarya birrea	54	58%
Schotia brachypetala	3	3%
TOTAL	93	

3.4 Discussion

3.4.1 Diet Composition

The hand-raised elephants were accustomed to, and even sought out, human attention. They stayed around areas with people rather than making use of the whole property available to them. They ranged further from the lodge compound during the evening and night, but because of the time of day I observed them, I could only document the species they fed on around the lodge. Therefore, the number of species recorded in their diet during the observation periods must be regarded as an absolute minimum of what they would normally consume. Similarly, the vegetation quadrats were based on the same locations where the animals were observed, so are also limited in their scope. Considering this, the elephants ate 31 of 43 woody species encountered during the study.

Barnes (1982) reported that the number of browse species recorded in the diet of wild bull elephants at Ruaha increased with the number of feeding records. In other words, the number of food species recorded is likely to be a function of observation time. Keeping this in mind, Tshukudu elephants ate at least 31 woody plant species during the 3490 minutes of observation whereas the Ruaha elephants fed on a maximum of 12 species during any one season (Barnes 1982). In addition to the obvious explanation that the Tshukudu elephants may have a more species diverse diet, the ease with which the Tshukudu elephants were observed probably allowed improved recording of the plants they consumed.

Elephants are most reliant on woody species during the dry season (Barnes 1982, Lindsay 1994). My study began at the end of the dry winter and proceeded into the rainy summer season, but the year preceding the study was the wettest year in recent history (see also rainfall data in section 1.5.1), so reliance on woody plants was probably much lower than usual. I anticipate that during drier seasons and drier years, elephants would consume more species of woody vegetation and would also have a heavier impact on preferred species.

The Tshukudu elephants were heavily reliant on grass, which comprised 57-95% of daily feeding events. Hand-raised calves in Tsavo East in Kenya ate grass 78.3% of the time they were feeding in natural settings, while nearby free-living calves ate grass 77.5% of the time (McKnight 1995). This high level of grass consumption in the Tshukudu elephants is somewhat surprising since southern African elephants are expected to be more dependent on the abundant woody layer: Van Wyk and Fairall (1969) reported that woody species were far more important in the diet of elephants living in the Kruger National Park than those living in the more open savanna of East Africa. If elephants are reliant on low quality browse their body condition may deteriorate: in the mid to late-dry season in Ruaha, Barnes (1982) reported that woody browse contributed about 80% of the diet of female elephants, and was accompanied by a noticeable loss of body condition. In spite of limiting their own movements to a heavily utilized periphery around the inhabited areas, the Tshukudu elephants were able to eat a diet primarily of grass throughout the study period.

McKnight (1995) reported that after grass, creepers were the most frequently eaten food item of hand-raised elephants (5-18% of the feeding activities), followed by woody species (2% to 8% of feeding activities). In my study, woody species were the second most important food item in the diet of the Tshukudu elephants, amounting to 5% to 43% of feeding events per day.

3.4.2 Favoured Woody Species

By quantity, the elephants consumed *Sclerocarya birrea, Grewia bicolor, G. monticola, Combretum apiculatum,* and *Acacia nigrescens* most often. Both the female and the male elephant fed on each of these five species in more than 5% of feeding events on woody plants.

The selection index values show *Sclerocarya birrea* to be the highest ranking species (SI = 1.07), followed by *Combretum apiculatum* (SI = 0.28), and *Acacia nigrescens* (SI = 0.20). Each of these three species comprised more than 5% of feeding events in the diet of the male and the female elephants as well as having high selection indices, therefore are both important and favoured food items.

3.4.3 Impact on Seedlings

Stems smaller than 2 cm in diameter were a very minor part of the elephants' diet (0.14% of all feeding events). Seedlings were eaten in extremely small amounts by comparison to their overall availability and did not appear to be a preferred food item. The seedling size class did not appear to be seriously affected by elephant feeding. When woodlands decrease in size or density, elephant removal of young saplings is often suggested as an explanation (Laws *et al* 1975, Barnes 1983, Jachmann and Croes 1991). The present study indicates that elephant browsing alone had very little effect on woody species composition at the seedling level. Previous studies have suggested that elephants have the greatest impact upon seedlings (Barnes 1983, Jachmann and Croes 1991), but other studies have found that seedlings were not being depleted by elephants. As mentioned in section 2.4.1. Pellew (1983) found that elephants did not eat or destroy stems less than 1 m in height. In a study of *Acacia tortilis* at Lake Manyara, Tanzania, Mwalyosi (1987) reported that smaller trees were less susceptible to being killed than large trees. Jachmann and Bell (1985) hypothesized that elephants forage on smaller stems only when woody stems in the favoured 2-3m height group are not present. Anything which reduces the amount or quality of grass available to elephants causes an increase in elephant intake of woody species (Dublin 1992). In combination with fires and heavy browsing by other herbivores (Pellew 1983), elephants may feed heavily on seedlings, but this was not presently evident at Tshukudu.

3.4.4 Bark Removal

Bark removal by elephants can kill woody plants directly or by increasing susceptibility to fire or to infection by boring insects (Weyerhauser 1985, Barnes 1980). The Tshukudu elephants most frequently removed bark from *S. birrea* (54 tusk gouges), followed by *A. nigrescens* (31 tusk gouges). The elephants removed bark from *A. tortilis, G. monticola, L. schweinfurthii* and *S. brachypetala* only on single occasions. In all cases, fewer than 3 strips of bark were peeled off. My interpretation is that the elephants gouged the trees with their tusks, then tasted or smelled the bark and found it undesirable. Bark stripping does have a seasonal component, possibly coinciding with sap rising (Guy 1981). On the single occasion that *A. nigrescens* had bark removed, both elephants removed and ate bark until the tree was denuded of bark to 3.5 m. The consumption of *A. nigrescens* is similar to reports from the Kruger National Park, where the species was in decline in some areas due to heavy utilization by elephants, particularly bark stripping and felling (Van Wyk and Fairall 1969, Owen-Smith 1988). More than half of the *A. nigrescens* trees near the Linyanti river in Botswana had bark stripping on greater than 50% of the circumference. The uniqueness of this event during my observations may indicate that bark stripping of *A. nigrescens* is also highly seasonal. *Sclerocarya birrea* was repeatedly the target of bark stripping. Tusk gouging varied from one to 32 gouges on a single tree. Severe bark stripping again confirms reports in the Kruger Park that elephants have heavy impact on *S. birrea* (Van Wyk and Fairall 1969, Owen-Smith 1988).

Many species which are commonly bark stripped elsewhere were not stripped by elephants during the present study. *Acacia tortilis* was tusk gouged, but extremely infrequently in comparison to its abundance at Tshukudu. Elsewhere in Africa, elephants extensively remove the bark from *A. tortilis* (Anderson and Walker 1974, Croze 1974, Pellew 1983, Mwalyosi 1987). *Combretum imberbe* was bark stripped in 82% of stems found in the Sengwa Wildlife Research Area (Anderson and Walker 1974). *Terminalia prunioides* had bark removal in 50% of stems found along the Linyanti river (Wackernagel 1992). In addition to limited observation time, seasonality of bark removal and prevalence of alternate food may have precluded prominent bark stripping during my study.

CHAPTER 4. THE IMPACT OF ELEPHANTS ON THE MARULA TREE *SCLEROCARYA BIRREA*

4.1 Introduction

Marula trees *Sclerocarya birrea* have great economic, cultural and aesthetic value. Furthermore, they were found in this study to be the dominant tree species in the area in terms of overall basal cover (Chapter 2). Managers of protected areas, game rangers and tourists widely believe that elephants preferentially eat or break marula trees and attention is often focused on this "destructive" habit (pers. obs.). My primary objective was to ascertain the fraction of marula trees that had been damaged or killed by elephants at Kapama, Thornybush and Tshukudu Game Reserves.

Elephants are known to walk on dirt and paved roads and it has been suggested that they may in fact browse more heavily on plants in the immediate vicinity of roads (Van Wyk and Fairall 1969). Large broken trees visible from roads perpetuate this belief, but the theory has not been rigorously tested. Thus, a secondary aim was to establish whether roadside damage is representative of overall damage, or whether elephants push over more trees near roads. In the following pages, I will discuss the marula tree density, size class distribution, percentage of fruit-bearing trees, and extent of utilization by elephant in the three study areas.

4.2 Materials and Methods

Between 6 December and 13 December 1996, thirty 1 000 x 5 m quadrats were surveyed at each of the three game reserves. The properties were divided into blocks delineated by roads or cutlines. Fifteen blocks on each property were sampled with one transect inside the block and the second transect on the block edge (the road encircling the block).

Tshukudu Private Game Reserve had 15 distinct blocks, but Kapama and Thornybush had 144 and 129 blocks respectively, so a random number generator was used to select sample blocks. Sampling was stratified to include a representative number of blocks in each of the geographically distinct sections of the properties.

The starting point for the transect was chosen at random, generally at the first point at which the block was intercepted by vehicle. My field assistant and I counted the number of steps required to travel 1 000 m in similar terrain beforehand and paced off the transect length. Internal transects began approximately 10 m from the roadside and were oriented randomly by picking a distant landmark or reference point and heading towards it without avoiding thickets or other obstacles. If internal blocks were less than 1 000 m in length and roads had to be crossed, counting was stopped and resumed in the contiguous block 10 m from any road edges.

Roadside transects were adjacent to one edge of the road encircling the block and extended from the road edge to 5 m inside the block. If blocks were less than 1 000 m in perimeter, the road transect was extended onto the adjacent block.

The diameter above the basal swelling of every marula tree within the 1 000 x 5 m strip was measured. Tree height was estimated to the nearest 0.5 m. Each tree was examined for presence/absence of fruit, presence of bark damage, and presence of branch breakage. When bark damage was present, the minimum and maximum height of damage, percent of circumference and percent of total bark removed between ground level and 3m were noted. When breakage was present, it was categorized as main stem breakage, branch breakage, and/or old branch breakage. Breakage qualified as branch breakage, rather than main stem breakage, when the stem had forked into two or more branches below the breakage point. The proportion of the overall plant which was removed was visually estimated as the fraction of biomass which had been removed, judging from the size of the break in relation to the remaining branches at the break point (after Anderson and

Walker 1974). Main stem breakage was 100% removal of above-ground biomass, but did not necessarily mean the tree had been killed.

Recent or current season impact was distinguished from old impact by the pinkish fleshy colour of the exposed stem in the former. Exposed stems which had weathered over time were grey inside and were categorized as old impact.

In the following pages, the marula trees are discussed with respect to presence or absence of fruit, rather than as male and female because small or sickly female trees may not have borne fruit, but were indistinguishable from male trees.

The χ^2 test (Zar 1996) was used to detect significant differences between the number of trees on each property, and incidence of breakage on fruiting and non-fruiting trees. Each pair of transects (inside and road) had a common starting point so a paired t-test (Zar 1996) was used to test for a significant difference in the incidence of elephant impact on marula trees inside and on the edge of blocks.

4.3 Results

A total of 615 marula trees were found. Tshukudu had the highest density of marula trees of 1567 trees km^{-2}. Thornybush had 1527 trees km^{-2}, and Kapama had 1007 trees km^{-2}. Mean ± SD of the number of trees was 1367 ± 312.41. The difference in density was significant at the 0.05 level (χ^2 = 142.79, df = 1).

4.3.1 Population Characteristics

The smallest size class, less than 10 cm in stem diameter, accounted for an average of 8% of the population (Figure 4.1). The 30-40 cm size class was the most numerous size on two of the three properties, amounting to 31% at Thornybush and 44% at Tshukudu. Trees greater than 60 cm in diameter were rare on all three properties, amounting to less than 1% of the overall sample.

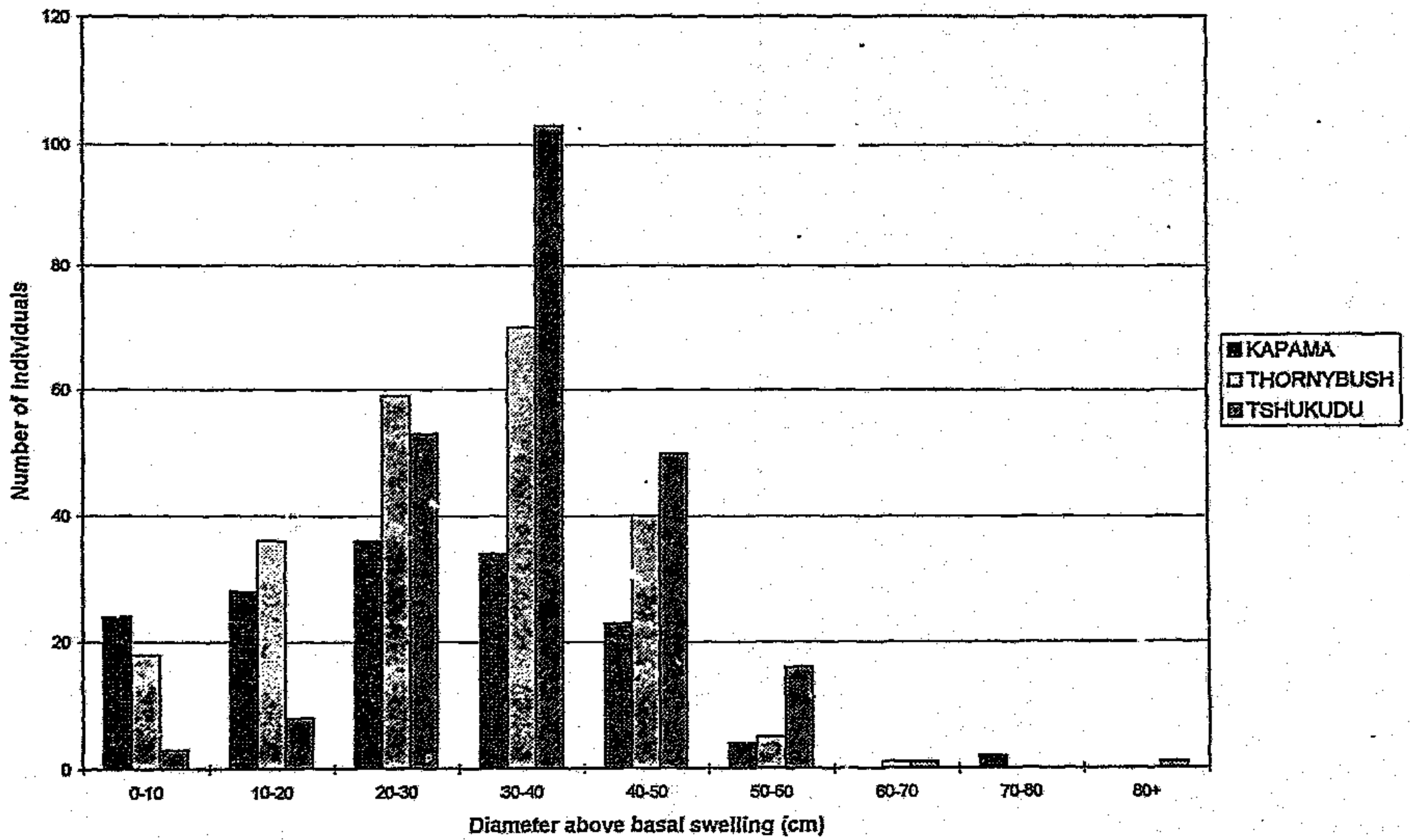

Figure 4.1. *Sclerocarya birrea* size distribution at Kapama, Thornybush and Tshukudu Game Reserves.

4.3.2 Bark Damage

In total, 59 trees had evidence of bark damage (9.6%) (Figure 4.2). Forty trees had recent bark stripping or ring barking (6.5% of all trees), 14 bore single tusk gouges (2.2% of all trees), and an additional five had old bark removal (0.8%).

None of the 45 trees in the smallest size class, 0-10 cm in diameter, had any bark damage whatsoever. Of the 30 trees in the sample greater than 50 cm in diameter, seven (3%) had bark damage. Only five trees were greater than 60 cm in diameter, one of which had been bark-stripped.

In total, four marula trees with ring-barking by elephants were dead. Three of the four trees had bark completely removed from ground level to 3m. The fourth dead tree had 50% of the bark surface to 3m removed. However, it was almost contiguously ring-barked (90%) at one height. Elephants had completely stripped the bark from a fifth tree from ground level to 3m, but it was still alive and bearing fruit.

Five trees with 50% bark removed to a height of 3m, but less than 75% contiguously at any height, were still alive. Trees with 25-33% bark removal also appeared viable, bearing leaves and, in some cases, fruit. Three trees with old bark removal up to 25% overall appeared to be healthy.

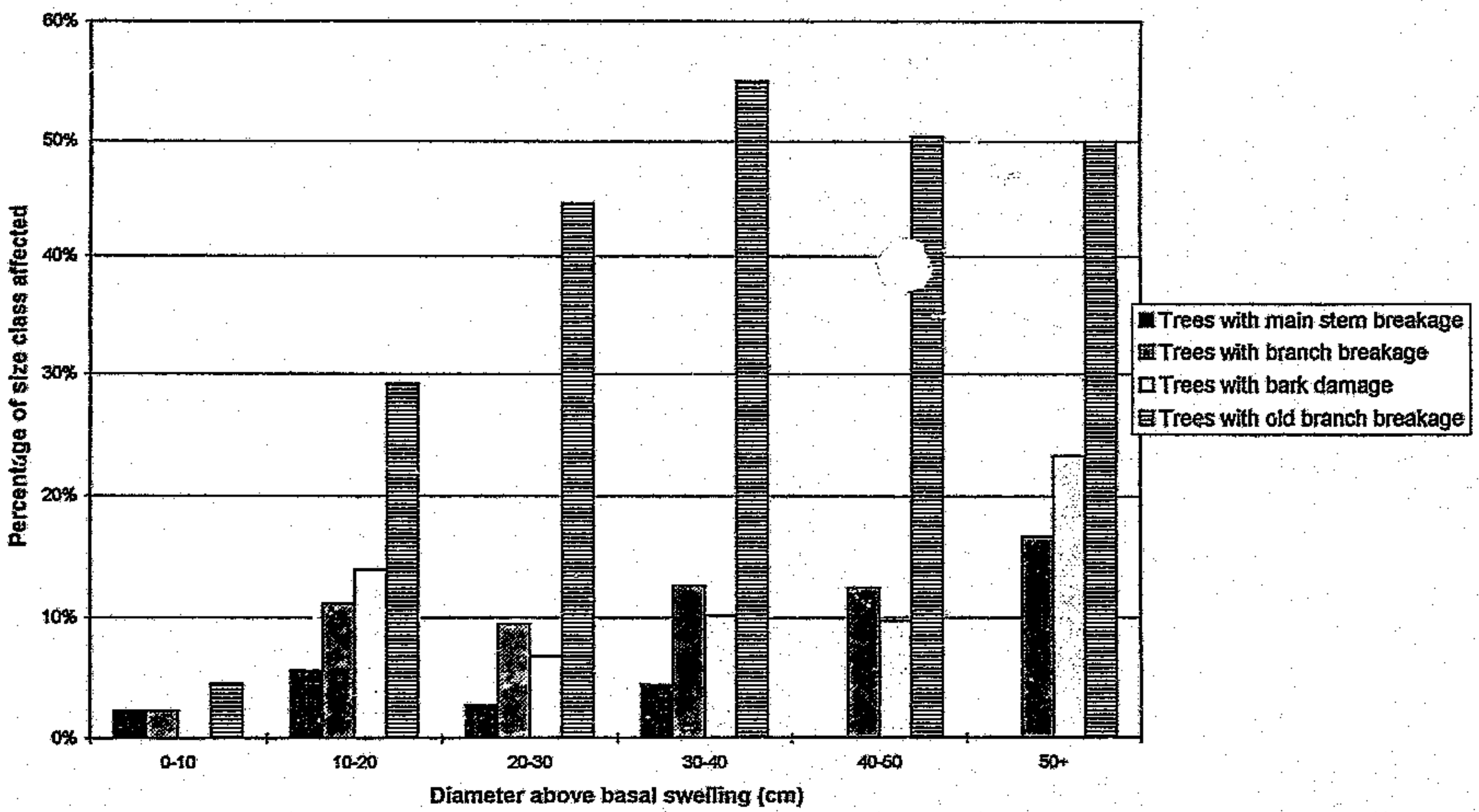

Figure 4.2. Percentage of *Sclerocarya birrea* trees in each size class with main stem breakage, branch breakage, bark removal or old branch breakage.

4.3.3 Breakage

Elephants broke the main stems of 18 marula trees (3% of all trees) during the year prior to the survey. Of these 18 broken trees, seven had visible new green leaves sprouting from the broken stem, and were obviously not killed. All trees with broken main stems were smaller than 40 cm in diameter (Figure 4.2). Trees in the 10-20, 20-30, and 30-40 cm size categories were most heavily affected with main stem breakage. However, even the most severely affected class (10-20cm) had fewer than 6% of stems broken.

Elephants recently broke branches on an additional 68 of the 615 trees (11%). Branch breakage was least frequent in the 0-10 cm size class (Figure 4.2). Size classes greater than 10 cm in diameter had branch breakage on 9 to 17% of stems.

Old branch breakage was evident on 45% of trees (Figure 4.2), but was particularly difficult to attribute to elephants because elephant damage was virtually indistinguishable from breakage due to other forces, such as wind or lightning. The incidence of branch breakage increased with increasing diameter; old breakage rose from 4% in small stems to approximately 50% of stems in trees greater than 30 cm in diameter.

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4.3.4 Severity of Breakage

Extent of breakage for the 86 marula trees with recent branch or main stem breakage was estimated (Figure 4.3).

The great majority of trees had no branch breakage whatsoever (529 of 615 trees, 86%). Breakage of 1-24% of all branches was found on 31 trees (5.0% of all trees). Twenty trees had 25-49% of branches broken (3.3% of all trees). Breakage from 50-74% was found on 15 trees (0.2%). One tree had 75-99% breakage. Of the 68 trees with fresh branch breakage, one had all of its branches broken (100%) and was dead. Including the 18 trees with main stem breakage, 19 trees had 100% damage.

As noted in section 4.3.3, seven of the 19 trees with 100% breakage had new coppice regrowth and had not been killed. All 67 trees with branch breakage less than 100% were still alive. Two trees with 60% of their branches broken, three with 66% and one with 75% still appeared healthy.

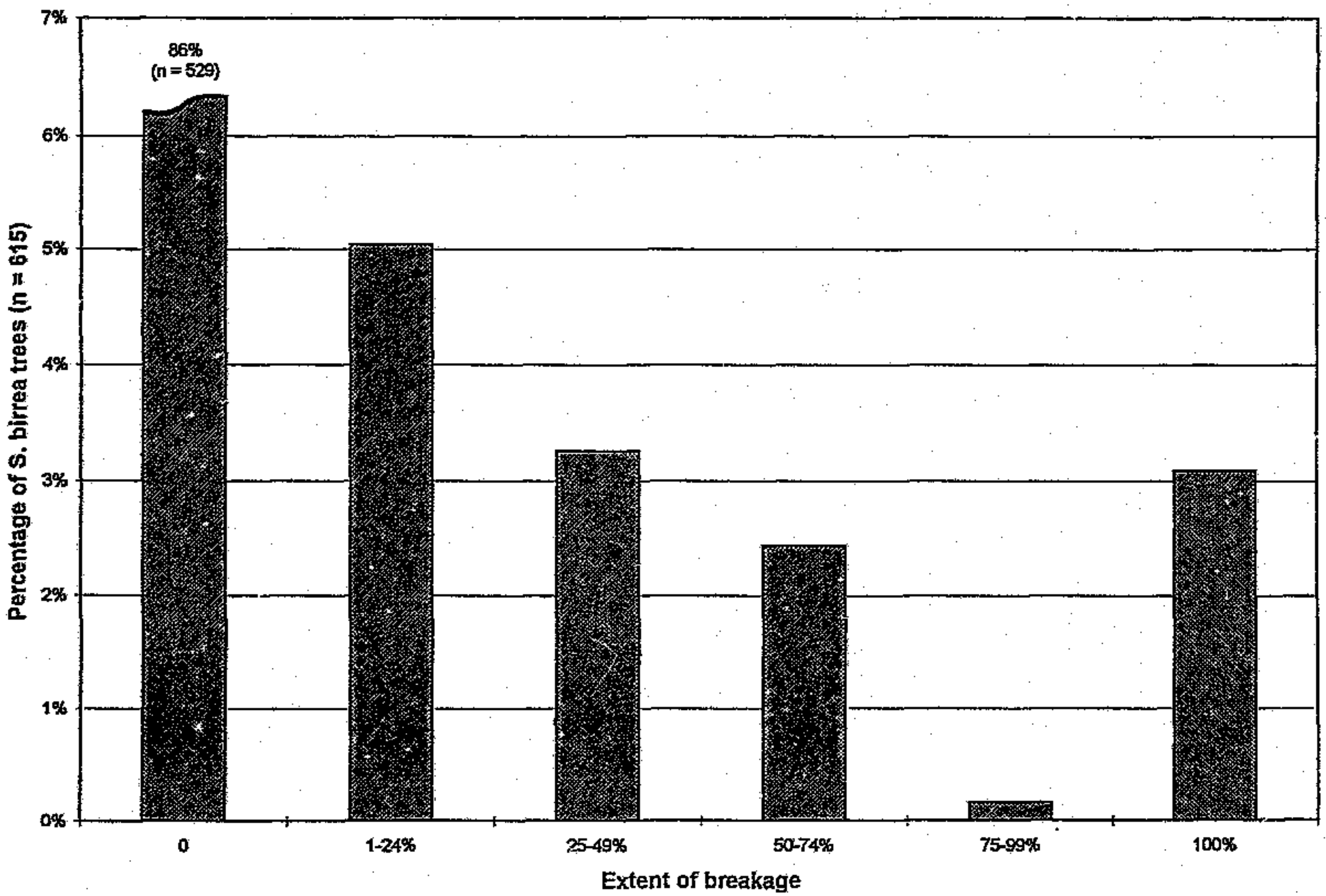

Figure 4.3. Severity of branch or main stem breakage on 615 *Sclerocarya birrea* trees.

4.3.5 Importance of Roads

In 45 interior and 45 road transects, four road transects had no marula trees. The 45 interior transects included 363 marula stems (59% of total), while the roadside blocks had 252 trees (41%). The difference between the number of trees inside each block and along the road of each block was not significant (paired two-tail t-test, $t = 0.011$, $p > 0.05$). There was no significant difference between the fraction of trees with elephant impact inside the blocks or along the road (paired two-tail t-test, $t = 0.058$, $p > 0.05$).

4.3.6 Importance of Fruit

Fruiting trees amounted to 36% of the overall population. Sixteen of 615 trees (3%) were leafless (dead or regrowing from coppice) and did not bear any fruit, but were assigned to a third category of unknown fruiting status.

Trees with and without fruit suffered nearly identical incidences of bark damage and branch breakage (Table 4.1). Sixteen trees which were severely broken or dead had unknown fruiting status, but did not significantly alter the percentage of trees with impact when pooled with either the non-fruiting or fruiting trees ($\chi^2 = 0.0002$ when pooled with the non-fruiting trees, $\chi^2 = 0.0983$ when pooled with the fruiting trees; both at $p > 0.05$).

Table 4.1. Percentage of fruit-bearing marula trees and incidence of recent elephant impact.

	Trees	Bark Damage	% of Trees	Branch Breakage	% of Trees
Fruit	223	22	9.8%	134	59.3%
No Fruit	376	34	9.0%	216	57.5%
Unknown	16	3	18.8%	11	68.8%
TOTAL	615	59	9.6%	361	58.7%

4.4 Discussion

4.4.1 Population Characteristics

The dearth of trees smaller than 30 cm in diameter is reason for concern since many tree species have more individuals in the smaller classes. Young seedlings may undergo high mortality, and *S. birrea* seedlings in particular, are highly palatable and may be killed by herbivores when not protected by other vegetation (Walker *et al* 1986). The clumped nature of marula seedlings could lead to undercounting or underrepresentation in my randomly chosen transects, but the little information that is available on the population dynamics of *S. birrea* seems to indicate that the species typically has few trees in the smallest size classes. In a survey of the *S. birrea* population in the Nylsvley Provincial Nature Reserve, Walker *et al* (1986) found a markedly unstable population structure with no immature trees and no evidence of successful regeneration. Size classes between 125 and 300 cm circumference (40-95 cm diameter) were evenly represented, but an absence of trees smaller than 50 cm circumference (16 cm diameter) led the authors to the conclusion that successful regeneration was highly episodic. A later publication suggested that marula trees were introduced to Nylsvley by early human settlers and the species struggled to maintain itself naturally (Scholes and Walker 1993). A survey in Waza National Park, Cameroon, where *S. birrea* is a dominant species, also revealed very weak regeneration and recruitment classes; regeneration accounted for less than 1% of trees (2 of 203), recruitment size trees amounted to 22% (44 of 203) and mature made up 77% (157 of 203) (Tchamba 1995).

This population size structure is not atypical for southern African trees. Wackernagel (1992) found similar bell-shaped distributions, most like the marula trees here, in *Combretum hereroense, C. molle, Colophospermum mopane, Croton megalobotrys, Peltophorum africanum, Terminalia sericea,* and *T. prunioides.* McDonald (1992) reported a dearth of small stems but abundant large stems in populations of *Acacia tortilis, Diospyros mespiliformis, Combretum imberbe, Lonchocarpus capassa, Croton megalobotrys, Ficus sycomorus,* and *Trichilia emetica.*

In addition to the risk of insufficient regeneration, elephant pressure may be exacerbated when trees grow in even-aged or even-sized stands. This phenomenon has been implicated in a die-off of *Acacia xanthophloea* in Amboseli National Park in Kenya (Young and Lindsay 1988). Environmental factors which can impede tree growth for an extended period include shade, fire, browsing, soil chemistry and water content. When the trees are released from these suppressing factors, even-sized stands of different aged trees form. Such stands are known to occur in many East African trees, and uniformity in size/age distribution may render them highly susceptible to size-specific stressors, like elephant feeding, increased water salinity or other micro-climatic changes (Young and Lindsay 1988). The *S. birrea* sub-populations at Kapama, Thornybush, and Tshukudu show enough variation in size that their resilience to elephants does not appear to be compromised by even-sized stands.

4.4.2 Bark and Branch Damage

During the year prior to my study, elephants broke branches of 11%of marula trees, broke the main stems of 3% of trees and removed bark from 10% of trees. Elephant impact contributed to the deaths of 12 trees (<2%): seven trees died from main stem breakage, one from branch breakage, and four from bark stripping.

Branch breakage and bark stripping increased in frequency with increasing stem sizes. Elephants broke branches in all size classes, whereas bark stripping only affected trees greater than 10 cm in diameter and main stem breakage was confined to stems smaller than 40 cm diameter.

There was no evidence of disproportional impact on the smaller size classes. If small trees were ring barked and killed, little sign would remain, but elephants observed in this study did not frequently eat small marulas (pers. obs., Chapter 3) so minor elephant impact on the smaller classes is not unexpected.

Evidence from my study indicates that *S. birrea* may withstand up to 50% ring barking from ground level to 3m high, but is likely to succumb to ring barking in excess of 50%. Contiguity of bark removal may also affect the ability of the tree to persist.

Trees died from branch breakage by elephants only when 100% of branches were broken. All 67 trees with less than total branch breakage appeared healthy. Most trees with broken branches had fewer than 50% of their total branches broken (51 trees, or 8.3% of the sample). Breakage of small branches is likely to have been under-reported owing to the inconspicuousness of such scars. The marula tree was found to be capable of coppicing after main stem breakage.

4.4.3 Importance of Roads and of Fruiting

Proximity to roads appeared to have no significant effect on either density of marula trees or frequency of use by elephants. Fruiting did not appear to encourage or discourage use by elephants.

4.4.4 Accumulation of Damage

The results of this study must be interpreted bearing in mind that rainfall in the preceding year was extremely high and elephants may have been less reliant on woody vegetation than is normally the case (Barnes 1979, 1980).

Old branch breakage was evident on 45% of the sampled population of *Sclerocarya birrea*. Annual breakage affected 14% of the population and bark stripping affected an additional 10%. Elephant usage resulted in death of 2% of the marula tree population.

The number of trees with old bark stripping (0.8%) was lower than predicted by the occurrence of fresh bark stripping (9.6%). Bark stripping can weaken trees to the point that they fall over or break (Weyerhaueser 1985). If trees did collapse from old bark stripping they have been recorded as old main stem breakage. Some trees are capable of regrowing bark over the exposed stem, e.g. *Acacia nigrescens* (Wackernagel 1992), which I did observe in some *S. birrea* stems, but I believe it is more likely that I mistakenly attributed old damage to the current season. Current branch breakage also exceeded accumulated branch breakage if branch breakage is visible for more than three years. Alternatively, elephants could have been using *S. birrea* more extensively in the past year, but in light of the abundant rainfall and high quality grass, I believe this is unlikely.

Elephant impact on *Sclerocarya birrea* was higher at Kapama, Thornybush and Tshukudu Game Reserves than elsewhere in the tree's range. In a survey of marula trees in Waza, Cameroon, Tchamba (1995) found cumulative impact of 14% of the *S. birrea* population, which is much lower than the 45% cumulative impact I found.

Trees in the present study appeared to be capable of surviving any breakage less than 75% of branches, and some even survived 100% breakage. When trees were affected, less than 25% of the tree's biomass was removed in 36% of cases. Less than 50% of the tree's biomass was broken in 59% of breakages. At the level of the individual tree, one year's impact of 25% is unlikely to kill the tree. However, repeated breakage on the same tree could lead to its demise.

If elephant impact is accumulated at a rate which exceeds annual growth on a given marula tree, it is not sustainable for the individual tree. Without knowing marula growth rates, it is difficult to estimate how quickly biomass is gained. However, if elephants affect 14% of trees each year, and select different trees every year, an individual marula tree may suffer branch breakage only every seventh year. The typical damage level in this study was <50% of the tree's biomass. It is possible that the individual tree will have recovered from the initial biomass loss in the period between impacts and damage to it will therefore not accumulate beyond the tolerable level of 75%.

At the population level, the current level of elephant impact appears sustainable; regeneration and recruitment stage trees did not appear to be depleted and a substantial number of reproducing trees were found.

CHAPTER 5. CONCLUSIONS

5.1. Impact of elephants on woody vegetation along feeding pathways

Conclusions

The first part of this study aimed to provide information on the type and extent of impact on woody vegetation caused by recently-introduced elephants in three study areas. Vegetation quadrats in areas where elephants had been feeding were successful for measuring the vegetation available to the elephants, and establishing species and sizes of woody plants eaten or broken by elephants.

The first section of the study showed size-related trends in elephant impact types. Branch breakage and leaf stripping affected stems of all sizes. The frequency of branch breakage increased with increasing stem diameter. Main stem breakage was most common in stems smaller than 30cm diameter. The incidence of bark stripping increased in stems larger than 10cm in diameter. Elephants apparently had very little impact on seedlings.

Data from the vegetation quadrats revealed that certain common species are broken or eaten more frequently and more severely than others. In agreement with the findings of researchers elsewhere, *Combretum collinum, Acacia gerrardii, Albizia harveyi, Sclerocarya birrea, Dalbergia melanoxylon*, and *Pterocarpus rotundifolius* were species favoured by elephants. It was surprising to find that elephants had impact on *Acacia tortilis, Terminalia sericea*, and *Terminalia prunioides* very infrequently, whereas in other parts of Africa, these are species which elephants browse extensively. Within certain genera, there was wide variation in impact levels. Elephants frequently broke the stems or branches of *Acacia gerrardii* and *A. nigrescens* but rarely or never altered *A. exuvialis, A. nilotica* and *A. tortilis*. Elephants also showed preferences for *Combretum collinum* and *C. imberbe*, but neglected *C. apiculatum, C. hereroense*, and *C. zeyheri*.

Limitations

This study was conducted after a period of exceptionally high rainfall. Since elephants are more reliant upon woody species during dry periods, elephant impact during drier times could be much heavier. Impact may increase in severity and shift or expand to include a wider diversity of species. Data were collected from August to December and do not reflect changes in species use which may occur with seasonal change.

The vegetation quadrats had an inherent bias towards areas with elephant impact since they were placed specifically on feeding pathways. Therefore the quadrats were not representative of overall elephant impact on the entire property, and impact rates and severity could not be extrapolated over the entire area. The methods were, however, sufficient to fulfill the objective of identifying target sizes and species.

Elephant density was relatively low at all three of my study areas. Increased elephant pressure may lead to different selectivity and magnitude of impact on woody vegetation.

5.2 Elephant feeding behaviour

Conclusions

Behavioural observation of hand-raised elephants gave insight into the relative importance of woody species in the diet, how elephants affect particular trees, and which trees suffer more severe biomass removal as a result of this feeding. Grass was the major constituent of the elephants' diet throughout the study and they were not as reliant on woody species as anticipated. The elephants ate *Acacia nigrescens, Combretum apiculatum, Grewia bicolor, G. monticola,* and *Sclerocarya birrea* most frequently, but in relation to the abundance of each species, *S. birrea, Combretum apiculatum,* and *A. nigrescens* were the most preferred species. The hand-raised elephants removed sizable portions of bark from stems of *Acacia nigrescens* and *S. birrea*. Although seedlings were the most common size of woody stems in the area where they foraged, the elephants ate seedlings very infrequently, fewer than 0.2% of all feeding events.

Limitations

Interpreting the ecological implications of the observed behaviour proved to be quite difficult. Each feeding observation was not paired directly with a vegetation quadrat because quadrats were only done once every ten minutes, so the comparison of feeding event frequency to species abundance was less exact than I would have liked. The young age and unnatural behaviour of the hand-raised animals has unknown effects on their similarity to wild herds with respect to impact on woody vegetation.

5.3. The impact of elephants on the marula tree *Sclerocarya birrea*

Conclusions

A survey of *Sclerocarya birrea* was designed to determine how seriously trees of this species have been affected by elephants. I found that elephants broke or bark stripped 24%of the marula trees in the preceding year. Elephants killed 3% of the sampled trees during the preceding year by completely removing bark or breaking the main stem or all branches. However, individual trees were found to withstand removal of up to 75% of branches and most branch breakage was not severe. If elephants revisit the same trees though, the trees may become seriously damaged. Smaller marula trees were relatively free from elephant damage while bigger trees were increasingly more prone to branch breakage and bark stripping. Intermediate sized trees were most susceptible to main stem breakage, but showed some capacity to regrow by coppicing. Neither fruiting nor proximity to road had any significant effect on elephant impact.

Limitations

Fresh elephant impact was greater than predicted from incidence of old impact, so fresh impact may include some older impact. The frequency of fresh impact is therefore probably exaggerated. Estimates of annual damage therefore err towards over-estimating rates and may include an additional year of impact.

5.4. Complementarity

The vegetation quadrats, behavioural observations, and marula tree survey allowed synthesis of information which would have been overlooked when assessing each study independently.

The vegetation quadrats and behavioural observations both provided insight into how elephants eat woody vegetation and the resultant consequences for the woody vegetation. *Sclerocarya birrea* was the only species found to be highly preferred by vegetation-based acceptance frequencies and by behaviour-based forage index values. Feeding on *Grewia villosa* and *Terminalia prunioides* was not evident in vegetation quadrats, but was seen in behavioural observations of hand-raised elephants. Similarly, some species appeared to be favourite forage items of the hand-raised elephants, but the vegetation data indicated that they were not favoured relative to their abundance: for example, *Grewia bicolor, G. flavescens, G. hexamita,* and *G. monticola*. Leaf stripping was frequently observed during my behavioural observations and is probably underreported in the vegetation quadrats because it was inconspicuous.

The marula survey was an extension and expansion of the vegetation quadrats and behavioural studies to include a detailed assessment of elephant impact on a single species at a large geographic scale. The size distribution of the various impact types on *S. birrea* were very similar to the distribution of impact types on all species in the vegetation quadrats. In addition to pinpointing the level of impact on marula trees, this segment of the study provided unique insight into the tree's ability to survive breakage and bark stripping.

5.5 Recommendations

Long-term monitoring is necessary to detect change in size and species composition of the vegetation. The data from the current survey are a baseline to which future data can be compared. Variation due to forces other than elephant pressure is bound to occur, but unusual trends should be detectable. Furthermore, this study revealed which species were currently undergoing the most use by elephants and these species can be carefully regulated as indicators of change. I believe any of the species highlighted as preferred in either the site-based acceptance frequencies or the forage index may be good indicators of elephant use in the future. If future vegetation surveys reveal severe decrease in the area of woodlands or density of trees, it may be important to assess the contribution of other factors to the decline as well. The effects of elephant utilization on the woody layer can be intensified by combination with fires or intensive use by other browsing ungulates.

Further investigation of the nutritional differences in preferred and non-preferred plants would be very interesting. A strong preference for some *Acacia* and *Combretum* spp. and not for others may reflect underlying biochemical or structural differences.

A study which more thoroughly integrates feeding behaviour and vegetation availability would be extremely valuable. Expanding the duration of the observation over entire days and across seasons would also provide useful information on daily and seasonal variation in both habitat choice and food choice.

Follow-up studies would be extremely valuable to elucidate details of marula tree population dynamics. A single survey is insufficient to provide the necessary information to calculate survivorship and growth in marula trees. Without knowledge of the capacity of the species to replenish itself, it is difficult to determine what level of use by elephants is sustainable. Repeating the marula tree surveys at Kapama, Thornybush and Tshukudu a number of years from now would provide interesting information on both the tree population and the level of elephant impact.

If repeat studies confirm a decline in the marula tree population, excluding elephants from selected areas (as is currently done on some of the game reserves) may enhance marula survivorship. Data from my study indicate that selectively excluding elephants from selected areas should counter mortality of seedlings and mature trees: small trees could be protected from early removal and medium sized trees could be allowed to grow beyond the critical sizes most susceptible to main stem breakage.

REFERENCES

Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour.* 49: 227-267.

Anderson, GD, and BH Walker. 1974. Vegetation composition and elephant damage in the Sengwa Wildlife Research Area, Rhodesia. *Journal of the South African Wildlife Management Association.* 4: 1-14.

Anderson, JL. 1991. The introduction of elephant into medium-sized conservation areas. In *Proceedings of a Symposium on the African elephant as a game ranch animal,* Wildlife Group of the South African Veterinary Association.

Barnes, RFW 1979. Elephant ecology in Ruaha National Park, Tanzania. PhD dissertation. University of Cambridge.

Barnes, RFW. 1980. The decline of the baobab tree in Ruaha National Park, Tanzania. *African Journal of Ecology.* 18: 243-252.

Barnes, RFW. 1982. Elephant feeding behaviour in Ruaha National Park, Tanzania. *African Journal of Ecology.* 20: 123-136.

Barnes, RFW. 1983. Effects of elephant browsing on woodlands in a Tanzanian National Park: measurements, models and management. *Journal of Applied Ecology.* 20: 521-540.

Barnes, RFW. 1985. Woodland changes in Ruaha National Park (Tanzania) between 1976 and 1982. *African Journal of Ecology.* 23: 215-221.

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

Caughley, GJ. 1976. The elephant problem - an alternative hypothesis. *East African Wildlife Journal.* 14: 265-283.

Coates Palgrave, K. 1977. *Trees of Southern Africa.* C. Struik Publishers. Cape Town.

Corfield, TF. 1973. Elephant mortality in Tsavo National Park, Kenya. *East African Wildlife Journal.* 11: 339-368.

Croze, H. 1974. The Seronera bull problem. Part II. The trees. *East African Wildlife Journal.* 12: 29-47.

Croze, H, AKK Hillman, and EM Lang. 1981. Elephants and their habitats: how do they tolerate each other? In *Dynamics of Large Mammal Populations*, CW Fowler and TD Smith, eds. John Wiley & Sons, New York.

Cumming, DHM. 1981. The management of elephant and other large mammals in Zimbabwe. In *Management of Locally Abundant Wild Mammals*, PA Jewell, S Holt and D Hart, eds. Academic Press, New York.

De Villiers, PA, EW Pietersen, TA Hugo, HH Meissner, and OB Kok. 1991. Method of sampling food consumption by free-ranging elephant. *South African Journal of Wildlife Research*. 21: 23-27.

Dublin, HT. 1995. Vegetation dynamics in the Serengeti-Mara Ecosystem: the role of elephants, fire, and other factors. In *Serengeti II*, ARE Sinclair and P Arcese, eds. University of Chicago Press, Chicago.

Du Toit, JG. 1991. The African elephant *Loxodonta africana* as a game-ranch animal. In *Proceedings of a Symposium on the African elephant as a game ranch animal*. Wildlife Group of the South African Veterinary Association.

Guy, PR. 1976. The feeding behaviour of elephant *(Loxodonta africana)* in the Sengwa Area, Rhodesia. *South African Journal of Wildlife Research*. 6: 55-63.

Guy, PR. 1981. Changes in the biomass and productivity of woodlands in the Sengwa Wildlife Research Area, Zimbabwe. *Journal of Applied Ecology*. 18: 507-519.

Ishwaran, N. 1983. Elephant and woody-plant relationships in Gal Oya, Sri Lanka. *Biological Conservation*. 26: 255-270.

Jachmann, H, and RHV Bell. 1985. Utilization by elephants of the *Brachystegia* woodlands of the Kasungu National Park, Malawi. *African Journal of Ecology*. 23: 245-248.

Jachmann, H, and T Croes. 1991. Effects of browsing by elephants on the *Combretum/Terminalia* woodland at the Nazinga Game Ranch, Burkina Faso, West Africa. *Biological Conservation*. 57: 13-24.

Laws, RM, ISC Parker, and RCB Johnstone. 1975. *Elephants and their habitats*. Clarendon Press, Oxford.

Leuthold, W. 1977. Changes in tree populations of Tsavo East National Park, Kenya. *East African Wildlife Journal*. 15: 61-69.

Leuthold, W, and JB Sale. 1973. Movements and patterns of habitat utilization of elephants in Tsavo National Park, Kenya. *East African Wildlife Journal.* 11: 369-384.

Lindsay, WK. 1994. Feeding ecology and population demography of African elephants in Amboseli, Kenya. PhD thesis. University of Cambridge.

McDonald, I.R. 1992. Impacts of large herbivores on the vegetation landforms of the riparian zone of the Letaba River, Kruger National Park. Unpublished data. University of the Witwatersrand.

McKnight, BL. 1995. Behavioural ecology of 'hand-reared' African elephants (*Loxodonta africana* (Blumenbach)) in Tsavo East National Park, Kenya. *African Journal of Ecology.* 33: 242-256.

Moolman, HJ, and RM Cowling. 1994. The impact of elephant and goat grazing on the endemic flora of South African succulent thicket. *Biological Conservation.* 68: 53-61.

Moore, RJ. 1991. Can the African elephant earn its keep? In *Proceedings of a Symposium on the African elephant as a game ranch animal.* Wildlife Group of the South African Veterinary Association.

Moroka, DN. 1984. Elephant-habitation relationships in northern Botswana. Department of Wildlife and National Parks, Gaborone.

Mulder, PFS. 1991. The African elephant: legislation and management. In *Proceedings of a Symposium on the African elephant as a game ranch animal.* Wildlife Group of the South African Veterinary Association.

Mwalyosi, RBB. 1987. Decline of *Acacia tortilis* in Lake Manyara National Park, Tanzania. *African Journal of Ecology.* 25:51-53.

Owen-Smith, RN. 1988. *Megaherbivores: the influence of very large body size on ecology.* Cambridge University Press. Cambridge, UK.

Owen-Smith, RN and SM Cooper. 1987a. Assessing food preferences of ungulates by acceptability indices. *Journal of Wildlife Management.* 51: 372-378.

Owen-Smith, RN and SM Cooper. 1987b. Palatability of woody plants to browsing ruminants in a South African savanna. *Ecology.* 68: 319-331.

Pellew, RAP. 1983. The impacts of elephant, giraffe and fire upon the *Acacia tortilis* woodlands of the Serengeti. *African Journal of Ecology.* 21: 41-74.

Petrides, GA. 1975. Principal foods versus preferred foods and their relations to stocking rate and range condition. *Biological Conservation.* 7: 161-169.

Ruess, RW, and FL Halter. 1990. The impact of large herbivores on the Seronera woodlands, Serengeti National Park, Tanzania. *African Journal of Ecology.* 28: 259-275.

Scholes, RJ, and BH Walker. 1993. *An African Savanna: Synthesis of the Nylsvley Study.* Cambridge University Press. Cambridge, UK.

Tchamba, MN. 1995. The impact of elephant browsing on the vegetation in Waza National Park, Cameroon. *African Journal of Ecology.* 33: 184-193.

Thomson, PJ. 1975. The role of elephants, fire and other agents in the decline of a *Brachystegia boehmii* woodland. *Journal of the South African Wildlife Management Association.* 5: 11-18.

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

Van Wyk, P, and N Fairall. 1969. The influence of the African elephant on the vegetation of the Kruger National Park. *Koedoe.* 9: 57-95.

Vesey-Fitzgerald, D. 1973. Browse production and utilization in Tarangire National Park. *East African Wildlife Journal.* 11: 291-305.

Viljoen, PJ. 1991. Elephants and habitats. In *Proceedings of a Symposium on the African elephant as a game ranch animal.* Wildlife Group of the South African Veterinary Association.

Von Teichman, I, JCG Small, and PJ Robbertse. 1986. A preliminary study on the germination of *Sclerocarya birrea* subsp. *caffra.* *South African Journal of Botany.* 52: 145-148.

Wackernagel, A. 1992. Impact of elephants on riverine vegetation of the Linyanti River in northern Botswana. Unpublished MSc dissertation. University of the Witwatersrand.

Walker, BH, L Stone, L Henderson, and M Vernede. 1986. Size structure analysis of the dominant trees in a South African savanna. *South African Journal of Botany.* 52: 397-402.

Walker, CH. 1991. Factors that may influence the establishment of new elephant populations onto private land. In *Proceedings of a Symposium on the African* *elephant as a game ranch animal.* Wildlife Group of the South African Veterinary Association.

Weyerhaeuser, FJ. 1985. Survey of elephant damage to baobabs in Tanzania's Lake Manyara National Park. *African Journal of Ecology.* 23:235-243.

Young, TP, and WK Lindsay. 1988. Role of even-age population structure in the disappearance of *Acacia xanthophloea* woodlands. *African Journal of Ecology.* 26: 69-72.

Zar, JH. 1996. *Biostatistical analysis (3rd edition).* Prentice Hall, New Jersey.

APPENDIX 1. Scientific, common, and family names of species found in the vegetation quadrats at Kapama, Thornybush or Tshukudu Game Reserves. Nomenclature according to conventions used in Coates Palgrave (1977) and Van Wyk (1984).

Genus	species	Author	Common name	Family
Acacia	*exuvialis*	Verdoorn	Flaky thorn	Mimosaceae
Acacia	*gerrardii*	Benth.	Red thorn	Mimosaceae
Acacia	*karroo*	Hayne	Sweet thorn	Mimosaceae
Acacia	*nigrescens*	Oliver	Knob thorn	Mimosaceae
Acacia	*nilotica*	(L.) Willd. ex Delile	Scented thorn	Mimosaceae
Acacia	sp.			Mimosaceae
Acacia	*tortilis*	(Forsk.) Hayne	Umbrella thorn	Mimosaceae
Albizia	*harveyi*	Fourn.	Common false thorn	Mimosaceae
Balanites	*maughamii*	Sprague	Torchwood	Balanitaceae
Berchemia	*zeyheri*	(Sonder) Grubov	Red ivory	Rhamnaceae
Bolusanthus	*speciosus*	(Bolus) Harms	Tree wisteria	Fabaceae
Bridelia	*cathartica*	Bertol. f.	Knobby bridelia	Euphorbiaceae
Canthium	sp.			Rubiaceae
Carissa	*edulis*	Vahl	Numnum	Apocynaceae
Cassia	*senepetersiana*	(Bolle)	Monkey pod	Caesalpiniaceae
Cassine	*aethiopica*	Thunb.	Koobooberry	Celastraceae
Cassine	*transvaalensis*	(Burtt Davy)	Transvaal saffron	Celastraceae
Cissus	*cornifolia*		Wild grape	Vitaceae
Combretum	*apiculatum*	Sonder	Red bushwillow	Combretaceae
Combretum	*collinum*	Fresen.	Rhodesian bushwillow	Combretaceae
Combretum	*hereroense*	Schinz	Russet bushwillow	Combretaceae
Combretum	*imberbe*	Wawra	Leadwood	Combretaceae
Combretum	*molle*	R. Br. ex G. Don	Velvet bushwillow	Combretaceae
Combretum	*zeyheri*	Sonder	Large-fruited bushwillow	Combretaceae
Commiphora	*africana*	(A. Rich.) Engl.	Hairy corkwood	Burseraceae
Commiphora	*glandulosa*	(Schinz)	Tall common corkwood	Burseraceae
Commiphora	*mollis*	(Oliver) Engl.	Velvet corkwood	Burseraceae
Commiphora	*neglecta*	Verdoorn	Sweet-root corkwood	Burseraceae
Cordia	*monoica*	Roxb.	Snot berry	Boraginaceae
Cordia	sp.			Boraginaceae
Croton	*menyhartii*	Pax	Rough-leaved croton	Euphorbiaceae

Genus	species	Author	Common name	Family
Dalbergia	*melanoxylon*	Guillemin & Perrottet	Zebrawood	Fabaceae
Dichrostachys	*cinerea*	(L.) Wight & Arn	Sicklebush	Mimosaceae
Diospyros	*mespiliformis*	Hochst. ex A. DC.	Jackalberry	Ebenaceae
Dombeya	*rotundifolia*	(Hochst.) Planchon	Wild pear	Sterculiaceae
Ehretia	*amoena*	Klotzsch	Sandpaper bush	Boraginaceae
Ehretia	*rigida*	(Thunb.) Druce	Puzzle bush	Boraginaceae
Erythrina	*lysistemon*	E. Mey.	Common coral tree	Linaceae
Euclea	*divinorum*	Hiern	Magic guarri	Ebenaceae
Euclea	*natalensis*	A. DC.	Natal guarri	Ebenaceae
Euclea	*racemosa*	Murray	Bush guarri	Ebenaceae
Euphorbia	sp.			Euphorbiaceae
Gardenia	*volkensii*	K. Schum.	Transvaal gardenia	Rubiaceae
Gossypium	*herbacium*		Wild cotton	
Grewia	*bicolor*	Juss.	White raisin	Tiliaceae
Grewia	*flavescens*	Juss.	Square-stemmed raisin	Tiliaceae
Grewia	*hexamita*	Burret	Giant raisin	Tiliaceae
Grewia	*monticola*	Sonder	Silver raisin	Tiliaceae
Grewia	*villosa*	Willd.	Mallow raisin	Tiliaceae
Hippocratea	sp.		Paddle-pod	Celastraceae
Lannea	*discolor*	(Sonder) Engl.	Live-long	Anacardiaceae
Lannea	*schweinfurthii*	(Engl.) Engl.	False marula	Anacardiaceae
Lonchocarpus	*capassa*	Rolfe	Apple-leaf	Fabaceae
Maerua	*angolensis*	DC.	Bead-bean	Capparaceae
Maerua	sp.			Capparaceae
Manilkara	*mochisia*	(Baker) Dubard	Lowveld milkberry	Sapotaceae
Maytenus	*heterophylla*	(Ecklon & Zeyher) N.K.B. Robson	Common spike thorn	Celastraceae
Maytenus	*senegalensis*	(Lam.) Exell	Red spike-thorn	Celastraceae
Mundulea	*sericea*	(Willd.) Chev.	Cork bush	Fabaceae
Nuxia	*oppositifolia*	(Hochst.) Benth.	River nuxia	Loganiaceae
Olea	*europaea*	L.	Olive	Oleaceae
Ormocarpum	*trichocarpum*	(Taub.) Engl.	Caterpillar pod	Fabaceae
Ozoroa	*paniculosa*	(Sonder) R. & A. Fernandes	Resin tree	Anacardiaceae
Ozoroa	sp.			Anacardiaceae
Ozoroa	*sphaerocarpa*	R. & A. Fernandes	Bastard currant resin tree	Anacardiaceae
Peppea	*capensis*	Ecklon & Zeyher	Jacket plum	Sapindaceae

Genus	species	Author	Common name	Family
Pavetta	*calophylla*		Bride's bush	Rubiaceae
Pavetta	sp.			Rubiaceae
Peltophorum	*africanum*	Sonder	Weeping wattle	Caesalpiniaceae
Protasparagus	sp.		Wild asparagus	Asparagaceae
Pterocarpus	*rotundifolius*	(Sonder) Druce	Round-leafed klaat	Fabaceae
Rhus	*dentata*	Thunb.	Nana-berry	Anacardiaceae
Rhus	*gueinzii*	Sonder	Thorny karee	Anacardiaceae
Rhus	*pentheri*	Zahlbr.	Common crow-berry	Anacardiaceae
Rhus	*rehmanniana*	Engl.	Blunt-leaved currant	Anacardiaceae
Rhus	sp.			Anacardiaceae
Schotia	*brachypetala*	Sonder	Weeping boer bean	Caesalpiniaceae
Sclerocarya	*birrea*	(A. Rich.) Hochst	Marula	Anacardiaceae
Securinega	*virosa*	(Roxb. ex Willd) Pax & K. Hoffm.	White-berry bush	Euphorbiaceae
Spirostachys	*africana*	Sonder	Tamboti	Euphorbiaceae
Strychnos	*madagascariensis*	Poiret	Black monkey orange	Loganiaceae
Terminalia	*prunioides*	C. Lawson	Lowveld cluster-leaf	Combretaceae
Terminalia	*sericea*	Burch. ex DC.	Silver cluster-leaf	Combretaceae
Ximenia	*caffra*	Sonder	Sourplum	Olacaceae
Ziziphus	*mucronata*	Willd.	Buffalo thorn	Rhamnaceae

APPENDIX 2. Woody species abundance by number of stems, pooled from vegetation quadrats at Kapama, Thornybush and Tshukudu Game Reserves.

Rank	Species	Stems	%of all stems
1	*Grewia flavescens*	878	6.73%
2	*Dalbergia melanoxylon*	762	5.84%
2	*Grewia monticola*	762	5.84%
4	*Strychnos madagascariensis*	689	5.28%
5	*Combretum apiculatum*	625	4.79%
6	*Combretum collinum*	595	4.56%
7	*Ormocarpum trichocarpum*	586	4.49%
8	*Pterocarpus rotundifolius*	576	4.41%
9	*Ehretia amoena*	539	4.13%
10	*Acacia gerrardii*	530	4.06%
11	*Combretum hereroense*	501	3.84%
12	*Acacia exuvialis*	495	3.79%
13	*Grewia bicolor*	446	3.42%
14	*Acacia nigrescens*	414	3.17%
15	*Albizia harveyii*	390	2.99%
16	*Securinega virosa*	387	2.97%
17	*Dichrostachys cinerea*	379	2.90%
18	*Maytenus heterophylla*	349	2 67%
19	*Euclea divinorum*	325	2.49%
20	*Cissus cornifolia*	299	2.29%
21	*Combretum zeyheri*	240	1.84%
22	*Grewia hexamita*	174	1.33%
23	*Terminalia sericea*	169	1.29%
24	*Grewia villosa*	141	1.08%
25	*Cassine transvaalensis*	114	0.87%
25	*Mundulea sericea*	114	0.87%
27	*Ziziphus mucronata*	110	0.84%
28	*Commiphora mollis*	108	0.83%
29	*Commiphora glandulosa*	92	0.70%
30	UNKNOWN	86	0.66%
31	*Cordia monoica*	81	0.62%
32	*Euclea natalensis*	78	0.60%
33	*Lonchocarpus capassa*	74	0.57%
34	*Bolusanthus speciosus*	73	0.56%
35	*Ehretia rigida*	69	0.53%

Rank	Species	Stems	%of all stems
36	*Maytenus senegalensis*	67	0.51%
37	*Gardenia volkensii*	47	0.36%
38	*Manilkara mochisia*	46	0.35%
39	*Peltophorum africanum*	43	0.33%
40	*Lannea schweinfurthii*	40	0.31%
41	*Protasparagus* sp.	38	0.29%
42	*Balanites maughamii*	37	0.28%
42	*Carissa edulis*	37	0.28%
44	*Sclerocarya birrea*	34	0.26%
45	*Acacia tortilis*	33	0.25%
46	*Berchemia zeyheri*	28	0.21%
46	*Rhus rehmanniana*	27	0.21%
48	*Canthium* sp.	26	0.20%
49	*Maerua* sp.	22	0.17%
50	*Diospyros mespiliformis*	21	0.16%
50	*Terminalia prunioides*	21	0.16%
52	*Hippocratea* sp.	18	0.14%
53	*Cassine aethiopica*	17	0.13%
54	*Combretum imberbe*	16	0.12%
55	*Rhus* sp.	15	0.11%
55	*Rhus pentheri*	14	0.11%
57	*Lannea discolor*	13	0.10%
57	*Schotia brachypetala*	13	0.10%
59	*Euphorbia* sp.	11	0.08%
59	*Pappea capensis*	11	0.08%
61	*Dombeya rotundifolia*	10	0.08%
61	*Ozoroa sphaerocarpa*	10	0.08%
63	*Cordia* sp.	9	0.07%
63	*Croton menyhartii*	9	0.07%
63	*Erythrina lysistemon*	9	0.07%
66	*Commiphora neglecta*	7	0.05%
67	*Gossypium herbacium*	6	0.05%
67	*Pavetta catophylla*	6	0.05%
69	*Acacia nilotica*	5	0.04%
69	*Spirostachys africana*	5	0.04%
69	*Ximenia caffra*	5	0.04%
72	*Pavetta* sp.	4	0.03%
73	*Rhus dentata*	3	0.02%

Rank	Species	Stems	%of all stems
73	*Rhus gueinzii*	3	0.02%
75	*Acacia karroo*	2	0.02%
75	*Combretum molle*	2	0.02%
75	*Euclea racemosa*	2	0.02%
75	*Ozoroa* sp.	2	0.02%
79	*Acacia* sp.	1	0.01%
79	*Bridelia cathartica*	1	0.01%
79	*Cassia senepetersiana*	1	0.01%
79	*Commiphora africana*	1	0.01%
79	*Maerua angolensis*	1	0.01%
79	*Nuxia oppositifolia*	1	0.01%
79	*Olea europaea*	1	0.01%
79	*Ozoroa paniculosa*	1	0.01%

APPENDIX 3. Size class distribution of each woody plant species included in the vegetation quadrats. Size classes are grouped by diameter (in cm).

Species	Total Stems	SIZE CLASS <2	2-5	5-'.	10-20	20-30	30-40	40-50	50+
Acacia exuvialis	495	51%	44%	5%	1%				
Acacia gerrardii	530	31%	16%	32%	19%	1%	0%		
Acacia karroo	2	100%							
Acacia nigrescens	414	62%	18%	12%	5%	1%	1%	0%	1%
Acacia nilotica	5	60%	40%						
Acacia sp.	1	100%							
Acacia tortilis	33	21%	42%	3%	18%	15%			
Albizia harveyi	390	58%	14%	18%	9%	0%			
Balanites maughamii	37	59%	24%	14%			3%		
Berchemia zeyheri	28	61%	39%						
Bolusanthus speciosus	73	21%	22%	38%	19%				
Bridelia catharlica	1		100%						
Canthium sp.	26	85%	15%						
Carissa edulis	37	89%	8%	3%					
Cassia senepetersiana	1	100%							
Cassine aethiopica	17	100%							
Cassine transvaalensis	114	82%	16%	2%					
Cissus cornifolia	299	92%	8%	0%					
Combretum apiculatum	625	42%	22%	27%	9%	1%			
Combretum collinum	595	31%	35%	23%	10%	1%	0%		

Species	Total Stems	SIZE CLASS <2	2-5	5-10	10-20	20-30	30-40	40-50	50+
Combretum hereroense	501	63%	12%	21%	4%	0%	0%		
Combretum imberbe	16		31%	56%	6%				6%
Combretum molle	2	50%	50%						
Combretum zeyheri	240	63%	19%	16%	3%				
Commiphora africana	1		100%						
Commiphora glandulosa	92	79%	17%	2%		1%			
Commiphora mollis	108	45%	21%	21%	11%	1%			
Commiphora neglecta	7	43%	29%	14%	14%				
Cordia monoica	81	40%	47%	14%					
Cordia sp.	9		78%		22%				
Croton menyhartii	9	89%	11%						
Dalbergia melanoxylon	762	56%	22%	17%	5%	0%			
Dichrostachys cinerea	379	39%	37%	22%	2%				
Diospyros mespiliformis	21	57%	19%	10%	10%			5%	
Dombeya rotundifolia	10	40%	50%		10%				
Ehretia amoena	539	94%	5%	1%					
Ehretia rigida	69	96%	3%	1%					
Erythrina lysistemon	9	100%							
Euclea divinorum	325	65%	25%	9%	2%				
Euclea natalensis	78	82%	14%	4%					
Euclea racemosa	2	100%							
Euphorbia sp.	11	100%							
Gardenia volkensii	47	72%	21%	6%					

Species	Total Stems	<2	2-5	5-10	10-20	20-30	30-40	40-50	50+
		SIZE CLASS							
Gossypium herbacium	6	100%							
Grewia bicolor	446	69%	28%	3%	0%				
Grewia flavescens	878	86%	12%	1%					
Grewia hexamita	174	61%	32%	6%	1%				
Grewia monticola	762	67%	29%	3%	0%				
Grewia villosa	141	99%	1%						
Hippocratea sp.	18	94%	6%						
Lannea discolor	13	46%		8%	38%	8%			
Lannea schweinfurthii	40	45%	8%	13%	18%	10%	3%	5%	
Lonchocarpus capassa	74	59%	19%	11%	7%	3%	1%		
Maerua angolensis	1	100%							
Maerua sp.	22	100%							
Manilkara mochisia	46	35%	50%	13%	2%				
Maytenus heterophylla	349	48%	40%	10%	2%				
Maytenus senegalensis	67	100%							
Mundulea sericea	114	6[illegible]%	34%	2%					
Nuxia oppositifolia	1	100%							
Olea europaea	1		100%						
Ormocarpum trichocarpum	586	55%	28%	16%	1%				
Ozoroa paniculosa	1	100%							
Ozoroa sp.	2	100%							
Ozoroa sphaerocarpa	10		100%						
Pappea capensis	11	100%							

Species	Total Stems	SIZE CLASS <2	2-5	5-10	10-20	20-30	30-40	40-50	50+
Pavetta catophylla	6	100%							
Pavetta sp.	4	75%	25%						
Peltophorum africanum	43	21%	23%	23%	28%	2%	2%		
Protasparagus sp.	38	100%							
Pterocarpus rotundifolius	576	45%	26%	22%	7%				
Rhus dentata	3	100%							
Rhus gueinzii	3		100%						
Rhus pentheri	14	36%	43%	14%	7%				
Rhus rehmanniana	27	37%	30%	22%	11%				
Rhus sp.	15	67%	33%						
Schotia brachypetala	13	77%	23%						
Sclerocarya birrea	34	41%		6%		6%	15%	24%	9%
Securinega virosa	387	80%	18%	1%					
Spirostachys africana	5	60%	20%	20%					
Strychnos madagascariensis	689	64%	28%	7%	0%				
Terminalia prunioides	21	86%	14%						
Terminalia sericea	169	46%	18%	20%	15%	1%			
UNKNOWN	86	57%	37%	6%					
Ximenia caffra	5	40%	20%	40%					
Ziziphus mucronata	110	41%	26%	31%	2%				

APPENDIX 4. Acceptance frequencies for each woody species at each study area and at all areas combined (pooled). SA = site-based acceptance frequency.

Species	POOLED Quadrats with sp.	POOLED Quadrats with new impact	POOLED SA	KAPAMA Quadrats with sp.	KAPAMA Quadrats with new impact	KAPAMA SA	THORNYBUSH Quadrats with sp.	THORNYBUSH Quadrats with new impact	THORNYBUSH SA	TSHUKUDU Quadrats with sp.	TSHUKUDU Quadrats with new impact	TSHUKUDU SA
Acacia exuvialis	67		0.00	8		0.00	43		0.00	18		0.00
Acacia gerrardii	104	37	0.36	45	18	0.40	55	19	0.35	4		0.00
Acacia karroo	1		0.00	1		0.00			N/A			N/A
Acacia nigrescens	88	9	0.10	30	3	0.10	36	1	0.03	22	5	0.23
Acacia nilotica	4		0.00	2		0.00	1		0.00	1		0.00
Acacia sp.	1		0.00	[illegible]		0.00			N/A			N/A
Acacia tortilis	11		0.00			N/A			N/A	11		0.00
Albizia harveyii	75	20	0.27	42	16	0.38	30	4	0.13	3		0.00
Balanites maughamii	8		0.00	8		0.00			N/A			N/A
Berchemia zeyheri	14		0.00	8		0.00	6		0.00			N/A
Bolusanthus speciosus	18	1	0.06	2	1	0.50	16		0.00			N/A
Bridelia cathartica	1		0.00	1		0.00			N/A			N/A
Canthium sp.	5		0.00	2		0.00	3		0.00			N/A
Carissa edulis	5		0.00	3		0.00	2		0.00			N/A
Cassia senepetersiana	1		0.00	1		0.00			N/A			N/A
Cassine aethiopica	3		0.00	2		0.00	1		0.00			N/A
Cassine transvaalensis	20		0.00	9		0.00	11		0.00			N/A
Cissus cornifolia	39	1	0.03	23	1	0.04	5		0.00	11		0.00
Combretum apiculatum	87	4	0.05	39	3	0.08	34		0.00	14	1	0.07

Species	POOLED			KAPAMA			THORNYBUSH			TSHUKUDU		
	Quadrats with sp.	Quadrats with new impact	SA	Quadrats with sp.	Quadrats with new impact	SA	Quadrats with sp.	Quadrats with new impact	SA	Quadrats with sp.	Quadrats with new impact	SA
Combretum collinum	56	27	0.48	47	23	0.49	8	4	0.50	1		0.00
Combretum hereroense	72	3	0.04	28	2	0.07	43	1	0.02	1		0.00
Combretum imberbe	5	1	0.20	2		0.00	2		0.00	1	1	1.00
Combretum molle	2		0.00	1		0.00	1		0.00			N/A
Combretum zeyheri	19	2	0.11	17	2	0.12	2		0.00			N/A
Commiphora africana	1		0.00	1		0.00			N/A			N/A
Commiphora glandulosa	16	2	0.13	9	1	0.11	3		0.00	4	1	0.25
Commiphora mollis	38	5	0.13	27	5	0.19	6		0.00	5		0.00
Commiphora neglecta	6		0.00	2		0.00	4		0.00			N/A
Cordia monoica	10	1	0.10	7	1	0.14	2		0.00	1		0.00
Cordia sp.	1		0.00			N/A			N/A	1		0.00
Croton menyhartii	1		0.00	1		0.00			N/A			N/A
Dalbergia melanoxylon	92	21	0.23	51	15	0.29	40	6	0.15	1		0.00
Dichrostachys cinerea	84	8	0.10	31	3	0.10	36	3	0.08	17	2	0.12
Diospyros mespiliformis	11	1	0.09	6	1	0.17	5		0.00			N/A
Dombeya rotundifolia	7		0.00	1		0.00	6		0.00			N/A
Ehretia amoena	45		0.00	17		0.00	27		0.00	1		0.00
Ehretia rigida	7		0.00	1		0.00	6		0.00			N/A
Erythrina lysistemon	1		0.00	1		0.00			N/A			N/A
Euclea divinorum	61	2	0.03	25		0.00	36	2	0.06			N/A
Euclea natalensis	20		0.00	9		0.00	11		0.00			N/A
Euclea racemosa	2		0.00	2		0.00			N/A			N/A

Species	POOLED Quadrats with sp.	POOLED Quadrats with new impact	POOLED SA	KAPAMA Quadrats with sp.	KAPAMA Quadrats with new impact	KAPAMA SA	THORNYBUSH Quadrats with sp.	THORNYBUSH Quadrats with new impact	THORNYBUSH SA	TSHUKUDU Quadrats with sp.	TSHUKUDU Quadrats with new impact	TSHUKUDU SA
Euphorbia sp.	1		0.00			N/A			N/A	1		0.00
Gardenia volkensii	13		0.00	4		0.00	9		0.00			N/A
Gossypium herbacium	1		0.00			N/A			N/A	1		0.00
Grewia bicolor	53	2	0.04	29		0.00	15	1	0.07	9	1	0.11
Grewia flavescens	66	1	0.02	24	1	0.04	31		0.00	11		0.00
Grewia hexamita	21	4	0.19	16	4	0.25	4		0.00	1		0.00
Grewia monticola	96	10	0.10	29	2	0.07	44	4	0.09	23	4	0.17
Grewia villosa	8		0.00			N/A			N/A	8		0.00
Hippocratea sp.	3		0.00	3		0.00			N/A			N/A
Lannea discolor	7	2	0.29	5	2	0.40	2		0.00			N/A
Lannea schweinfurthii	20	2	0.10	5		0.00	9	1	0.11	6	1	0.17
Lonchocarpus capassa	16	1	0.06	13	1	0.08	2		0.00	1		0.00
Maerua angolensis	1		0.00			N/A	1		0.00			N/A
Maerua sp.	1		0.00			N/A			N/A	1		0.00
Manilkara mochisia	5		0.00	2		0.00	2		0.00	1		0.00
Maytenus heterophylla	53	6	0.11	23	2	0.09	29	3	0.10	1	1	1.00
Maytenus senegalensis	4		0.00	2		0.00	2		0.00			N/A
Mundulea sericea	28	1	0.04	16	1	0.06	12		0.00			N/A
Nuxia oppositifolia	1		0.00			N/A	1		0.00			N/A
Olea europaea	1		0.00			N/A	1		0.00			N/A
Ormocarpum trichocarpum	80	9	0.11	40	7	0.18	37	2	0.05	3		0.00
Ozoroa paniculosa	1		0.00	1		0.00			N/A			N/A

Species	POOLED			KAPAMA			THORNYBUSH			TSHUKUDU		
	Quadrats with sp.	Quadrats with new impact	SA	Quadrats with sp.	Quadrats with new impact	SA	Quadrats with sp.	Quadrats with new impact	SA	Quadrats with sp.	Quadrats with new impact	SA
Ozoroa sp.	1		0.00	1		0.00			N/A			N/A
Ozoroa sphaerocarpa	1		0.00	1		0.00			N/A			N/A
Pappea capensis	4		0.00			N/A	4		0.00			N/A
Pavetta catophylla	1		0.00	1		0.00			N/A			N/A
Pavetta sp.	2		0.00	2		0.00			N/A			N/A
Peltophorum africanum	14	1	0.07	8		0.00	5	1	0.20	1		0.00
Protasparagus sp.	15		0.00	9		0.00	5		0.00	1		0.00
Pterocarpus rotundifolius	48	10	0.21	32	7	0.22	16	3	0.19			N/A
Rhus dentata	1		0.00			N/A	1		0.00			N/A
Rhus gueinzii	2	1	0.50			N/A	2	1	0.50			N/A
Rhus pentheri	3	1	0.33	1		0.00	2	1	0.50			N/A
Rhus rehmanniana	6		0.00	3		0.00	3		0.00			N/A
Rhus sp.	5		0.00	2		0.00	3		0.00			N/A
Schotia brachypetala	5	1	0.20			N/A	5	1	0.20			N/A
Sclerocarya birrea	24	6	0.25	4		0.00	8	3	0.38	12	3	0.25
Securinega virosa	51		0.00	30		0.00	19		0.00	2		0.00
Spirostachys africana	3		0.00	1		0.00	2		0.00			N/A
Strychnos madagascariensis	22	3	0.14	22	3	0.14			N/A			N/A
Terminalia prunioides	3		0.00	1		0.00			N/A	2		0.00
Terminalia sericea	27	2	0.07	18	2	0.11	9		0.00			N/A
UNKNOWN	33	1	0.03	23	1	0.04	4		0.00	6		0.00
Ximenia caffra	2	1	0.50			N/A	1	1	1.00	1		0.00
Ziziphus mucronata	51	3	0.06	9	1	0.11	38	2	0.05	4		0.00