THE EFFECT OF ELEPHANT UTILISATION ON THE *STERCULIA ROGERSII* AND *ADANSONIA DIGITATA* POPULATIONS OF THE KRUGER NATIONAL PARK

by

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ABSTRACT

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This study asseses elephant induced damage and mortality of baobab and common star-chestnut trees in the northern Kruger National Park. Comparisons are made between the populations north and south of the Luvuvhu River. The density, population size and age structure are estimated.

The population structure of neither species has been shaped by elephant utilisation. While the baobab population has a healthy age distribution, that of the star-chestnut population shows that recruitment has declined in recent decades.

Utilisation has been found to be higher in the south as a result of higher elephant densities, although recently damage has been greater in the north. Damage increases with tree size. The mortality of baobabs is lower than in other areas where elephants and baobabs co-exist. Elephants are not playing a significant role in mortality of either tree species and management of factors other than elephant is required to improve regeneration rates of these species.

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CHAPTER 1

INTRODUCTION

GENERAL

Elephant populations are major agents of habitat change and are second only to man in their capacity for altering their environment (Ben-Shahar 1993; Smithers 1983). This can be attributed to the pushing over and uprooting of trees by elephants for social display, as well as to increase the availability of browse and fruits, especially during the dry season, (Jachmann & Bell 1985). Elephants are thus able to alter the composition and structure of the natural vegetation, by means of their foraging activities.

The habitat changes wrought by elephants in eastern, central and southern Africa has attracted much attention over the last few decades. In some areas, regeneration has been suppressed and mature trees ringbarked or felled. This trend of converting forest to woodland or open savannah has been termed "the elephant problem" (Caughley 1976).

The influence elephants can have on the habitat has become one of the most hotly debated topics in African conservation (Hall-Martin 1986). In areas where elephant movements are restricted or where they exceed their food supply, elephant induced damage to habitats increases and they can cause retrogression of the habitat towards complete devastation (Ben-Shahar 1993; Smithers 1983). Although the destruction of trees by these animals is a natural phenomenon, elephants today occur almost exclusively in small, isolated parks and they are therefore able to sway the system to a point which may be undesirable as it affects the ability of the park to reach its management objectives.

Despite intensive utilisation, the affected plant species may survive, and hence not be lost to the ecosystem, but if their density and numbers are affected, the habitat may be altered sufficiently to make it unsuitable for other faunal and floral species. Where elephants convert woodland into grassland, these effects are most pronounced. The species richness of woodland ants and birds has been found to be significantly lower in areas where elephants had removed the tree canopy (Cumming *et al.* 1997; Herremans 1995). This situation may however benefit other species which are better adapted to grassland living, and trees which have been pushed over provide a microhabitat suitable for the establishment of seedlings and grass and provide refuge for small mammals, reptiles and numerous invertebrates.

Elephants are therefore, essential agents of disturbance in many ecosystems but can result in the loss or gain of species (Moolman & Cowling 1994; Smithers 1983). In some conservation areas where elephant numbers increase locally, woody vegetation declines, and the control of elephant numbers is necessary (Ben-Shahar 1993).

Studies have shown that elephants have had damaging effects on baobabs (*Adansonia digitata*) in numerous African reserves, including Mana Pools, Zimbabwe (Swanepoel 1993; Swanepoel & Swanepoel 1986), Ruaha National Park, Tanzania (Barnes 1980; Barnes *et al.* 1994) and Lake Manyara National Park, Tanzania (Weyerhaeuser 1985). Elephants eat the bark and wood of these trees and, by gouging out the wood with their tusks, can excavate large cavities in the trunk. If large enough, these cavities can result in the collapse and death of the trees (Weyerhauser 1985).

Since 1967, an average of seven percent of the elephant population of the Kruger National Park (Kruger National Park) has been removed annually by culling (Joubert 1986; Whyte *et al.* 1998). The impact these animals were able to have on the habitat has therefore been limited. During 1995 and 1996, the National Parks Board, however, reviewed the Kruger National Parks' elephant management policy and decided that controlled fluctuations of elephant numbers were acceptable. The culling programme was therefore, suspended until a revised management plan for the reserve could be approved. This plan was finally accepted in 1999. In this plan, elephant management is based on six zones of elephant density. Two of these zones are botanical reserves, two are high-impact elephant zones in which elephant numbers will be allowed to increase indefinately, and two are low impact zones where elephant numbers will be reduced to allow recovery of vegetation.

Although their numbers have been tightly controlled, it has been suggested that even at these relatively low densities, the Kruger National Park elephant population may be responsible for a decline in the baobab (*Adansonia digitata*) population. Concern has also been voiced that elephant utilisation may have been impacting negatively on other plant species. One of these species is the common star-chestnut (*Sterculia rogersii*), a plant which is very rare in the Kruger National Park (Van Wyk 1984).

The mission of the Kruger National Park is to maintain biodiversity in all its natural facets and fluxes. Therefore any elephant induced habitat degradation is unacceptable as this would be followed by a decline in species richness and hence biodiversity. Baobabs are especially important for species richness due to the large number of faunal species associated with them. Both Mottled Spinetail (*Telecanthura ussheri*) and Bohm's Spinetail (*Neafrapus boehmii*) use baobabs almost exclusively for breeding in the park, and the loss of these bird species would almost certainly follow the loss of baobabs. Numerous other birds also utilise baobabs for breeding. These include Cape Parrots (*Poicephalus robustus*), Barn Owls (*Tyto alba*), Whiteheaded Vultures (*Trigonoceps occipitalis*), Redheaded Weavers (*Anaplectes rubriceps*), Dickinson's Kestrels (*Falco dickinsoni*) and Redbilled Buffalo Weavers (*Bubalornis niger*). Due to the limited potential for recolonisation of the Kruger National Park by extirpated species, every effort needs to be made to avert any threat to the species richness of the area.

The attempts by many African reserves to conserve biodiversity has in a number of cases been affected by international public pressures against reducing elephant densities in game reserves (Cumming *et al*. 1997). A need therefore, existed to determine whether the populations of *Adansonia digitata* and *Sterculia rogersii* in the Kruger National Park were being negatively affected, and if so, whether these effects would affect the long term survival of the species. If the populations were diminishing, it was necessary to establish if this could be attributed to an overabundance of elephants. If elephant management is required in the Kruger National Park, documented evidence is needed to justify this.

This project was therefore implemented to assess the current status of the *Sterculia rogersii* and *Adansonia digitata* populations of the Kruger National Park and to obtain baseline data which can be used to monitor elephant impact on these species. A proper management policy regarding elephants requires information on the trends of the elephant populations and, especially, their patterns of resource utilisation (Ben-Shahar 1993). Monitoring of the utilisation of rare species such as *Adansonia digitata* and *Sterculia rogersii*, can provide an indication of when elephant numbers have exceeded the threshold of the area and therefore, when management intervention is warranted.

Until recently, the density of elephants on either side of the Luvuvhu River has differed due to different land use and management of these two areas. The area of the Kruger National Park, north of the Luvuvhu River, was only incorporated into the reserve in 1969. Due to the perceived ecological sensitivity and botanical importance of the area, because of the relative abundance of trees such as the baobab (*Adansonia digitata*) and common star-chestnut (*Sterculia rogersii*), elephant numbers were kept at a relatively low density through culling. By comparing the populations of tree species in the two areas, an indication of the long term effects of differing elephant densities can be gained.

RATIONALE AND OBJECTIVES OF THE STUDY

Many factors contribute in a complex manner to determine elephant impact on a plant species or community and the management of elephant numbers (Coetzee *et al.* 1979). Studies of isolated aspects are necessary from time to time (Coetzee *et al.* 1979) as they can contribute to an understanding of these interrelated factors. Recent criticism of the Kruger National Park elephant management policy and its resultant suspension heightened concerns that the elephant population, if left unchecked, could drive certain plant species to extinction and thus affect the biodiversity of the region. These concerns warranted investigation.

For these reasons, this study was implemented to establish and document the current status of, and elephant impact on the *Adansonia digitata* and *Sterculia rogersii* populations of the Kruger National Park, to establish whether the populations are in decline and if so to determine the magnitude of the decline.

The objectives could be achieved by fulfilling the following:

(i) Estimate the density of *Sterculia rogersii* and *Adansonia digitata* in the Kruger National Park north and south of the Luvuvhu River.

(ii) Determine and compare the structure of the *Sterculia rogersii* and *Adansonia digitata* populations in the Kruger National Park north and south of the Luvuvhu River and ascertain if the utilisation of these species by elephant has affected the structure of the populations.

(iii) Determine the extent of elephant damage north and south of the Luvuvhu River for each of the two species and determine if any correlation between damage and elephant density exists as well as determine which size class of tree is most affected.

(iv) Ascertain whether elephant damage causes death of *Sterculia rogersii* trees.

(v) Determine if any correlation exists between damage to *Sterculia rogersii* and to *Adansonia digitata*; the population structure of these two species.

Although this study only deals with a small aspect of elephant management, utilisation of these two tree species has been causing concern. It is hoped that the information will be of value in making decisions concerning the management of the Kruger National Park's elephant population.

THE BAOBAB (*Adansonia digitata* Linnaeus)

The first recognisable reference to a baobab tree in the literature is by the Arab traveller, Ibn Batuta, who in 1352, wrote of a weaver in Mali taking shelter in a hollow trunk while working (Wickens 1982). Since then, the baobab has probably been described more often than any other African tree. The baobab belongs to the family Bombacaceae which contains around 21 genera (Palmer 1977). In 1941, the baobab was brought under the protection of the forestry act, and was the first tree in South Africa to be given universal state protection (Palmer & Pitman 1961).

The name *Adansonia* is derived from the surname of the eighteenth century French botanist Michel Adanson and was coined in his honour by Linnaeus after publication of the results of his exploration of Senegal in 1757 (Wickens 1982). The species name (*digitata*) refers to the shape of the leaf, which resembles a hand (Venter & Venter 1996) and is derived from the Latin word for finger, *digitus* (Van Wyk 1974).

The baobab is a massive tree, which can grow to a height of over 20 m in this region. The bole is extremely thick and in large specimens, can gain a circumference exceeding 20 m. The flowers which occur from October to December are large and white. The fruit too is large, with a hard outer shell covered in fine hairs. The leaves of seedlings are simple, but later become palmately compound, usually with five leaflets (Van Wyk 1984). Saplings often retain their simple seedling leaf form for many years, but observations have shown that the variation in leaf shape can occur from a very early age (Wickens 1982). Baobabs grow best in areas of dry woodland where the soil is well drained (Venter & Venter 1996; Wilson 1988).

Although the baobab tree is not indigenous to Egypt, the fruits of this tree were known to the ancient Egyptians and were sold in the markets of Cairo, probably for use as a febrifuge (Wickens 1982). It was from these merchants that the tree's common name was derived, as they referred to it as *bu hobab* (Wickens 1982).

The wood of baobab trees is very soft and light and can be used only for paper production (Van Wyk 1984). As a fodder plant, the baobab is of value to a number of herbivores. Elephant, kudu (*Tragelaphus strepsiceros*), nyala (*Tragelaphus angasii*) and impala (*Aepyceros melampus*) eat the leaves of the tree, while the fallen flowers are also relished by various species (Venter & Venter 1996). As already mentioned, elephant also make use of the trunks of baobabs, sometimes causing large-scale damage to the trees. The fruit is eaten by primates (Van Wyk 1984).

These trees are also utilised by man in a number of ways. The roots can be used as a source of water, while young roots and leaves can be cooked and eaten. The pith of the fruit can be used to make a refreshing drink, while seeds can be roasted to produce a coffee substitute. Seeds can also be eaten fresh or dry. The most useful part of the tree , is the bark, which when stripped from the tree, pounded and soaked in water can be used to produce an excellent fibre (Palmer & Pitman 1961). Rope, mats, sacks, clothing, baskets, nets and fishing lines are made from the inner bark (Palmer & Pitman 1961; Venter & Venter 1996). The bark has even been used by Europeans to treat fevers.

Another interesting feature of these trees is the high proportion of water contained in the wood. A tree with a volume of 200 m^3 contains an estimated 136 kl of water (Palmer & Pitman 1961). Due to the fact that baobabs are able to survive even when the trunks are hollow, they have served as houses, prisons, storage barns and places of refuge from wild animals (Coates Palgrave 1984). In Sudan, baobabs are often hollowed out and used as water tanks which are filled during the rainy season, enabling people to survive in the countries' extremely dry climate. Rain water also accumulates naturally in hollow trunks, and people travelling through baobab areas, such as the bushmen, regularly used this source of water (Palmer & Pitman 1961).

Numerous myths and superstitions have evolved surrounding the baobab tree. This is probably due to the size attained by some trees as well as their unusual appearance. Among these is a belief by some Africans that young baobabs no longer exist (Coates Palgrave 1984). Other beliefs are that God planted these trees upside down and that spirits inhabit the flowers and a lion will therefore devour anyone who plucks one from a tree. It is also believed that protection from an attack by a crocodile can be derived from drinking a draught of water in which the seeds of a baobab have been soaked and stirred. Another belief is that a man who drinks an infusion of the bark will become mighty and strong (Coates Palgrave 1984).

Baobab trees occur in most sub-Saharan African countries although it has been introduced into some countries in which it occurs (Wilson 1988). Specimens can also be found on the Cape Verde Islands, and on the islands of the Gulf of Guinea (Wilson 1988). There are a total of nine *Adansonia* (baobab) species, seven of which occur on Madagascar (Wilson 1988) and one each in Australia and Africa. The baobabs present in India were probably introduced by man early in the thirteenth century at the start of the African slave trade (Wickens 1982). There is much uncertainty over the origins of trees growing on the Arabian peninsula as these specimens may occur there naturally or may have been introduced by Arab traders (Wickens 1982; Wilson 1988). The most suitable habitat for these trees consists of deep well-drained soils at altitudes between 450 m and 600 m above sea level and an annual rainfall of between 300 mm and 500 mm (Wickens 1982).

In South Africa, the natural distribution of baobabs is limited to the Northern Province and Mpumalanga as the trees are susceptible to frost. Baobabs are conspicuous in the Limpopo basin, especially in the dry, frost-free country north of the Soutpansberg mountains and the Olifants River in the east. A few stragglers occur to the south of this, with a number of trees growing in the Waterberg region and one near Rustenburg (Wickens 1982). The popularity of the baobab as an ornamental tree has resulted in its introduction into numerous parts of the world, including Cairo, Mauritius, Malaysia, Java, New Caledonia, Hawaii, the Philippines, the West Indies, the Antilles, Guyana, Cuba and Florida (Wickens 1982). South Africans have also cultivated these trees, with specimens occurring as far afield as Durban and Cape Town.

AGEING OF BAOBABS

The massive size which mature baobab trees can attain has often been thought to be associated with great age, but this is a debatable point (Coates Palgrave 1956). Due to the interest and uncertainty surrounding the age of these trees, and the relevance of baobab age to this study, some of the ageing techniques and results of attempts at ageing these trees have been reviewed here. The ageing of baobabs is especially pertinent to discussion in later chapters.

Some Africans believe that young baobabs no longer exist (Coates Palgrave 1984). Although this is known to be untrue, the speculation which has always surrounded the age of baobab trees, has resulted in ageing of baobabs having a long and colourful history which began during the eighteenth century. The Frenchman after whom the tree was named, Michel Adanson was the first to attempt estimates of baobab age. He believed some specimens to be over 5000 years old (Swart 1963) and placed the age of one at 5500 years (Palmer & Pitman 1961). The trees he aged in 1749 were situated on the Magdalene Islands west of Cape Verde and had been inscribed with the names of European sailors who had landed there between 1400 and 1600 AD (Wickens 1982). David Livingstone however did not believe that trees older than the great biblical flood could exist, and according to calculations made by Bishops Usher and Lightfoot that the earth's creation took place in 4004 BC, the trees which Adanson had aged were alive before the flood. This implied that the flood could not have taken place and angered Livingstone who used growth rings to assess the age of a number of trees, the largest of which he believed was over 4000 years old (Wickens 1982).

Although baobabs do show well-defined growth rings, the extraction of cores is time consuming and due to the size of the trees, the labour involved in obtaining a complete section with a smooth surface is enormous (Swart 1963). The centre of the trunks are also porous, many of the trees being entirely hollow, making ring counting impossible (Swart 1963). There has also been speculation that these rings are not annual (Coates Palgrave 1956; Palmer & Pitman 1961), but are formed irregularly, after a rainy season, or even a storm or for other reasons (Palmer & Pitman 1961).

Swart (1963) reported on a baobab tree which was felled in the Zambezi valley during bush clearing operations in the Lake Kariba area in 1960. This tree had a girth of over 14 m and samples were obtained from various parts of it for use in carbon dating. The heartwood was 1010 ± 100 years old, while the sample midway between the centre and outside of the tree gave an age of 740 ± 100 years. Indications were that the tree increased in radius more slowly over the latter half of its life, with an annual average increment in radius of 0.0015 m over the last 1.14 m of the total radius (Swart 1963).

According to Palmer and Pitman (1961), it is fairly well established that young trees put on about one foot (0.305 m) in diameter in 10 years, but that older trees grow more slowly.

These authors quote records of the growth rates of individual trees from scattered localities. One baobab, planted in Dongola, grew to 7.6 m in 15 years, one in the Transkei reached a height of 6.1 m in 20 years, while one tree in Messina took only two years to reach a height of 3 m. In this same garden in Messina, most trees grew to five or 6 m in 17 years after receiving water and manure only in the nursery stages.

According to Venter and Venter (1996), the growth rate of cultivated trees is moderate to fast in the first 5 years, during which time they grow at a rate of 0.5 to 0.8 metres per year. Similarly, Coates Palgrave (1984) states that baobab plants which receive good treatment reach 7 m in 20 years and also that trees with a girth of 25 m have been estimated to be over 3000 years old.

Tree features which have been correlated with age include radial width and transverse area of sapwood, diameter and basal area (Sellin 1994; Sellin 1996; Stephenson & Demetry 1995; Tyrrel & Crow 1994; Yang & Murchison 1993). Numerous attempts have been made to correlate the girth of baobab trees with their age (Caughley 1976; Swanepoel 1993; Weyerhauser 1985; Wilson 1988). These attempts have met with varying degrees of success and have in some instances, even come in for criticism (Guy 1982).

Caughley (1976) worked in Zambia's Luangwa valley, and aged baobabs by measuring girth and converting this to age using the equation:

$$\text{Age (years)} = 0.213 \times \text{girth (cm)}.$$

This equation was calculated by using growth rings and determining the increase in radius for each ring laid down. It was found that growth was faster for the first 30 years but slowed as the tree aged.

Barnes (1980) studied Baobabs in Ruaha National Park, Tanzania. He used core samples obtained from trees and used the ring width of the core samples to determine the annual increment in radius. No difference in growth rate of the different size classes was obtained and there was no difference in growth rate of trees growing in three different soil and vegetation types. The radius of the 71 trees assessed, increased by a mean of 0.43 cm annually.

Weyerhauser (1985), worked in Lake Manyara National Park in Tanzania, and used the growth rate figure calculated by Barnes (1980) in which a linear relationship between girth and age exists. Using this method, each metre of the girth at breast height (GBH) represents 40 years of growth. Barnes' calculations were made in Ruaha National Park, Tanzania where the climate is similar to that at Lake Manyara.

Guy (1982) cautions against the use of girth as a method for calculating age, and states that growth rates of baobabs vary through the life of the plant and in general decrease with age.

Wilson (1988) assessed five baobab populations in Zambia, Sudan, Mali, Kenya and Tanzania and used either growth rings or empirical observations to determine growth rates and convert size to age classes. It was determined that very few trees live to an age in excess of 400 years. The multiplication factors for converting girth (cm) to age in the various populations were 0.370 for Tanzania, 0.213 for Zambia, 0.91 for Sudan, 0.164 for Mali, and 0.114 for Kenya. The data used for calculating the Tanzania and Zambia growth rates were from the trees studied by Barnes (1980) and Caughley (1976) respectively.

In Mali, baobabs are cultivated as an agricultural crop and the ages of these trees are therefore known. Wilson (1988) derived the equation ($y = 3.25 + 0.081\,x$) to calculate the age of these trees where x is the girth at breast height (cm). According to this equation, a tree with a GBH of 25 m is only 206 years old. Trees of known age in central-southern Africa gave girth conversion factors of 0.174 (mean of three trees), 0.191 (three other trees close together in the same garden), while one tree at Bagomoyo in Tanzania had a factor of 0.116 (Wilson 1988).

Baobabs in Mana Pools National Park, Zimbabwe, grew slowly initially, increasing in girth at a rate of 0.2 m annually (Swanepoel 1993). This was the rate of growth until the tree had a girth of 2.5 m, whereafter the rate increased to 0.78 m per year until the trees had attained a girth of 6.0 m. Thereafter growth was extremely slow, with the girth of trees only increasing by 0.10 m each year (Swanepoel 1993).

Von Breitenbach (1985) used a different approach to the ageing of baobabs. Instead of ageing the trees based purely on the size of the stem, he combined measurements of stem diameter, tree height and crown width with the shape and growth form of the tree to obtain rough estimates of the tree age.

From the above discussion, it is obvious that a number of opinions exist as to the growth rates of baobab trees. Although many of these studies were conducted in areas with vastly different climates, and therefore different growth rate figures were obtained, the one common aspect appears to be that baobabs grow quickly during the early part of their lives, with the rate of growth slowing later.

THE COMMON STAR-CHESTNUT (*Sterculia rogersii* N.E. Brown)

Sterculia rogersii forms part of the Sterculiaceae or cacao family. The family is distributed throughout the world in tropical and subtropical regions and is famous as the source of chocolate and cocoa. This is produced from the fermented seeds of the tropical American tree, *Theobroma cacao* (Pooley 1993). The African members of the family are of negligible economic value. They are used to a certain extent as sources of medicine, fibre, firewood, timber and as decorative plants (Van Wyk 1974). The family has 60 genera with well known South African trees belonging to the *Dombeya* and *Sterculia* genera (Germishuizen 1997; Palmer & Pitman 1961). There are about 700 Sterculiaceae species, of which about 230, from six genera occur in southern Africa (Germishuizen 1997). In the Kruger National Park, this family is represented by 21 species, from six genera, including one exotic genus. Five of these species are trees (Van Wyk 1974). Trees of the Sterculiaceae family are used by skipper butterflies (Hesperiidae) for breeding (Pooley 1993). The *Sterculia* genus consists of about 300 species of deciduous and evergreen trees, three of which occur in South Africa (Kruger 1973; Palmer 1977).

The name, *Sterculia* is derived from the Latin Sterculius. This was the name of the Roman god whose responsibility it was to fertilise the lands. His name was in turn derived from the word 'stercus', which means manure. This name was coined as a reference to the foul-smelling flowers of certain members of the genus (Van Wyk 1974). The species, *rogersii*, was named after Archdeacon F.A. Rogers, an amateur botanical collector, who collected extensively in southern Africa during the early 1900s (Germishuizen 1997). This species is now known as the common star-chestnut, but has in the past also been known as the succulent chestnut, ulumbu tree and squat sterculia.

The common star-chestnut is a small, deciduous tree, which resembles a *Commiphora*, or small baobab (Pooley 1993; Van Wyk 1974). Specimens have a thick stem which usually branches from near the ground into a number of thinner stems. The flowers are small, red and green, the fruits are slightly larger and consist of a number of lobes. The flowers usually appear during July, while the fruit is present on the tree from September to March. The common star-chestnut is a slow growing tree (Van Wyk 1984).

Sterculia rogersii trees occur at low altitudes in Mozambique, Botswana, Zimbabwe, Swaziland and South Africa (Coates Palgrave 1984). It is a species which is confined to southern Africa (Van Wyk 1974). The common star-chestnut occurs throughout the Kruger National Park, but are very rare in all areas except for the Pafuri region where the species is fairly common (Van Wyk 1984). Many specimens are present on the Pafuri ridges and in the area between the Limpopo and Luvuvhu Rivers. A few plants occur in rocky places in other locations, some close to Malelane and some in the Punda Maria and Olifants rest camps (Van Wyk 1974). The preferred habitat of these trees is in dry areas, and it grows almost exclusively in stony environments (Coates Palgrave 1984; Van Wyk 1974). Although dense stands of this species do not occur, it is sometimes associated with dense plant communities, of which *Colophospermum mopane* is the most important component (Van Wyk 1974).

The wood of *Sterculia rogersii* trees is very soft, light, fibrous and coarse in texture. It's air-dry mass is only 540 kg/m^3 (Van Wyk 1984). As a result of these poor qualities, the timber is worthless and not put to any known use (Van Wyk 1974). Fibre made from the bark is used by Africans to weave fishing nets and to sew sleeping mats (Coates Palgrave 1984) as well as in the construction of huts (Pooley 1993). The seeds are eaten by people, birds and game, while the leaves and young stems are browsed (Pooley 1993). The tree is also used in decorative gardens in frost free areas (Pooley 1993; Van Wyk 1984).

AGEING OF THE COMMON STAR-CHESTNUT

Ageing of *Sterculia rogersii* trees is of relevance in later chapters and is therefore discussed here. The common star-chestnut, resembles the baobab in a number of ways, and can even be confused with a young baobab (Pooley 1993; Van Wyk 1974). One reason for these similarities is that both these trees have very soft, fibrous wood. The wood of *Sterculia rogersii* does exhibit growth rings. The rings are very thin, finely sinuous, darker than the rest of the wood and extremely close together. As with the baobab, there is doubt as to whether these rings each represent a full years growth. (Van Wyk 1974). This makes it exceedingly difficult to estimate the age of *Sterculia rogersii* trees.

If each ring does represent a years growth, then a branch with a 0.10 m diameter is 170 years old (Van Wyk 1974). This is an extremely slow growth rate and indicates an increase in girth of only 0.0018 m per year. This implies that some star-chestnut trees in the Kruger National Park are more than 2500 years old. If *Sterculia rogersii* trees do live to this age, then some specimens are among the oldest trees in the world, and have attained an age usually associated with extremely long-lived plants such as *Welwitshia mirabilis*. Although common star-chestnuts are slow growing trees (Van Wyk 1984), it is unlikely that they live to such an age, and these growth rings are probably not annual.

It is more likely that these growth rings are formed more often, their formation possibly linked to rainfall. If each growth ring is laid down after rainfall, there could be up to 38 rings laid down per year as there are, on average, 38 days in the year on which rain falls in Pafuri. However, some of these rainfall events take place over more than one day and there are therefore probably fewer rings than this laid down annually. The actual number probably lies somewhere between one and 38.

If a rainfall event is considered to be the period from when the rain falls until there is no longer water available for the plant in the ground, then there will be fewer rainfall events than days of rain in a year. Such a rainfall event and a rain day are most probably not distinguishable by the plant. At the height of the wet season (November to March), there will be water available to the plant between different rains and more than one day of rain would therefore, become one rainfall event. Rain which falls in the form of showers often continues for a number of days and in such cases more than one rain day will only be one rainfall event. As there are probably around ten rainfall events per year, approximately ten growth rings are produced by these trees annually. The larger *Sterculia rogersii* plants in the Kruger National Park are thus estimated to be around 300 years old. Little is known of the lifespan of indigenous tree species, but some trees used for timber have known lifespans of 400 years (Hemlock) and 450 years (Douglas Fir) (Tyrrell & Crow 1994).

RECENT HISTORY OF THE KRUGER NATIONAL PARK ELEPHANT POPULATION

During the early part of the twentieth century, hunters eliminated elephants from most of the area now occupied by the Kruger National Park. Elephants were still present in the Portuguese territory east of the Lebombo Mountains and occasionally did wander across (Stevenson-Hamilton 1937), but a small nucleus is believed to have survived in the remote and secluded forested area near the Olifants Gorge (Pienaar 1963). No information on elephant numbers is available prior to their discovery in 1905. Since this time, regular estimates on the number of the population have been recorded. The first such report was by the parks first warden, Colonel James Stevenson-Hamilton who mentioned the existence of 10 elephant in the area between the Olifants and Letaba Rivers in 1905 (Van Wyk & Fairall 1969). In 1912, the population was estimated at 25, and grew steadily, due to the absolute protection afforded it, and also augmented by the immigration of elephant from the then Portuguese territory in the east (Pienaar 1963). Regular estimates of the population were made (1926: 100; 1931: 131; 1936: 250; 1946: 480; 1947: 560; 1954: 740; 1958: 995) until 1960 when the first aerial census was undertaken and 1186 elephant were present (Pienaar

1963; Whyte *et al.* 1998). In 1964 a complete census by helicopter was undertaken. There were 2474 elephants in the Kruger National Park at this time (Van Wyk & Fairall 1969).

Undoubtedly, the replacement of ground counts with aerial ones resulted in greater accuracy and hence, the apparent growth spurt of the elephant population. The population was, however, increasing during this time due to immigration of large numbers of elephants into the Kruger National Park from the neighbouring countries of Portuguese East Africa (Mozambique) and Rhodesia (Zimbabwe). These animals moved into the reserve where they received protection from the hunting activities in the adjacent regions (Van Wyk & Fairall 1969).

The elephant recolonisation of the Kruger National Park, was initially centred in the area around the Letaba River, and this was where the population initially increased and from where it dispersed. This dispersal was led by the scouting patrols of solitary bulls, followed by small groups who slowly began infiltrating the entire reserve (Van Wyk & Fairall 1969). The process was extremely slow, but in 1931, elephants began recolonising the northern mopani-veld, and then moved in a southerly direction during 1939 - 1941 (Pienaar 1963). During 1941, they were seen in the area south of the Sabie River for the first time in almost 100 years. During the summer of 1952, the Pretoriuskop area was first re-entered by two bulls, completing the recolonisation process (Pienaar 1963; Van Wyk & Fairall 1969).

The growth of the elephant population continued and inclined steeply during the 1960's (Joubert 1986), until 1967, when the first culling campaigns were initiated to maintain the population at around 7000 animals (Whyte *et al.* 1998). The population limit was imposed to ensure the perpetuation of viable populations of all large mammal species in the Kruger National Park and to minimise possible elephant damage to the vegetation (Coetzee *et al.* 1979). Culling of elephant continued for the next three decades, removing an average of seven percent of the population annually (Whyte *et al.* 1998).

CHAPTER 2

THE STUDY AREA

LOCATION

The Kruger National Park occurs along South Africa's eastern and north-eastern boundaries (Fig. 1). It occupies the eastern parts of both the Northern and Mpumalanga Provinces which are separated by the Olifants River. The Lebombo Mountains form the eastern border of the Kruger National Park, and also separate South Africa from Mozambique. This range is prominent in the south of the park as far north as the Shingwedzi River. The northern boundary of the park as well as the international border with Zimbabwe is formed by the Limpopo River. The Crocodile River forms the southern boundary. The western boundary of the Kruger National Park is generally not demarcated by natural features although it does follow the courses of the Nsikazi, Sabie, Klein Letaba and Luvuvhu Rivers in some areas. The western and eastern boundaries of the reserve are fenced.

The Kruger National Park is situated along the upper reaches of the Mozambique coastal plain in the area known as the Lowveld. It lies between latitudes 22° 25′ S and 25° 32′ S and longitudes 30° 50′ E and 32° 02′ E. The reserve has a north to south distance of approximately 320 km and an average east to west distance of approximately 65 km. The Kruger National Park currently has an area of 1 948 528 ha.

Generally the topography of the Kruger National Park is flat with undulating plains. Mountainous areas occur along the eastern boundary, in the south-west corner and in the area north of Punda Maria. The altitude varies between 839 m at Khandizwe near Malelane and 122 m along the Sabie River. Drainage takes place from west to east by the nKomati river system in the south and the Limpopo river system in the north.

Baobabs have a geographical distribution limited to areas which receive frost on a maximum of one day per year and are therefore only common in the extreme north of the Kruger

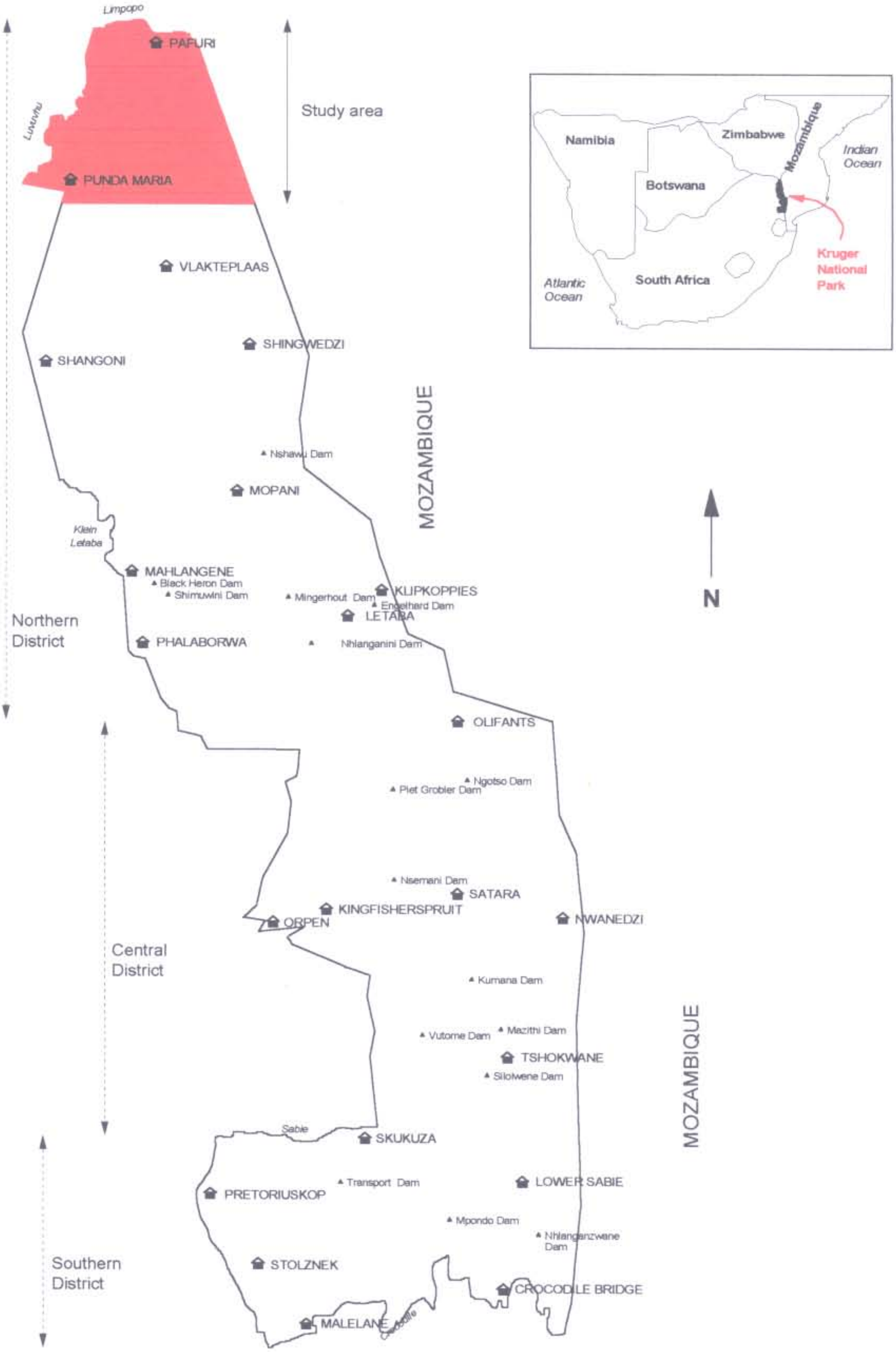


Fig. 1: Location of the study area in the Kruger National Park.

National Park. These trees are, however, not confined to this area and individuals are found almost as far south as Tshokwane. Similarly, the common star-chestnut, though present in suitable habitat throughout the reserve, is common only in the Pafuri region of the Kruger National Park. The study area was therefore, determined by the distribution of these two plant species. The study took place in the extreme northern part of the Kruger National Park (Fig. 1), in the area between the Punda Maria restcamp and the Limpopo River. A line with latitude 22° 45′ S formed the southern boundary of the study area. This area has a size of approximately 154 104 ha. The Luvuvhu River, which flows from west to east through the study area, divides the area into a northern and a southern section (Fig. 2). Plant populations in these two sections were compared as they have different histories of land-use.

HISTORY

The area in which the Kruger National Park is situated has been inhabited by people since the time of the nomadic bushmen and isolated settlements of the Early Stone Age inhabitants (Joubert 1986). The prevalence of diseases which affected both man and livestock prevented the establishment of high-density or extensive settlements. The numbers of people fluctuated considerably until the mid 1800's, their lifestyle, one of the hunter-gatherer. It was around 1840 that the first European settlers slowly began to move into the area, despite the climate, diseases and remoteness. The winter months, when the climate was more hospitable and diseases less prevalent, saw an insurgence of hunters, traders, farmers and adventurers (Joubert 1986).

Following the discovery of gold in the Lydenburg district in 1869 the popularity of the area as a hunting ground and winter pasture soared (Fourie & De Graaf 1992). The accessibility of the area improved greatly during the 1870's with the establishment of the Lydenburg-Delagoa Bay trading route and in the 1890's when the Selati railway line was built. The insurgence of hunters which invaded the area in the late 1800's, resulted in the decimation of the animal populations (Joubert 1986). The situation for the game worsened during the construction of the railway line when thousands of labourers were employed and were paid

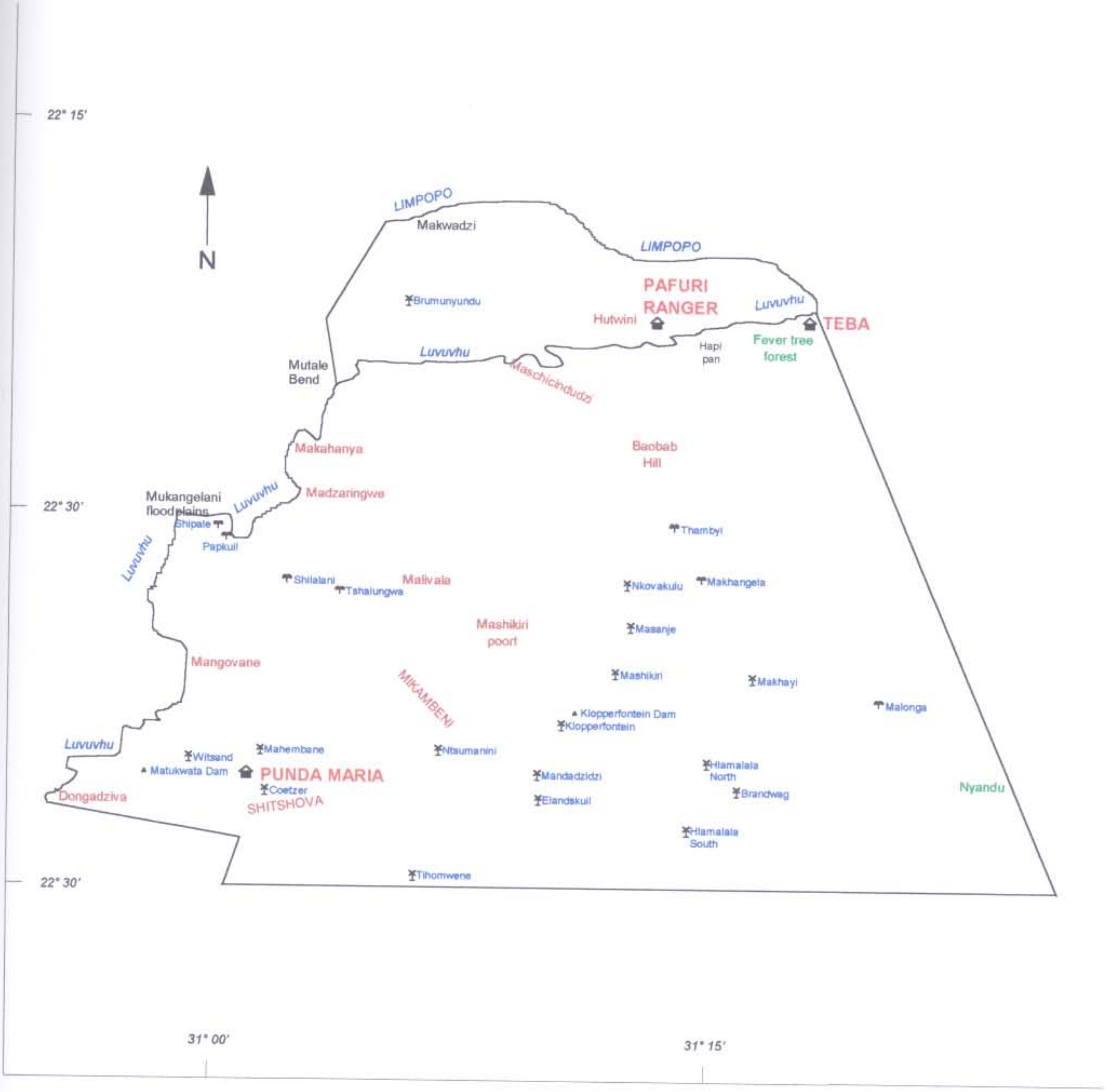


Fig. 2: The northern Kruger National Park.

mainly in game meat (Stevenson-Hamilton 1937). Game in the vicinity of the line, which had been numerous before was exploited to the utmost, and many men made a living solely by killing buck (Stevenson-Hamilton 1937). Species such as white rhinoceros (*Ceratotherium simum*) had been eliminated from the area, while other species were threatened with extinction (Joubert 1986).

This decline in game numbers led to President Kruger's proposal that a game sanctuary be established to protect the regions fauna. Eventually, 14 years later in 1898, some land between the Crocodile and Sabie Rivers was proclaimed as the Government Game Reserve (Fourie & De Graaf 1992; Joubert 1986). This area was reproclaimed in 1902 as part of the Sabi Game Reserve which stretched from the Crocodile River in the south to the Olifants River in the north (Joubert 1986). Although the Government Game Reserve had been established a number of years earlier, it was only after the appointment of Col. Stevenson-Hamilton as warden in 1902 that control of the area as a wildlife sanctuary began in earnest.

In 1903, a section of land between the Letaba and Luvuvhu Rivers was proclaimed as the Shingwedzi Game Reserve. Land to the west of the Sabi Game Reserve and an area between the Olifants and Letaba Rivers were later added. These areas were all included in the Kruger National Park which was formed in 1926 (Joubert 1986). The land between the Luvuvhu and Limpopo Rivers did not originally form part of the Kruger National Park, but was only incorporated into the reserve in 1969.

CLIMATE

Climate can be described as the physical state of the atmosphere and is a result of the sun's radiation on the atmosphere which surrounds the earth (Gertenbach 1987). Climate is one of the many abiotic factors that have a major influence on vegetation. Sunlight, temperature and moisture are important for vegetation but temperature and moisture have the greatest influence on plants.

Koppen's classification, places the study area entirely within the BShw-class (Schulze 1947), where:

B - arid climate
S - steppe
h - hot and dry
w - dry season in winter.

The major part of the study area lies in the DB'd-class according to Thornthwaite's classification although the area around Punda Maria is classed as DB'w. This means the study area has a semi-arid, warm (steppe) climate with the latter portion having a relatively dry winter (Schulze 1947).

The climate of the Kruger National Park is characterised by a hot wet summer from October to March/April and a dry relatively milder winter from April/May to August/September. Temperatures frequently exceed 40 °C. The mean annual rainfall for the region is 500 mm - 550 mm and is highest in the south-west and lowest in the north-east of the park (Joubert 1986).

The climate of the Lowveld and hence the Kruger National Park is influenced by anticyclonic systems moving semi-rhythmically from west to east over the subcontinent. During summer, hot and dry conditions are caused by the presence of anticyclonic conditions present in the interior of the country. A low pressure cell usually then develops over the interior, resulting in moist equatorial air moving in from the north and north-east causing thunder storms. Showers are also caused by equatorial low pressure troughs which become established over southern Africa. In such cases rain is continuous and widespread over the Lowveld and the occurrence of thunder is rare (Venter & Gertenbach 1986).

Rainfall also results from the occurrence of tropical cyclones which originate in the tropical regions of the Indian ocean, move south along the Mozambique channel and then move inland over the Lowveld. Tropical cyclones usually result in heavy rainfall and often cause flooding (Venter & Gertenbach 1986).

The anticyclonic conditions usually present over the countries' interior during winter result in fine and mild conditions over the Lowveld, but are occasionally replaced by cooler, cloudy conditions when cold frontal systems penetrate from the south (Venter & Gertenbach 1986).

Generally, rainfall in the Kruger National Park decreases from south to north and from west to east. This is due to the increasing distance from the Indian ocean and the decreasing altitude respectively. The high lying area surrounding Punda Maria is an exception to this (Gertenbach 1980; Venter & Gertenbach 1986).

In the study area, rainfall is recorded at Punda Maria and Pafuri, which receive an annual average of 556.5 mm and 423.2 mm respectively. Rainfall in the study area is highly seasonal, falling mainly during the summer. A rainfall map has been compiled for the Kruger National Park (Fig. 3); (Gertenbach 1980). This map shows a range in annual rainfall in the study area from less than 450 mm to more than 650 mm. This data may, however, be slightly inaccurate as there are insufficient rainfall recording stations in the Kruger National Park to enable the accurate plotting of rainfall isohyets (Gertenbach 1980).

The rainfall pattern in the summer rainfall areas of South Africa consists of regular fluctuations. This quasi twenty-year regional oscillation results in 10 years of above and 10 years of below average rainfall (Tyson 1978). Rainfall in the Kruger National Park also follows this pattern with the difference between the average annual rainfall of wet and dry cycles of approximately 26 % (Gertenbach 1980; Venter & Gertenbach 1986).

Air temperature plays a major role in photosynthesis and can affect growth rate, size, seed germination and flowering of plants. Temperatures in the Kruger National Park vary between 0 °C and 44 °C although temperatures beyond these extremes are occasionally recorded. Frost seldom occurs (Venter & Gertenbach 1986). The average temperature for Punda Maria is 23.2 °C, with a minimum and maximum of 17.1 and 29.3 °C, respectively. The lowest temperatures occur during June (average minimum = 12.2 °C) (Fig. 4), and the

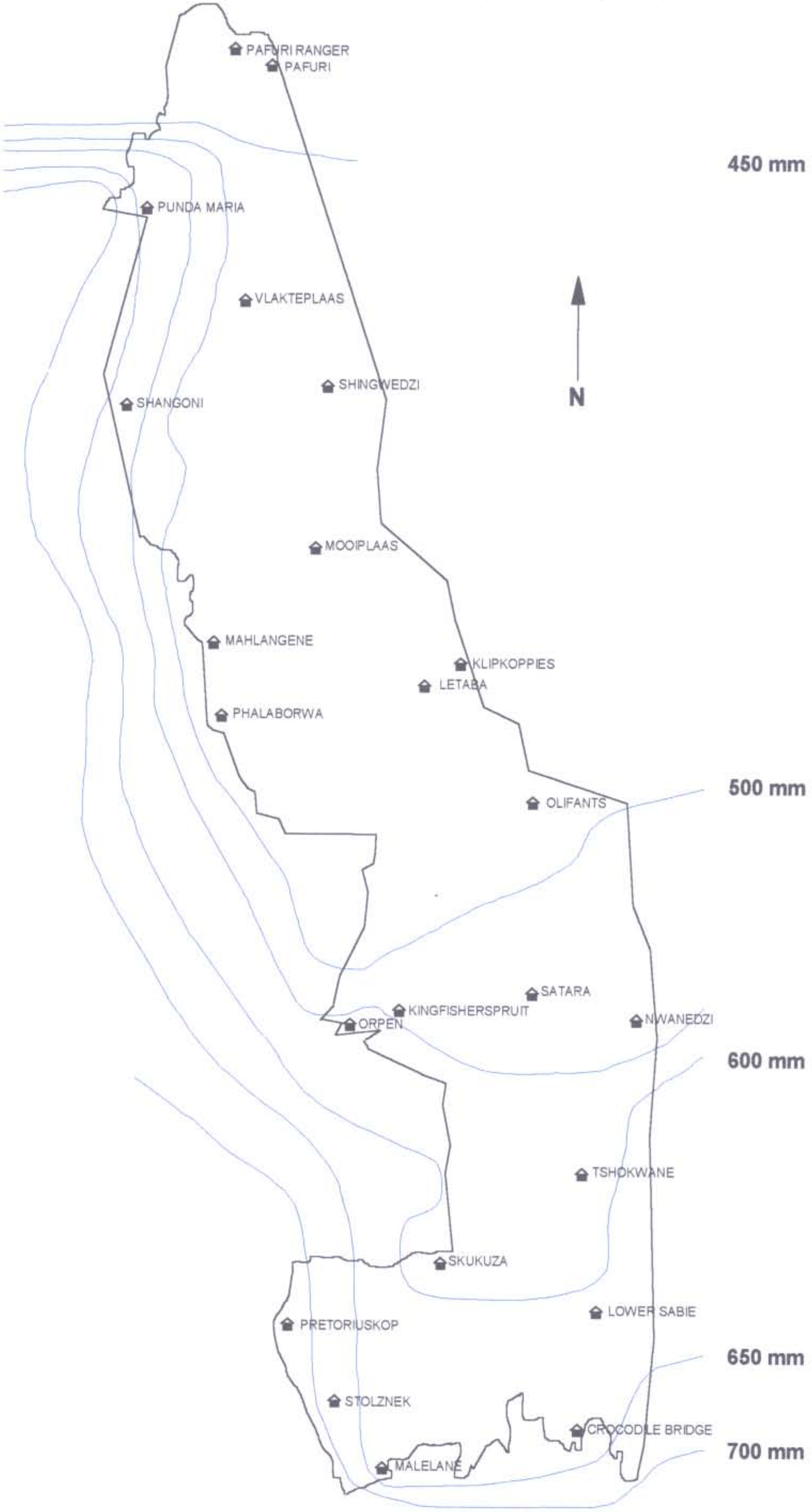
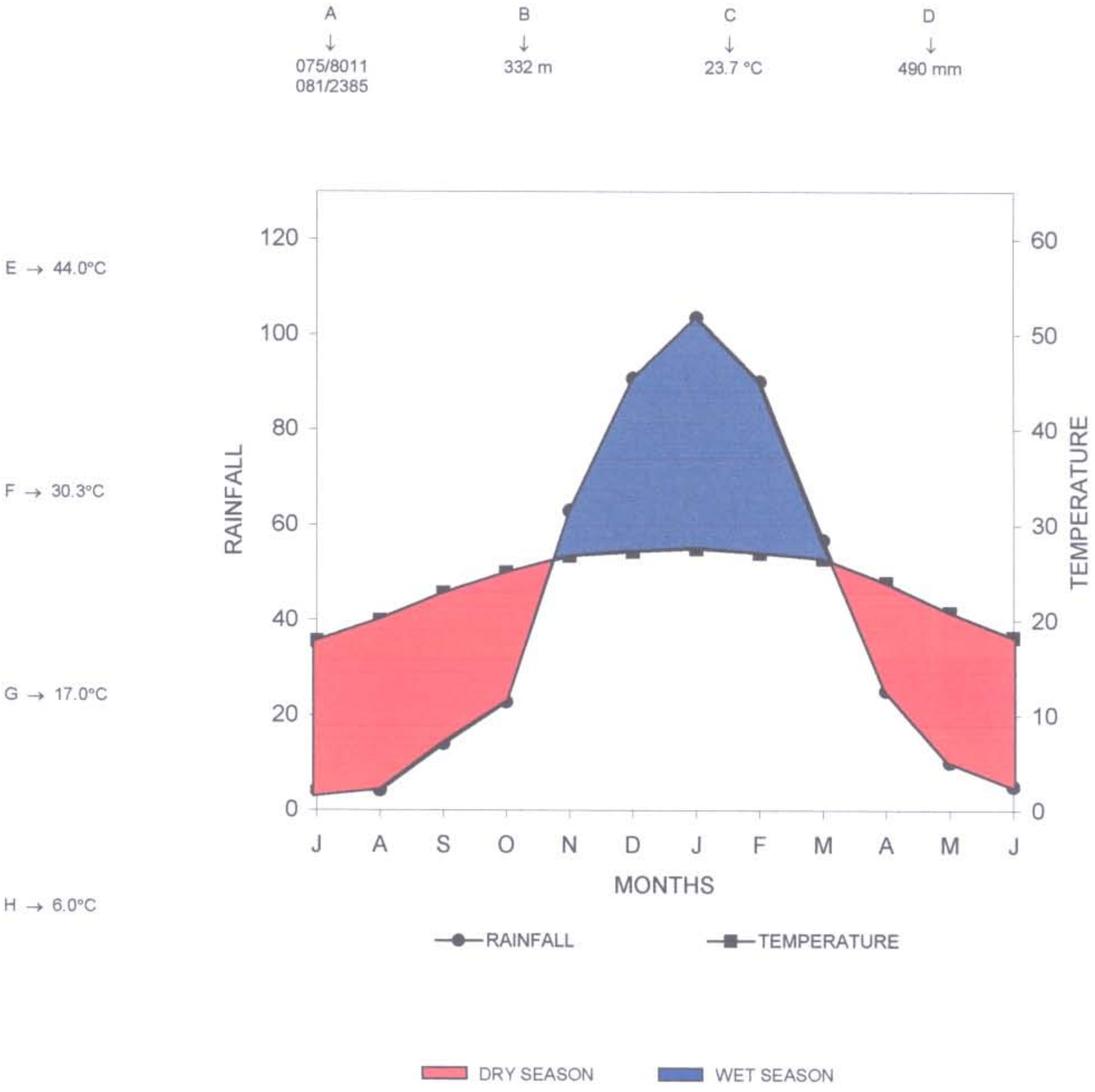


Fig. 3: Rainfall map of the Kruger National Park illustrating isohyets (Gertenbach 1980).



LEGEND: A-weather station; B-altitude; C-mean annual temperature; D-mean annual rainfall; E-highest recorded temperature; F-mean daily maximum; G-mean daily minumum; H-lowest recorded temperature

Fig. 4: Climate diagram for temperature (°C) and rainfall (mm) based on Walter's (1963) convention. Pooled data from Punda Maria (no. 0758011; 22° 41' S; 31° 01' E 462 m) and Pafuri (no. 0812385; 22° 27' S; 31° 19' E 202 m) weather stations were used.

highest during January (32.3 °C). The greatest temperature fluctuation occurs during August.

Pafuri has an average daily minimum temperature of 16.8 °C and an average daily maximum of 31.3 °C. The average temperature is 24.1 °C. The lowest temperatures occur during June (average minimum = 7.9 °C) and the highest during November (average maximum = 34.7 °C). The largest daily fluctuation in temperatures also occurs during June.

Due to the regions sub-tropical climate, summer months are usually hot and humid, while the winter is dry. The mean annual relative humidity for the Punda Maria weather station ranges between a minimum of 11 % and a maximum of 99 %.

GEOLOGY

The regions geological formations are important for the formation of soil, especially as the area has a semi-arid climate. In such a region, the parent material influences the type of profile that arises, the fertility of the soil and its stability against degradation.

The Kruger National Park is divided geologically into almost two equal sections with predominantly granitic formations in the western half and basalts in the eastern half. A narrow belt of shale and sandstone divides these two formations (Joubert 1986). The western granitic areas are undulating, while the east consists of fairly level plains, bordered on the east by the rhyolitic Lebombo Mountains. The sandstone reefs were formed by Karoo sediments and surface in patches throughout most of the reserve. In the region around Punda Maria, however, these reefs occur over a vast area. Dolerite intrusions are found throughout the park, but none of importance are present in the study area (Van Wyk 1984).

As can be seen from Figure 5, the geology of the study area is not highly complex and is represented by only four systems. These are the Karroo, Waterberg, Loskop and Dominion reef systems. Rocks of the Karroo System underlie most of the area, with the latter three

Fig. 5: Geology of the northern Kruger National Park.

systems only occurring in the south-western corner of the study area around the Punda Maria restcamp. Sandstone reefs of the Dominion Reef System occur to the west with intrusions of the Waterberg and Loskop Systems (Van Wyk 1984). The granite which runs along the western half of the rest of the Kruger National Park terminates just to the south of the study area. These systems are bordered by bands of the sandstone of the Stormberg and Ecca series' which run the length of the Kruger National Park. The geology of the northern and western half of the study area consists almost entirely of basalt and limburgite of the Stormberg series. It is, however, interrupted in the north by two sandstone patches (Stormberg series) which are associated with the two faults in this region. These two dykes run in a south-east direction. Along the eastern boundary, there is an area of Kalahari sand which lies on basalt, rhyolite and Cretaceous gravel of the Stormberg series. This sand is aeolian in origin, and up to 30 m deep in places (Gertenbach 1983). The vegetation which occurs in this area is known as the Nwambia Sandveld.

GEOMORPHOLOGY

The Lowveld forms the footslope of the Drakensberg escarpment and is classified as a pediplain with a gentle slope towards the east. The terrain morphology is determined by geological structures and differences in resistance of various rock formations against weathering. In the study area, rugged areas with low mountains have been formed by the sandstones and quartzites of the Clarens and Soutbansberg Formations (Venter & Bristow 1986).

The Lebombo mountains form the most outstanding topographic feature of the Kruger National Park, but north of the Shingwedzi River the range dwindles. In the study area, all that remains of the range is a broad platform that is about 90 m higher than the adjacent plains formed by the mafic lavas (Venter & Bristow 1986).

In the eastern part of the study area, unconsolidated conglomerates and coarse sands of coastal origin overlie rocks of the Malvernia Formation. This is the Nwambia Sandveld which forms an extremely flat plain which continues towards the east (Venter & Bristow 1986).

DRAINAGE

The study area is drained by two perennial rivers, the Limpopo River and the Luvuvhu River, which flow from west to east. The Luvuvhu River originates in the Drakensberg along the Great Escarpment and feeds the Limpopo System on the eastern boundary of the park. A number of smaller streams also flow through the area, many of which only carry water after heavy rainfall. Some of these streams are the Nkovakulu, Madzaringwe, Thambyi, Shihahlandonga, Hlamalala, Shidzivane, Mangovane and Matukwala. The Mutale River flows into the Kruger National Park from the west and supplies a substantial amount of water to the Luvuvhu River. In the Nwambia Sandveld, a deranged pattern of pseudo drainage lines (elongated depressions) of extremely low density occur, occasionally linking some of the many pans which are found in the region (Venter & Bristow 1986).

VEGETATION AND SOIL

The study area includes three of Acocks' veld types. These are Number nine (Lowveld Sour Bushveld), Number 15 (Mopani veld) and Number 18 (Mixed Bushveld) (Acocks 1988). According to the classification of Low and Rebelo (1996) the Kruger National Park forms part of the savanna biome. Four veld types occur in the study area. These are Mopane Shrubveld, Mopane Bushveld, Soutpansberg Arid Mountain Bushveld and Sour Lowveld Bushveld (Low & Rebelo 1996).

The structure, texture, chemical composition and colour of the numerous soil types in the Kruger National Park shows considerable variation, but three major groups of soil can be differentiated based on their origin (Joubert 1976). Soils which are derived from granite are light in colour, generally sandy, with some clay elements in the subsoil, or depressions due to leaching or erosion. Soils of sandstone origin are usually deep and sandy, while dark soils heavy in clay, which attain depths of up to a metre or more are derived from basalt (Joubert 1976).

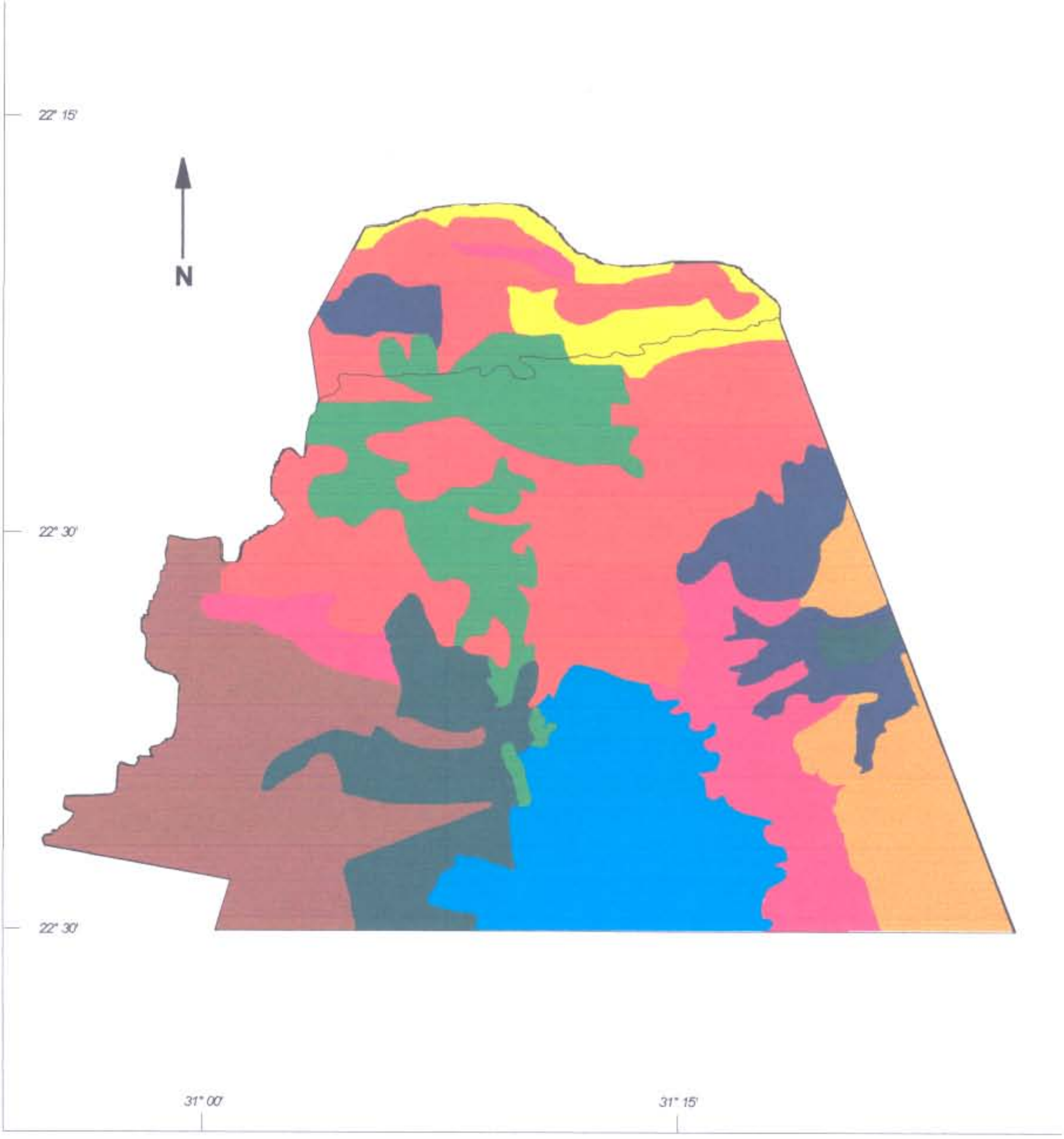
The Kruger National Park is home to approximately 1968 different plant species on which several detailed studies have been conducted (Venter & Gertenbach 1986). Due to the size and number of plant communities which have been identified, practical use of the information is difficult which has resulted in the development of the landscape system. A total of 35 landscape types have been identified in the Kruger National Park based on both the biotic and abiotic components of the area. Gertenbach (1983) defines a landscape as an area with a specific geomorphology, macroclimate, soil and vegetation pattern and associated fauna. There are nine such landscapes which occur in the study area (Fig. 6) and due to their relevance to this study, are discussed in more detail below. The following descriptions are summarised from Gertenbach (1983).

15: *Colophospermum mopane* Forest

This landscape occurs in the southern part of the study area and is not represented at all in the north. Ecca shales underlie the flat to concave topography. Deep soils, rich in salts, with a strong structure in the subsoil occur in this landscape. The soils are mainly of the Swartland (orthic A, over pedocutanic B horizon, over saprolite) and Valsrivier (orthic A, over pedocutanic B horizon, over unconsolidated material) forms although Hutton (orthic A, over red apedal B horizon) and Sterkspruit orthic A, over prismacutanic B horizon) also occur. The vegetation is a high tree savannah, with *Colophospermum mopane* trees of between 10 and 15 m high making up the most important component of this landscape. The landscape is unique to South Africa and deserves special priority in conservation. The thick mopane forest is also ideal habitat for elephant breeding herds.

16: Punda Maria Sandveld on Cave Sandstone

The majority of this landscape occurs south of the Luvuvhu although a small section does occur just north of the river. The Cave Sandstone of the Clarens Formation forms koppies or outcrops which have sand plateaus and bottomlands. These plateaus and bottomlands have deep grey to yellow sandy soil of the Clovelly (orthic A, over yellow brown apedal B horizon) or Fernwood (orthic A, over E horizon) forms. The soils otherwise consist of



🟩 15. *Colophospermum mopane* Forest
🟩 16. Punda Maria Sandveld on Cave Sandstone
🟦 23. *Colophospermum mopane* Shrubveld on Basalt
🟥 25. *Adansonia digitata / Colophospermum mopane* Rugged Veld
🟦 26. *Colophospermum mopane* Shrubveld on Calcrete
🟪 27. Mixed *Combretum* spp. / *Colophospermum mopane* Woodland
🟨 28. Limpopo / Luvuvhu Floodplains
🟧 32. Nwambia Sandveld
🟫 34. Punda Maria Sandveld on Waterberg Sandstone

Fig. 6: Landscapes of the northern Kruger National Park (Gertenbach 1983).

lithosols or solid rock with a thin layer of soil (orthic A horizon) (Mispah) in the hollow places. The vegetation on the deep sandy soils consists of a tall shrub savannah

23: *Colophospermum mopane* Shrubveld on Basalt

This landscape only occurs in the south of the study area and consists of flat to concave plains with a number of drainage channels in the form of marshes or vleis. The basalt has dolerite intrusions in places. Where the topography is flat or even concave, soils with vertic properties occur. A large number of soil forms occur, including Milkwood (melanic A horizon over hard rock), Mayo (melanic A, over a lithocutanic B horizon), Mispah, Bonheim (melanic A, over a pedocutanic B horizon), Swartland, Arcadia (vertic A horizon over an unspecified G horizon) and Glenrosa (orthic A, over a lithocutanic B horizon). Multi-stemmed mopane shrubs 1 - 2 m high dominate the woody vegetation in this area. Stands of these *Colophospermum mopane* shrubs may be as dense as 600 individuals per hectare. Their dominance results in other woody species being relatively scarce. Elephant bulls are common in this landscape and breeding herds may occasionally occur while moving between other landscapes.

25: *Adansonia digitata / Colophospermum mopane* Rugged Veld

This landscape is included in its entirety in the study area, and parts of it are found both north and south of the Luvuvhu River. It occurs on Basalt. The terrain undulates strongly, has steep slopes and numerous koppies. The soil is dark in colour and has a relatively high clay content. The structure of the topsoil is sometimes poorly developed, with the Milkwood, Mayo, Mispah and Glenrosa forms being dominant. Shallow lithosols occur on the koppies. The vegetation structure is an open tree savannah, with the landscape deriving its name from the physiognomic dominance of baobab and mopane trees. *Sterculia rogersii* trees also occur regularly in this area. Elephant occur infrequently.

26: *Colophospermum mopane* Shrubveld on Calcrete

This undulating landscape occurs in two isolated areas, both within the study area. One section occurs on the eastern boundary of the Kruger National Park alongside the Nwambia Sandveld, while the other occurs on the western boundary between the Limpopo and Luvuvhu Rivers. Soil in this region is shallow and calcareous with a high occurrence of lime concretions. These are as a result of decomposition of the underlying geological material of the Malvernia formations. The most common soil forms are Milkwood, Mayo, Mispah and Glenrosa. Lithosols are common. The sub-unit on the eastern boundary is mainly a shrub savannah, while the sub-unit on the western boundary is a tree savannah. *Sterculia rogersii* is one of the dominant woody species of this landscape. Elephant occur in this region in small numbers. This landscape is unique in South Africa and therefore, necessitates special conservation status.

27: Mixed *Combretum* spp. / *Colophospermum mopane* Woodland

Three isolated sections of this landscape occur in the study area. One section occurs in the far north of the Kruger National Park, alongside the Limpopo floodplain. The other two areas occur south of the Luvuvhu River. A small section is found near the parks western boundary and the larger section, is a narrow strip running along the west of the Nwambia Sandveld. The underlying geological material consists of Quaternary white sand mixed with gravel and basalt. This landscape is relatively flat, the soil is deep and sandy in places and usually well drained. Hutton, Shortlands (orthic A, over red structured B horizon), Bonheim, Valsrivier, Swartland, Mayo, Mispah and Glenrosa are the dominant soil forms. The vegetation consists of an open tree veld with a large quantity of medium shrubs. *Sterculia rogersii* is one of the many dominant woody species. Elephant occur regularly in this landscape.

28: Limpopo / Luvuvhu Floodplains

This landscape occurs on the banks of the Limpopo and Luvuvhu Rivers. The topography is flat and the soil consists of alluvium which has been deposited by the rivers. Koppies are absent. This landscape also has a number of pans which fill up when the rivers flood. The soils originate from granite, Waterberg sandstone, Cave sandstone, basalt and dolerite. Inhoek (melanic A horizon), Dundee (orthic A horizon over stratified alluvium) and Oakleaf (orthic A, over neocutanic B horizon) are the main soil forms, with Arcadia and Willowbrook (melanic A, over G horizon) soils found in the pans. *Adansonia digitata* is a dominant woody species in some parts of this landscape with almost homogenous stands occurring in isolated patches. Elephant bulls are abundant on these floodplains.

32: Nwambia Sandveld

This landscape occurs along the eastern boundary of the study area. The terrain is flat and consists of sand deposits which can be present to a depth of 30 m. The soil forms are Hutton and Clovelly. Well defined drainage channels are absent but a number of pans are present. The vegetation is in the form of a tall shrubveld with very few trees. *Adansonia digitata* is one of the dominant tree species in the western part of this landscape. As with most of the larger mammals, elephant only occur in relatively small numbers in this region.

34: Punda Maria Sandveld on Waterberg Sandstone

This landscape occurs in the south-western corner of the study area. The area consists of both mountains and plains with springs being a common feature. The underlying geology consists of Waterberg sandstone into which diabase sills and dykes have intruded. Soils vary from lithosols in the mountains to deep sandy soils on the middleslopes and brackish soils in the bottomlands. Dominant soil forms on the mountains are Mispah and Glenrosa, while Hutton, Clovelly, and Glenrosa dominate the middleslopes. Valsrivier, Sterkspruit, Hutton, and Swartland dominate the bottomlands. Elephant are present in small numbers.

CHAPTER 3

SPATIAL DENSITY AND POPULATION SIZE OF *ADANSONIA DIGITATA* AND *STERCULIA ROGERSII* IN THE KRUGER NATIONAL PARK

INTRODUCTION

Density is by definition, numbers per unit area, per unit volume or per unit of habitat (Krebs 1994). Trees can occur in many different types of spatial arrangement, from single isolated trees to dense clumps with a closed or almost closed canopy (Wilson 1988). Baobabs occur in all such arrangements and have even been planted in the form of avenues in some places. Although common star-chestnuts usually occur in an isolated arrangement on rocky outcrops, they are sometimes found in dense groups.

The use of quadrats is the most common method for sampling plants, but for samples of density, relies on three factors (Krebs 1994):

- The population of each quadrat examined must be determined exactly,
- The area of each quadrat must be known,
- The quadrats counted must be representative of the whole area.

Elephants have differing effects on the numbers and density of different plant species. Density of baobabs has been related to elephant densities in some places, but in other situations, increases in elephant density have not affected the size of the baobab population (Barnes *et al.* 1994).

In this study, quadrats in the form of belt transects were used to determine the density of *Sterculia rogersii* and *Adansonia digitata* in the study area. Estimates were then made of the population size of each of these two species in the area.

METHODS

Density data were obtained using a belt transect method (Tchamba 1995; Tchamba & Mahamat 1992; Viljoen 1995). A random stratified sampling technique was used in which transects were laid out according to Gertenbach's (1983) landscape system. Transects were located proportionally both north and south of the Luvuvhu River in order for comparisons to be made between these two sections. Transects were randomly located in all nine of the landscapes which occur in the study area. The location of transects did, however, have to take into account the accessibility of each area which was dependant on the road network. The location of each transect was determined from a map before entering the area so that bias could be avoided. Transects were set up at right angles to roads and were parallel to each other in each area. Transects started 30 m from roads to avoid disturbed veld conditions next to roads.

Data were gathered by two observers walking along the predetermined transect line. All *Sterculia rogersii* and *Adansonia digitata* trees, within a predetermined distance from the centre line of the transect, were located. This distance was dependent on the visibility at the site of the transect. The horizontal visibility was determined for each transect. Ten visibility estimates were made for each kilometre walked, and the lowest of these was taken as the single visibility estimate for that transect. Transects were preferred to total counts to minimise the possibility of smaller trees being missed and thus giving rise to erroneous data. Swanepoel and Swanepoel (1986), recorded damage to baobab trees, while travelling in a vehicle in the Zambezi Valley. Weyerhaeuser (1985) assessed elephant induced bark damage to baobabs in Tanzania. Both admit to overlooking smaller trees while conducting these total area counts. It was felt, that for this survey, sampling methods would result in a more complete representation of all size classes and hence more accurate data. The location of each baobab and star-chestnut relative to the centre line of the transect was recorded.

The density of trees was calculated separately for each landscape, using the following equation:

$$d = [(t \div s) \times n] \div t$$

where: d = density

t = total area

s = area sampled

n = number of trees sampled

The population size for each of the species was calculated by determining the product of the overall density and the size of the study area. The overall density was determined by adding the products of the density of each landscape and the size of the particular landscape in the study area.

Comparisons were made between the tree density of both *Adansonia digitata* and *Sterculia rogersii* in the northern and southern sections of the study area.

RESULTS

Adansonia digitata

The baobab population in the study area consists of around 15 216 trees which occur at an average density of approximately 11.14 trees/km^2 ($s^2 = 90.07$). The densities for individual landscapes are shown in Table 1.

The baobab density north of the Luvuvhu River is 21.8 trees/km^2, considerably higher than the density of 7.0 trees/km^2 south of the river. The difference in density is highly significant (difference of proportions on the density, $z = 7.75$; $P < 0.001$)

Table 1

Density of trees in each landscape (Fig. 6)

LANDSCAPE	**SIZE** **(km^2)**	***A. DIGITATA*** **(per km^2)**	***S. ROGERSII*** **(per km^2)**
15. *Colophospermum mopane* Forest	157	10.813	10.813
16. Punda Maria Sandveld on Cave Sandstone	166	17.532	5.844
23. *Colophospermum mopane* Shrubveld on Basalt	156	0.316	0.000
25. *Adansonia digitata / Colophospermum mopane* Rugged Veld	313	11.436	80.550
26. *Colophospermum mopane* Shrubveld on Calcrete	166	2.397	73.108
27. Mixed *Combretum* spp. / *Colophospermum mopane* Woodland	155	8.222	1.370
28. Limpopo / Luvuvhu Floodplains	128	32.174	22.274
32. Nwambia Sandveld	100	12.029	10.614
34. Punda Maria Sandveld on Waterberg Sandstone	199	5.297	5.959

Sterculia rogersii

The average density of the *Sterculia rogersii* population in the study area is approximately 23.39 trees/km^2 ($s^2 = 963.18$). There are an estimated 45 849 trees which occur in this area. The densities of trees in the various landscapes are also given in Table 1.

The common star-chestnut density north of the Luvuvhu River is 61.42 trees/km^2, almost three times higher than the density of 22.06 trees/km^2 south of the river. The difference in density is highly significant (difference of proportions on the density, $z = 13.44$; $P < 0.001$)

DISCUSSION

Although many studies have been conducted on baobabs, and much has been written about these unusual trees, not many authors have bothered to include any information on their spatial density or the size of the populations. Barnes (1980), however, has calculated the density of baobabs in 15 transects and arrived at figures as dissimilar as 3 trees/km^2 and 723 trees/km^2. He calculated a median density of 69 trees/km^2 for the 15 transects in Ruaha National Park, Tanzania. No relationship between vegetation type or soil could be found. The transects with the highest and lowest baobab densities occurred on the same soil type. In a later study, Barnes *et al.* (1994) calculated densities which varied from 15 trees/km^2 to 1025 trees/km^2 in the same reserve. The mean densities of baobabs in Ruaha in 1976, 1982, and 1989 were 51, 28, and 35 trees/km^2 respectively (Barnes *et al.* 1994). Densities of baobabs in parts of Sudan and Mali have also been calculated (Wilson 1988). The densities for these regions were 11.2 trees/km^2 and 10.7 trees/km^2, respectively.

Ben-Shahar (1996) found that tree densities in three woodland types in northern Botswana were regulated by factors other than elephant, such as soil nutrients, water drainage and fire.

The density of baobabs in the Kruger National Park of 11.14 trees/km^2 is much lower than the densities of trees in Ruaha, Tanzania, but is similar to the density of trees in Sudan and especially Mali. The density of baobabs in the north of the Kruger National Park is, however, much greater, although still not as high as in Ruaha. With the exception of the occasional straggler, baobabs are only found in the north of the Kruger National Park. They are at the southernmost part of their range in this region as a consequence of the less suitable climate further south, with frost being the limiting factor. Both altitude and climate varies considerably in the study area and is probably more suitable for baobabs in the north. It is therefore, expected that the density of trees in the northern study section would be higher due to the more suitable climate. Parts of the southern section can also be regarded as unsuitable for baobab growth. These trees show an affinity for deep, well drained soils, but much of this section consists of vertic soils with a high clay content (*Colophospermum mopane* Shrubveld on Basalt) (Gertenbach 1983). The unsuitability of this region for baobabs is demonstrated by the near absence of these trees there, probably as a result of poor drainage. The density of baobabs does not show any other trends related to soil type. Deep sandy soils have densities ranging from 5.2 trees/km^2 (Punda Maria Sandveld on Waterberg Sandstone) to 17.5 trees/km^2 (Punda Maria Sandveld on Cave Sandstone). While the baobab density on the shallow soil of landscape 26 (*Colophospermum mopane* Shrubveld on Calcrete) is very low, the shallow soils of the *Adansonia digitata* / *Colophospermum mopane* Rugged Veld support a high density of baobabs.

Density of *Sterculia rogersii* is higher in the northern than in the southern section, but as with baobabs, this is most likely due to the more suitable habitat in the north rather than as a result of the overutilisation by herbivores. This species prefers dry conditions and does not tolerate cold (Van Wyk 1974). The soil of the *Adansonia digitata* / *Colophospermum mopane* Rugged Veld is shallow, calcareous and has a poorly developed topsoil layer (Gertenbach 1983). The soil of the *Colophospermum mopane* Shrubveld on Calcrete is also shallow and calcareous (Gertenbach 1983). The density of star chestnuts in the study area is highest in these two landscapes. The common soil properties of these areas suggests that *Sterculia rogersii* has an affinity for this particular type of soil. These trees are absent from the *Colophospermum mopane* Shrubveld on Basalt, again probably due to this landscape lying on vertic clay soils. The densities of *Sterculia rogersii* is low in all landscapes with deep sandy soils, but as with baobabs, these trees are fairly common on the alluvial floodplains.

The spatial distribution of *Sterculia rogersii* may also be affected by fire. This species occurs in highest density in rocky places and on ridges where the fire intensity is lower due to a sparse field layer and hence a poor fuel load. Gertenbach (1983) describes the field layer of landscapes 25 (*Adansonia digitata* / *Colophospermum mopane* Rugged Veld) and 28 (Limpopo / Luvuvhu Floodplains) as sparse and that of landscapes 27 (Mixed *Combretum* spp. / *Colophospermum mopane* Woodland) and 34 (Punda Maria Sandveld on Waterberg Sandstone) as moderate to dense. The latter two landscapes support low densities of *Sterculia rogersii*, while the former two support relatively high densities. These densities may be influenced by fire frequency or intensity, although more research is required in this regard before any conclusions can be made.

CHAPTER 4

POPULATION STRUCTURE OF *ADANSONIA DIGITATA* AND *STERCULIA ROGERSII* IN THE KRUGER NATIONAL PARK

INTRODUCTION

Four key parameters drive population changes, mortality, natality, immigration and emigration (Krebs 1994). The first two parameters are of particular importance in this study. Populations which have reached a constant size, in which the birth rate and death rate are the same, have a fixed age distribution and maintain this distribution. The age distribution of an increasing population is dominated by young organisms, while that of a stable or declining population is not (Krebs 1994). The age distribution of a self-maintaining tree population has a smooth decline in tree numbers from the youngest to the oldest age class (Wilson 1988). The structure of the population can therefore provide information on its long-term viability.

By damaging mature trees, elephant have the ability to alter the population dynamics and structure of certain tree species (Tchamba 1995). The killing or heavy browsing of particular sizes of trees by elephant can result in other sizes being most numerous (Tchamba & Mahamat 1992), thereby altering the age distribution from a favourable to an unfavourable one. Elephant browsing suppresses regeneration of certain tree species (Lock 1993). Insufficient regeneration to balance the loss of trees from the population can result in a change in habitat (Tchamba & Mahamat 1992). In parts of Ruaha National Park, Tanzania, elephant have been responsible for a decline in baobabs, but in other parts of the reserve, the age structure has remained healthy and the Park's baobab population is therefore not threatened (Barnes *et al.* 1994).

The goal of this part of the study was to obtain data on the age class distribution of the two species (*Adansonia digitata* and *Sterculia rogersii*) in order to establish if the populations were increasing, stable or decreasing.

METHODS

The transects used to obtain the density and population size data were also used to obtain data for determining the structure of the populations. This was achieved by locating and recording all seedlings and small trees. The size of each tree was determined by measuring its girth using a tape measure. The girth of *Adansonia digitata* trees was measured at breast height (GBH). This measurement was chosen as it had been used extensively for baobabs (Barnes *et al.* 1994; Wilson 1988; Weyerhaeuser 1985), and is both convenient and practical. The girth of *Sterculia rogersii* trees was measured at ground level as the growth form of the tree, in which it branches into multiple stems at the base, precludes the measurement of the girth of the majority of trees at breast height. In the case of baobab trees which could not be measured at breast height, either due to branching below this level or because they did not reach breast height, girth measurements were taken at ground level and converted to GBH.

The structure of the *Sterculia rogersii* and *Adansonia digitata* populations was determined by placing trees into various size classes. In the case of the former species, these size classes were based on 0.25 m girth increments, but girth intervals of 1.00 m were used for baobabs. For each of the two species, 22 size classes were formed. The girths of a number of specimens which occurred outside of the transects were also measured, but these data were recorded separately. The size class distributions were compared using Kolmogorov-Smirnov two-sample tests.

RESULTS

Adansonia digitata

The size class distribution of the trees in the transects only differs from the distribution of the total sample at the 0.05 significance level (Kolmogorov-Smirnov two-sample test, $D_{\max} = 0.12$; $P > 0.05$).

As is readily apparent, the size distribution of baobabs in the northern section indicates a healthy population with more young than old trees, of which almost 25 % of the trees occur in the smallest size class (Fig. 7). The basic structure of the population in the southern section is not significantly different (Kolmogorov-Smirnov two-sample test, $D_{\max} = 0.22$; $P > 0.05$). Trees with a girth of 1 to 2 m are most common in the southern section.

The mean GBH of trees in the northern section is 3.96 m and in the south is 4.50 m. The difference between these means is not significant (two-sample t-test assuming unequal variances, $t = -0.84$; df = 133; $P > 0.05$).

Sterculia rogersii

The size class distribution of the trees occurring within the sampling transects does not differ significantly from the size class distribution of the total sample as would be expected (Kolmogorov-Smirnov two-sample test, $D_{\max} = 0.0295$; $P > 0.05$). The larger dataset has therefore been used.

As can be seen in Figure 8, the smaller size classes of trees are poorly represented in the samples of both regions. The proportions of trees increase gradually, with common star-chestnuts with a girth of 1.75 m to 2.00 m best represented. The proportions of trees show a general decrease into the larger size classes after this point, with no trees having a girth larger than 5.50 m. The basic form of the population in the southern section is not significantly different from the form of the northern population (Kolmogorov-Smirnov two-sample test, $D_{\max} = 0.059$; $P > 0.05$).

The mean girth of star-chestnut trees in the northern section is 2.09 m and in the southern section is 1.96 m. The difference between these means is significant (two-sample t-test assuming equal variances, $t = 2.39$; df = 1159; $P < 0.05$).

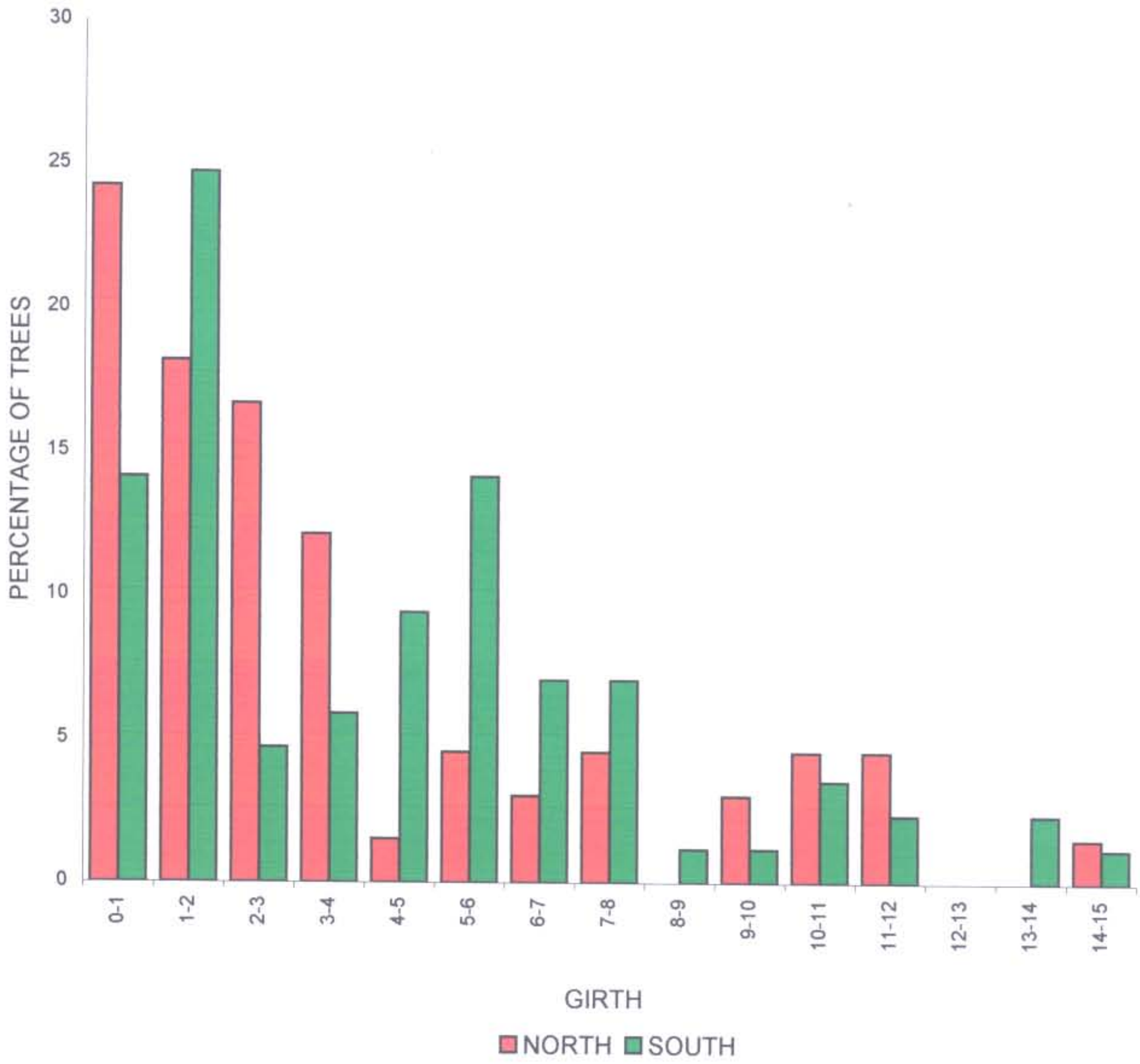


Fig. 7: Size class distribution (based on girth at breast height (m)) of *Adansonia digitata* in the Kruger National Park, north and south of the Luvuvhu River.

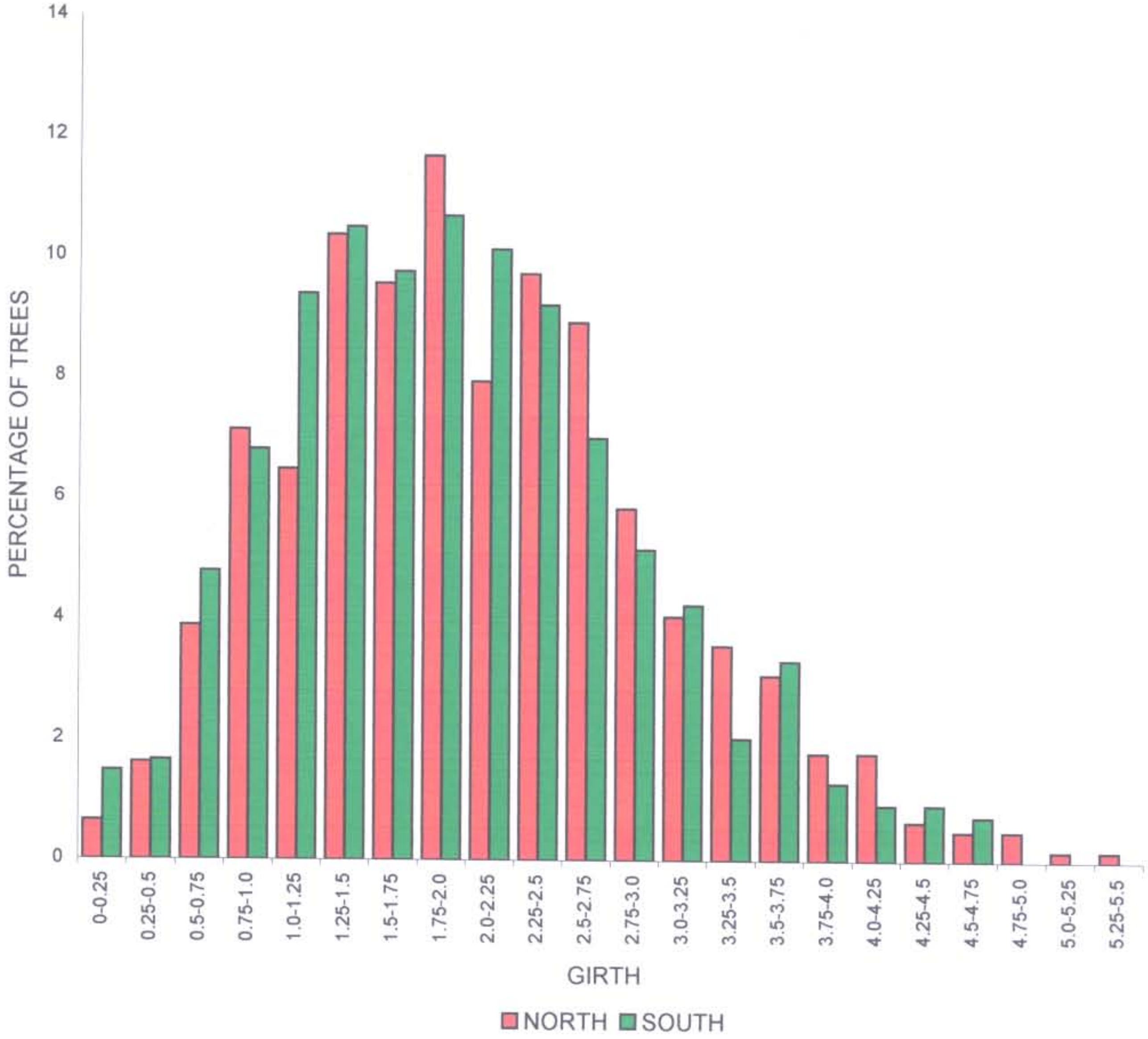


Fig. 8: Size class distribution (based on girth size at ground level (m)) of *Sterculia rogersii* in the Kruger National Park, north and south of the Luvuvhu River.

DISCUSSION

The results of this study are inconclusive in proving that elephants play any significant role in structuring the populations of either *Adansonia digitata* or *Sterculia rogersii* in the Kruger National Park. It would appear that the effect they have had on these populations has been overrated. Germination and recruitment of these trees into the population may be episodic, influenced by factors such as rainfall or fire. In northern Botswana, even moderate elephant browsing and fire damage in *Acacia erioloba* woodlands did not halt the recruitment of trees (Ben-Shahar 1996). Elephant were initially thought to have played a major role in structuring *Acacia tortilis* populations in east Africa, but this has been found not to be the case (Prins & Van der Jeugd 1993). It has been discovered that limited windows for recruitment play an important role in determining the population structure of these trees (Prins & Van der Jeugd 1993).

The population structure of other tree species has also been influenced by limited windows for recruitment. Catastrophic events have been shown to cause the establishment of tree species on the Galapagos Islands. In Australia, the establishment of *Astrebla lapacea* seedlings occurred only twice in the 42 years before 1983, while seedlings of *Callitris glaucophylla* have only become established when livestock numbers were reduced in 1876-1877 and when myxamotosis decimated the rabbit population during the 1950s (Prins & Van Der Jeugd 1993).

The likelihood that similar events in the past may have had an influence on the structure of the *Sterculia rogersii* and *Adansonia digitata* populations of the Kruger National Park warrants consideration. Windows for recruitment may have occurred in the past due to climatic factors, or more likely reduced herbivore populations. This situation could have resulted from hunting and human activity, but could also have been as a result of disease outbreaks.

Studies on baobab trees in Ruaha National Park, Tanzania show an overabundance of trees established between 1860 and 1870, while baobab establishment was above average in Lake Manyara National Park, Tanzania between 1870 and 1880. Although more accurate dating is required, this period corresponds quite well with the rinderpest epidemic in those areas which would have decimated the herbivore populations and thus created a period of reduced pressure on seedlings (Prins & Van Der Jeugd 1993). The rinderpest outbreak was probably indirectly responsible for this extremely successful period of baobab recruitment in Tanzania. Information from historical records also indicates that this rinderpest epidemic was a causal factor for the establishment of present day mature *Acacia* stands which occur in that region (Prins & Van Der Jeugd 1993).

Similarly the occurrence of anthrax epidemics in Lake Manyara have been linked to the establishment of stands of *Acacia tortilis* trees. This is due to the reduction in the impala population in that park (Prins & Van Der Jeugd 1993). Impala damage seedlings by foraging on them and also consume the seed pods. Despite the abundance in Botswana of herbivores which prevent new seedlings from becoming established, the effect of migratory herds in the Serengeti is much greater, due to the higher density of animals (Ben-Shahar 1996).

Although the population structure of baobabs in the Kruger National Park shows a general decline in the numbers of older trees, which would be expected from a self maintaining population, the curve is not as smooth as would be expected. It indicates that either mortality of baobabs or recruitment of seedlings into the population has not been consistent.

The population structure and these inconsistencies have been analysed by assigning ages to the size classes of trees and comparing the population structure with historical events. An average growth rate has been calculated from the baobab growth rates already discussed and this rate has been used to age trees for the following discussion. The growth rate is based on the average of all the growth rates, excluding the fastest and slowest figures. The growth rates of baobabs vary with age and any growth rates based on a sample of very large, or very small trees would be biased. The growth rate from Swart (1963) and Swanepoel (1993) have, therefore, been omitted when calculating the average growth rate.

According to this growth rate, baobabs with a girth of 20 m are only slightly older than 300 years. From available information, it can be concluded that the growth of large baobab trees is extremely slow, and therefore, these growth rates should probably not be applied to trees with a girth greater than 15 m, and certainly not to trees with a girth larger than 20 m. Many of the larger baobabs (GBH greater than 15 m) may be as young as 300 years which supports Wilson's (1988) statement that very few baobab trees live in excess of 400 years. Only the tree dated by Swart (1963) and those in Ruaha (Barnes 1980) had girths much less than 15 m when 300 years old. Comments are regularly made regarding the absence of noticeable change in large baobabs, and especially how trees which had had dates inscribed on them did not appear to have changed since the carvings were made a number of years previously. These baobab trees are generally noticed and selected as they are large and are therefore, probably already in the slow growth phase (i.e. older than 300 years). They do not change very much in size after this time.

The first white men recorded to have traversed the country now included in the Kruger National Park were those led in 1837, by the voortrekker Louis Trichardt (Stevenson Hamilton 1937). At the same time, another section of the party under Van Rensburg travelled near the Pafuri (Luvuvhu) River, where they were all massacred by the natives (Stevenson Hamilton 1937). Written records on the history of this area, before this time, are non existent. Due to the paucity of available information, no attempt will be made here to explain the population structure of trees which were in existence before this time.

At the end of the 19th and beginning of the 20th centuries, the herbivore populations in the area now comprising the Kruger National Park were affected by a number of factors. Numerous hunting parties invaded the area annually, harvesting the game, while inhabitants of the dispersed settlements and units of soldiers fighting in the Anglo-Boer War also took their toll on the animal populations (Joubert 1986). The rinderpest pan-zootic moved through the area in 1896 and large numbers of susceptible herbivores succumbed to this disease. During this period, the larger herbivore populations had been decimated and the populations of several species were reduced to the point of imminent extinction (Joubert 1986). The situation got to a point where the rather drastic measure of reducing predator populations was implemented in an attempt to allow the prey species to recover (Stevenson-Hamilton 1937). There is little doubt that the herbivore populations in the study area had been drastically reduced around the turn of the century (Stevenson-Hamilton 1937), and this could have provided an opportunity for above average recruitment of tree species.

The size class distribution of baobabs shows that good recruitment occurred during the latter half of the 19th century. Elephant numbers were also low during this period. Rinderpest is selective, highly susceptible animals being pigs (family Suidae), giraffe (*Giraffa camelopardalis*), buffalo (*Syncerus caffer*), kudu (*Tragelaphus strepsiceros*), eland (*Taurotragus oryx*), bushbuck (*Tragelaphus scriptus*) and reedbuck (*Redunca arundinum*) (Caughley 1976). Duiker (*Sylvicapra grimmia*), oribi (*Ourebia ourebi*), roan (*Hippotragus equinus*), sable (*Hippotragus niger*), and impala (*Aepyceros melampus*) are susceptible in some areas, but waterbuck (*Kobus ellipsiprymnus*), hartebeest(*Alcelaphus buselaphus*), elephant (*Loxodonta africana*), rhinoceros (family Rhinocerotidae) and hippopotamus (*Hippopotamus amphibius*) are largely immune (Caughley 1976). Caughley (1976) also suggests that the rinderpest epidemic killed many ungulates, causing a positive response in the vegetation, increasing the forage available to the remaining animals. The result of this would have been the large scale eruption of several herbivorous species.

This was followed by a period of inferior recruitment of baobabs in the Kruger National Park as is demonstrated by the rather low proportion of trees in the three to five metre size classes. Baobabs which are this size today would have established themselves in the mid 1920s and the thirty years thereafter. During the early years of the Kruger National Park, carnivore control operations took place as it was felt that the onslaught of hunting and the effect of the rinderpest epidemic on the game had decimated populations and that by reducing the predator pressure on them, these populations could recover. These predator reducing operations took place until the end of the 1920's when it was felt that the predator / prey ratio was finally in equilibrium (Joubert 1986).

From this action it can be deduced that the herbivore numbers increased dramatically during the 1920's, which is probably the reason for the low recruitment rates of baobabs during this period when compared with previous years. It was also around this time (1931) that elephants began to move into the area from the south and these animals may also have contributed to the low recruitment rates of baobabs. This period also includes the relatively dry 1940's (Gertenbach 1980), a period in which alarming losses of baobabs were recorded in neighbouring Zimbabwe (Piearce *et al.* 1994). The assumption made from this information is that sub-optimum conditions for the establishment of baobabs were present during this time.

Another characteristic of the baobab size class distribution is the large proportion of trees with girths of between one and two metres. When assessing the baobab size class frequency distribution, the proportion of trees in the smallest size class appears to be less than satisfactory, but this is probably apparent, due to the trees with a GBH of one to two metres being overabundant.

The anthrax outbreaks during the 1960's may have created an opportunity for baobab recruitment as occurred with *Acacia tortilis* in east Africa (Prins & Van der Jeugd 1993). Anthrax was rife in the north of the Kruger National Park during the 1960s. Although, the Pafuri area of the Kruger National Park is an enzootic anthrax region (De Vos *et al.* 1973) and sporadic outbreaks occur fairly regularly, during 1960 a very severe anthrax epidemic ravaged the greater northern section of the Park (Pienaar 1967). Between the 5th of June and 11th of October 1960, the disease reached epidemic proportions in parts and spread rapidly throughout the north of the Kruger National Park (Pienaar 1961). The Pafuri area, suffered a re-infection of the disease, after a considerable period without fatalities and the disease was therefore, present in this area for an extended period (Pienaar 1961). The kudu (*Tragelaphus strepsiceros*) population was most severely affected by the disease. Due to the susceptibility of these animals to anthrax, mortality was high, with 771 carcasses being found (Pienaar 1961). Waterbuck (*Kobus ellipsiprymnus*), and nyala (*Tragelaphus angasii*) were seriously affected, while in the Pafuri region, impala (*Aepyceros melampus*) also succumbed to the disease (Pienaar 1961). A total of 1054 animal carcasses were discovered in the Kruger National Park during the 1960 anthrax epidemic, the majority belonging to kudu and other herbivore species, while only three elephant carcasses were found (Pienaar 1961). Although a large number of carcasses were found, when the ruggedness of the terrain in the Punda Maria - Pafuri area is taken into consideration, it would be fair to assume that large numbers of carcasses may have been missed in which case the death toll would have been far greater. What is certain, however, is that the herbivore population in the north of the Kruger National Park was considerably reduced by the anthrax epidemic.

As occurred at the turn of the century, following the decimation of the herbivore populations, reduced browsing pressure on the baobabs, would once again have created an ideal situation for recruitment. The habitat at Pafuri was in an overgrazed state at the time of the outbreak forcing animals such as kudu and nyala to feed on the leaves and twigs of shrubs and trees (Pienaar 1961). Baobabs would have formed part of this diet and the reduction in herbivore numbers would therefore, have reduced the browsing pressure on these trees considerably. It is interesting to note that the highest mortality rate at Pafuri occurred among kudu and nyala, both browsing species (Pienaar 1967). It has also been shown that a lack of ground cover as a result of overgrazing in the vicinity of baobabs exacerbates their water deficit (Piearce *at al.* 1994). Therefore, high herbivore densities with the resultant high grazing pressure reduce the suitability of habitat for baobabs which are sensitive to drought.

The baobabs in the one to two metre girth size class probably emerged during the period following this anthrax epidemic. Only three elephant mortalities were recorded during this outbreak. However, a number of workers in the field are of the opinion that kudu and not elephant are mainly responsible for the destruction of baobab seedlings (De Jager, pers. comm.[1]; Sowry, pers. comm.[2]). Evidence of this can also be found in areas in which elephant are absent, but where young baobabs are extensively utilised. These plants have been damaged by browsers such as kudu, eland and giraffe. The large number of kudu fatalities during this period would therefore, have created a favourable environment for the establishment of baobab seedlings. This period of reduced pressure, also followed a period in the 1950's in which the number of herbivores increased dramatically in the region, and the area was considered to be overstocked. This has been attributed to the absence of lions in the area during that era (Pienaar 1963).

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During the 1960's, the area between the Luvuvhu and Limpopo Rivers did not form part of the Kruger National Park, but was occupied by human settlements. Although he mentions the simultaneous outbreak of anthrax in the Caprivi, Portuguese East Africa (Mozambique) and on farms to the south of the Kruger National Park, Pienaar (1961) makes no mention of any fatalities north of the Luvuvhu River. It can therefore, be assumed that the disease did not spread to this area, probably as a result of the vectors of the disease such as vultures (Anonymous 1979) not venturing into the region due to human activity. As a result, the size class distribution of baobabs in this northern study section does not show this overabundance of trees in the one to two metre girth size class. Smaller trees are most common in this section.

In both the northern and southern study sections a large proportion of trees have girths of less than 2 m. These baobabs are all less than 30 years old and it would appear that recruitment has not differed in the two study sections since the area north of the Luvuvhu River was incorporated into the Kruger National Park.

Recruitment of baobabs was better in the northern section for approximately 30 years before this, a period when the elephant density was higher in the south. However, it should also be noted that during this time, the populations of other browsers was also greater in the south. Between the turn of the century, the time the Shingwedzi Game Reserve was proclaimed until around 1940, recruitment of baobabs was generally better in the south. Comparisons of baobab recruitment rates in the two sections prior to this period, can give no indication of the influence of elephants on recruitment as elephant densities did not differ.

Unlike other herbivores, elephant numbers did not build up significantly until the mid 1900's. Baobab recruitment during the last 100 years showed fluctuations which coincide less with changes in the elephant population, than with the populations of other browsers. Evidence therefore, points towards other browsers such as antelope as having had the major impact on regeneration of baobabs. This study fails to provide conclusive evidence to indicate that elephant alone have played a deleterious role in the structuring of the baobab population of the Kruger National Park. The emphasis on the role of elephants in this process in the Kruger National Park is probably misplaced and it is unlikely that a reduction in the elephant population will have a significant impact on the regeneration of baobabs unless the numbers of other browsers are reduced simultaneously. The exclusion of fire may also have to be coupled with these herbivore reductions if the rate of regeneration of baobabs is to be improved (Ben-Shahar 1993; Hoft & Hoft 1995).

Messina Nature Reserve is situated approximately 120 km west of the Kruger National Park, and was formed to protect the baobab trees in the area. There are no elephant present in this reserve. A long term baobab monitoring programme has been in place since 1986, in order to determine if the population is sustainable. The programme makes use of two permanent line transects and two fixed point plots (Von Well 1997). The most recent monitoring was carried out during 1998 at which time, no baobabs were located in any of these sites which had not been present during monitoring in 1990 (De Jager, pers. comm.). Therefore, despite the absence of elephant, baobabs were not recruited into the population during this time. This suggests that either other herbivores are suppressing recruitment, or recruitment only occurs sporadically under certain ideal conditions. This is further proof that elephant are not solely, if at all responsible for suppressing baobab regeneration.

Sporadic recruitment of baobabs may be linked to the sporadic nature of viable seed production by the plant. In South Africa, baobab trees flower at 16 - 17 years old (Wickens 1980). Despite the large proportion (84 %) of baobab trees which produce flowers annually, seed production is far less regular (Swanepoel 1993). Trees sometimes produce immature pods with rudimentary seeds, but viable seeds are only produced in years when the pertinent conditions are correct (Swanepoel 1993). This fact has been borne out by four germination experiments in which as few as 8 %, 9 %, 7 %, and 1 % of seeds germinated, respectively (Wickens 1980)

The structure of the *Sterculia rogersii* population shows a relatively smooth decline in numbers from the abundant 1.75 m to 2.00 m class to the largest and smallest size classes. This indicates that *Sterculia rogersii* is less affected by short term windows of recruitment, but rather that the population has been shaped by a gradual decline in the suitability of the area as habitat for this species. The decline to the right of the peak on the chart is what would be expected in a healthy population, and can be attributed to the natural mortality of older trees. The decline in numbers to the left of the peak on the chart, will not be seen in a healthy population, and is indicative of a population in decline. This decline, is due to a steady reduction of recruitment of star-chestnuts into the population over time. The relatively small number of seedlings which were found in relation to numbers of larger plants, suggests that the future of the Kruger National Park population is a precarious one.

The recolonisation of the study area by elephants or other herbivores during the 1900's may have created an unsuitable environment for the establishment of individuals of *Sterculia rogersii* when compared with periods in the past. This recolonisation, however, did not occur at the same time in the two study sections. Therefore, if elephant or other large animal populations were the chief cause in the reduction of suitability of the habitat for this plant species, the population structure in these two areas would be vastly different for trees established during the period between 1930 and 1969.

In order to relate the population structure of star-chestnuts to historical events, information on the growth rate is required. The difficulties associated with this procedure have already been discussed. In the unlikely event of the rings in *Sterculia rogersii* wood representing a full years growth, each size class used in this study represents more than 100 years growth and the decline in the population would have started around 1000 years ago. Due to the lack of historical records for this area, prior to this century, no parallels can be drawn between animal populations and regeneration of *Sterculia rogersii* if the species is this long-lived. In such a case, it is highly unlikely that either man or the management of animal populations by man is responsible for this decline in the population.

If the rate of growth of *Sterculia rogersii* is faster, and approximates the more likely rate proposed in chapter one, the greatest proportion of trees in the population would have become established around the turn of the century. This coincides with the proclamation of part of the area as a game reserve. However, as is clear from the following discussion, comparisons between the two study sections fail to implicate elephant in the decline of the *Sterculia rogersii* population.

Of the trees which have become established this century, only in the 1 to 1.25 m size class do the northern and southern populations differ to any great extent. This is due to below expected numbers of trees in the northern section. According to this ageing scenario, recruitment of these trees would have taken place between 1929 and 1942. This roughly coincides with the recolonisation of the north of the Kruger National Park by elephant and also follows the build up of other herbivore populations after their decimation at the turn of the century. However, it is the northern and not the southern section where recruitment was poor. Elephant were absent from the northern area until 1969.

Except for this age class the populations in the north and the south do not differ markedly, especially with regards to trees established between the time of establishment of the area as a game sanctuary and the present. The older trees in the population would have been present during periods of low animal numbers during the latter part of the nineteenth century.

It can be argued that the population has not been regenerating in recent years as a result of increased herbivore pressures (elephants and others), but if herbivores were able to have such a profound impact on the population, massive differences in the northern and southern populations would be evident, due to the differing herbivore pressures on these populations during the first half of this century. This is not the case and it would therefore appear that neither elephant nor any other herbivore population is responsible for the decline in the *Sterculia rogersii* population.

The factor responsible for this decline is not restricted by the boundaries of the game sanctuary. Changes in the climate of the area would affect both populations equally, as would changes in the population of any vectors of pollination, or increased seed predation by invertebrates or rodents which are able to survive outside of the protected area. The frequency of fires in the area would also affect both populations equally.

Few studies have been published on the pollination ecology or breeding system of any *Sterculia* species. Taroda and Gibbs (1982), however, have investigated the floral biology and breeding system of the Brazilian species, *Sterculia chicha*. It was found that the flowers of this species are visited by a diverse array of insects, of which, species of Diptera are the most common. It was also discovered that the species of Diptera were the only insects able to carry sufficient pollen to facilitate pollination. They have determined that *Sterculia chicha* is self-incompatible as are the related *Theobroma cacao* and the West African *Cola nitida*. The other species of *Sterculia* which occur in Brazil have flowers resembling that of *Sterculia chicha*, and species of Diptera are also the pollination vectors. The flowers of *Sterculia rogersii* are similar in shape, size and colour to those of *Sterculia chicha*. It is therefore, probable that similar vectors facilitate pollination in *Sterculia rogersii*. If *Sterculia rogersii* possesses a self-incompatibility mechanism as do other species in the Sterculiaceae family, then pollination would not be possible in the absence of this vector.

However, the presence of fruit on *Sterculia rogersii* trees in the Kruger National Park indicates that pollination is in fact taking place, further evidence of which is the presence of a few trees, albeit a small proportion of the total population in the smallest size class. It is possible that insufficient fruit is being produced to provide enough seed to maintain the population, which may be as a result of too few flowers being successfully pollinated. The possibility also exists that sufficient seed is being produced, but it is being destroyed before it germinates.

Another possible explanation for the declining recruitment of the *Sterculia rogersii* population may be an increase in fire frequency this century. Fire has a profound effect on the dynamics of savannah ecosystems, and many studies have shown that the exclusion of fire can alter the grass-tree equilibrium in favour of trees (Bond & Van Wilgen 1996). Fire has been shown to prevent the regeneration of woody plants (Leuthold 1996) and with frequent fire damage, even in the absence of elephant effects, *Baikiaea plurijuga* woodlands are likely to decline (Ben-Shahar 1996). Brynard (1964) summarises the history of fire in the area occupied by the Kruger National Park as follows:

Little is known of the occurrence of fire in the area before the arrival of the bushmen, the earliest human inhabitants. They set fire to the veld occasionally to assist them during hunting. Bantu tribes and later (1838) voortrekkers from the south became established in the Lowveld. Both the Bantu tribes and white hunters used fire as a means of attracting game to hunting grounds. Thus began a period in which the vegetation was frequently burned.

During the tenure of Stevenson-Hamilton as warden of the Sabie and Shingwedzi Game Reserves in the early 1900's, both areas were devastated almost annually by fires which entered the reserves from outside the borders where they had been started by natives, hunters and stock farmers. Burning of the vegetation within the reserves also took place both deliberately and accidentally.

At the time of proclamation of the Kruger National Park in 1926, annual veld fires were still the norm, as no means of preventing fires from crossing the reserves' boundary from outside had yet been developed. Reports of disastrous fires, fanned by strong winds, burning deep into the reserve and lasting for two weeks or longer were made by the warden. A policy was also adopted whereby areas which had escaped accidental fires were burnt annually.

It was only in 1934, when firebreaks were prepared for the first time, that there was some means of controlling fires in place. Sandenbergh opposed veld burning in all its forms as he felt that it had a negative impact on the vegetation. When he became warden in 1946, burning of the veld was stopped, and in 1948 he brought in a new policy whereby veld was burned no more than once in five years and only after the first good spring rains.

In 1954, a rotational burning programme was introduced. Thereafter, burning of the veld took place at least every three years until 1992 when the fire management policy was changed from one of active prescribed burning on a fixed cycle to one of moving towards a more flexible and variable pattern of burning (Van Wilgen *et al*. 1998).

From the available evidence, it appears as though the arrival of people in the area increased the occurrence of fire dramatically. Until very recently, the frequency of burning has remained high. Although parts of the Lowveld and the area now occupied by the Kruger National Park were inhabited much earlier, even in 1903, what is now the north of the

Kruger National Park was uninhabited by whites and only very sparsely inhabited by natives (Stevenson-Hamilton 1937). Therefore, the increase in frequency of burning of the veld concomitant with human settlement probably only began during this century in the north of the Kruger National Park.

This increase in fire frequency by man has resulted in major changes in the botanical composition and structure of the area (Brynard 1964). The forest, and scrub forest vegetation which was once present in the area has been replaced by vegetation which has greater resistance to fire and drought (Brynard 1964). These frequent fires destroyed large numbers of trees, and even reduced the numbers of some species to such an extent that they neared extinction in the Kruger National Park (Brynard 1964). It is probable that the poor regeneration rates of *Sterculia rogersii* in recent times is as a result of the species` susceptibility to fire.

The susceptibility of trees to fire is dependant on the bark as well as any fire resistance strategies (Whelan 1995). The bark of *Sterculia rogersii* is rather thin (Van Wyk 1974). The bark of trees of this species is also regularly removed by browsers such as elephant. Most specimens have a canopy which is low above the ground and the fruits and flowers are therefore, borne at a height which makes them susceptible to destruction by fire. These characteristics indicate that the species has not adapted to withstand fire.

Tree species with thin bark are more susceptible to fire for two reasons. Thin bark is more easily destroyed by fire, leaving an open passage for bacterial infection, woodboring insects and further damage by fire (Brynard 1964). The time taken for cambial cells to reach a lethal temperature during a fire is also directly proportional to the thickness of the bark (Whelan 1995). Trees which have had bark removed by animal activity are therefore, also more susceptible to mortality by fire (Bond & Van Wilgen 1996). Mortality due to fire is also greater in smaller plants due to the allometric relationship between bark thickness and stem diameter (Bond & Van Wilgen 1996; Whelan 1995). Different types of bark also have different insulating properties (Whelan 1995). If bark recovery from a fire is not complete at the time of a successive fire, plant survival is affected (Whelan 1995). Frequency of fires as well as season of burning therefore, affects the ability of plants to survive fires.

In short, *Sterculia rogersii* is a species which does not appear to be adapted to withstand the onslaught of regular fires. The increase in the frequency of fires in the Kruger National Park area in recent times, may have had an effect on the population of this species. The susceptibility of small trees to fire may explain the poor regeneration of the population, while larger trees are able to survive. It is therefore possible that the structure of the *Sterculia rogersii* population in the Kruger National Park has been shaped by fire. It has not been shaped by elephants, although the browsing of these trees by elephants may have played a role by making the trees more susceptible to fire.

More research is required to determine if the cause of the decline in regeneration of the *Sterculia rogersii* population is due to an increase in fire frequency. A study of the pollination ecology and breeding system of *Sterculia rogersii* may also provide answers, but it is clear that large herbivores, especially elephant are not responsible for this disturbing trend.

CONCLUSION

The role of elephant utilisation in structuring the populations of various tree species in Africa has been heavily emphasised (Barnes 1983; Ben-Shahar 1993; Ben-Shahar 1996; Hoft & Hoft 1995; Tchamba 1995; Tchamba & Mahamat 1992). This is probably as a result of the apparently destructive feeding strategy of elephants (Prins & Van der Jeugd 1993). This has even led to attempts to find relationships between elephant populations and the age of trees (Barnes *et al.* 1994) and has also led to hypotheses suggesting cyclical interactions between elephants and trees (Caughley 1976). The results of this study suggest that in the Kruger National Park, more emphasis should be placed on determining the conditions required for successful recruitment of trees into the population as any role played by elephant is only of minor importance.

CHAPTER 5

UTILISATION OF *ADANSONIA DIGITATA* AND *STERCULIA ROGERSII* BY ELEPHANT IN THE KRUGER NATIONAL PARK

INTRODUCTION

Overwhelming evidence has emerged in the latter part of this century to indicate that elephants are major agents of habitat change. The effect of elephants on the habitat increases in areas where restrictions are placed on their movements and the control of elephant populations becomes necessary. Proper management of elephant populations however requires information on the trends of the populations and especially their patterns of resource utilisation (Ben-Shahar 1993). The effect of elephant utilisation on a tree is dependant on the type of damage, the ability of the tree to recover, the role played by the tree in the plant community and the relationship between the plant community and other ecosystem components (Engelbrecht 1979).

In certain cases, biomass removal by elephant has shown that they prefer particular age groups of certain plant species (Ben-Shahar 1993; Tchamba 1995), while in others, elephant have shown no preference for any size class of tree (Tchamba & Mahamat 1992). The amount of biomass which is removed from trees by browsing elephants also varies considerably in different areas. Ben-Shahar (1993) found that biomass removal from the canopy of trees in northern Botswana was low. Tchamba and Mahamat (1992) found that elephant had browsed 97 % of observed trees belonging to a number of species. Only 53 % of these trees in Kalamaloue National Park, Cameroon, had had less than 75 % of their biomass removed by elephant. In Waza National Park, Cameroon, 55 % of trees were undamaged, 36 % had less than three quarters of the biomass removed and only 9 % more than 75 % of biomass removed (Tchamba 1995).

The aim of this section of the study was to determine the patterns of elephant utilisation of *Adansonia digitata* and *Sterculia rogersii* in the Kruger National Park, to quantify this utilisation and to ascertain whether elephant browsing interferes with the progression of seedlings growing to mature trees.

METHODS

Adansonia digitata

The utilisation of 1314 baobab trees which occur in the study area has been assessed. This was achieved by using two methods. The first was an estimate of the percentage of the total bark which had been stripped from each tree and has been referred to as bark stripping. The second method was to subjectively classify the extent of utilisation into six categories in order to distinguish between superficial and deeper utilisation. This is the depth of utilisation scale, and trees were classified by using the following criteria:

Type 0	Undamaged trees.
Type I	Slightly scarred trees.
Type II	Trees which had been ringbarked, but damage was superficial.
Type III	Deeply scarred trees.
Type IV	Trees whose shape has been radically altered by utilisation.
Type V	Dead trees.

Sterculia rogersii

Similar methods were used to assess the utilisation of 1163 *Sterculia rogersii* trees which occur in the study area. The first method was carried out by determining the percentage of the tree volume from which plant material had been removed. This is the estimated percentage of biomass which was missing from an imaginary intact plant (Ben-Shahar 1993). Due to this species being deciduous (Coates Palgrave 1984; Van Wyk 1984), biomass was only considered missing if the removal of branches and not only leaves had occurred. This has been referred to as biomass removal.

A subjective assessment of the severity of damage was also carried out for this species using a six point classification of the intensity of utilisation. Once again this enabled a distinction to be made between superficial and deeper damage. The categories which were used for the assessment of the depth of utilisation of star-chestnuts were based on the following criteria:

Type 0	Undamaged trees.
Type I	Trees which showed signs of light browsing.
Type II	Trees with entire branches removed by browsing.
Type III	Trees with some but not all stems broken off.
Type IV	Trees with all stems broken off.
Type V	Dead or uprooted trees.

RESULTS

Adansonia digitata

Bark stripping

Bark stripping of baobab trees has been classified into five percent increments and the northern and southern populations compared (Fig. 9). In the northern section, the majority of trees have either none, or only small amounts of bark removed, but in the south trees have generally been stripped of more bark. The difference between the populations is highly significant (Kolmogorov-Smirnov two-sample test, $D_{max} = 0.34$; $P < 0.001$).

The average amount of bark which has been removed from the baobab trees is 18.37 %. On average, baobabs in the southern section (22.96 %) have had more bark stripped than those in the north (9.12 %) (two-sample t-test assuming unequal variances, $t = 15.01$; df = 1201; $P < 0.001$)

The mean percentage of bark stripping of each size class has been plotted against the midpoint of the size class in Figure 10. Trees with a girth larger than 15 m have been lumped together due to the small size of the sample. The relationship between debarking

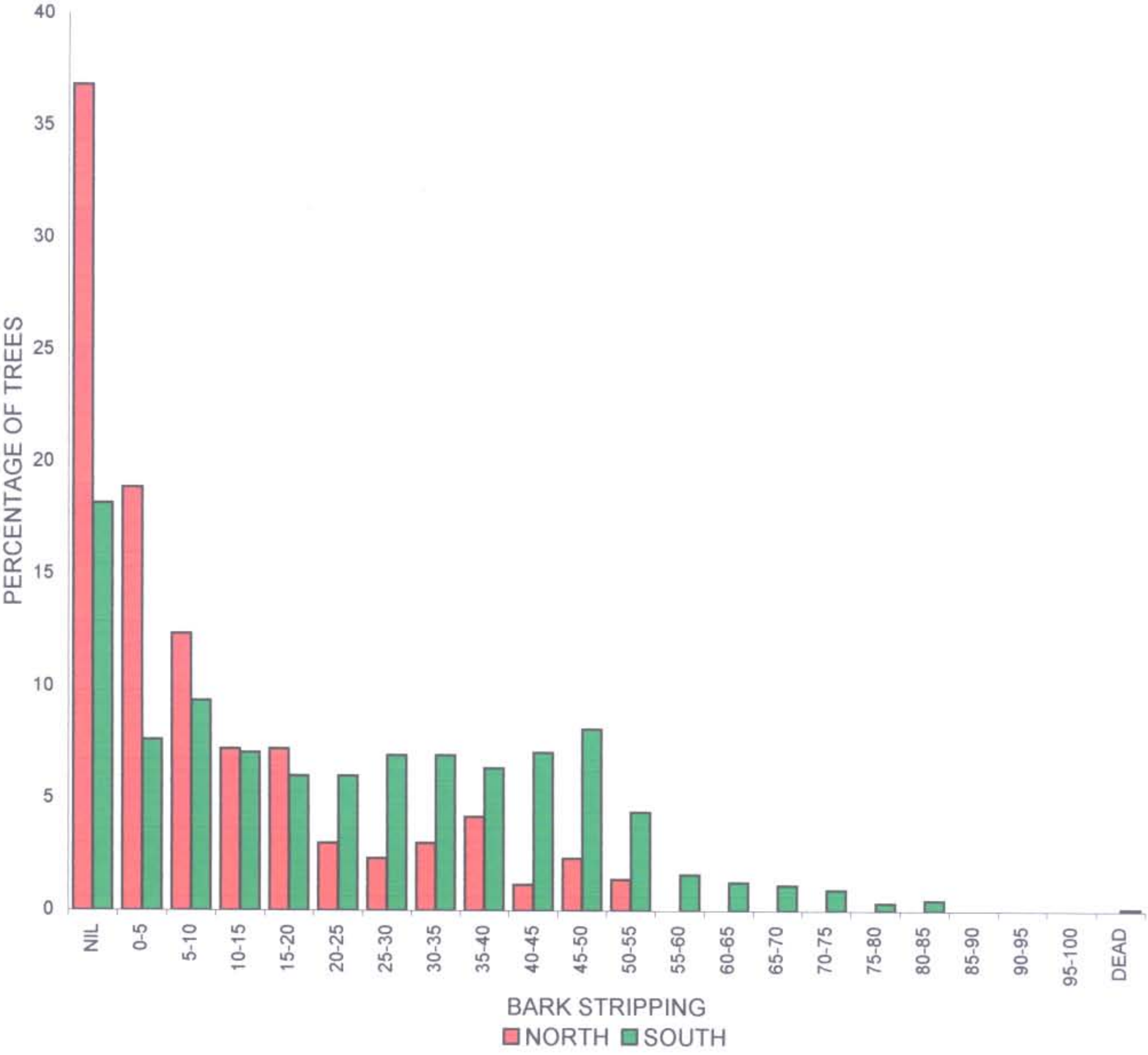


Fig. 9: Bark stripping (%) of *Adansonia digitata* in the northern and southern study sections of the Kruger National Park.

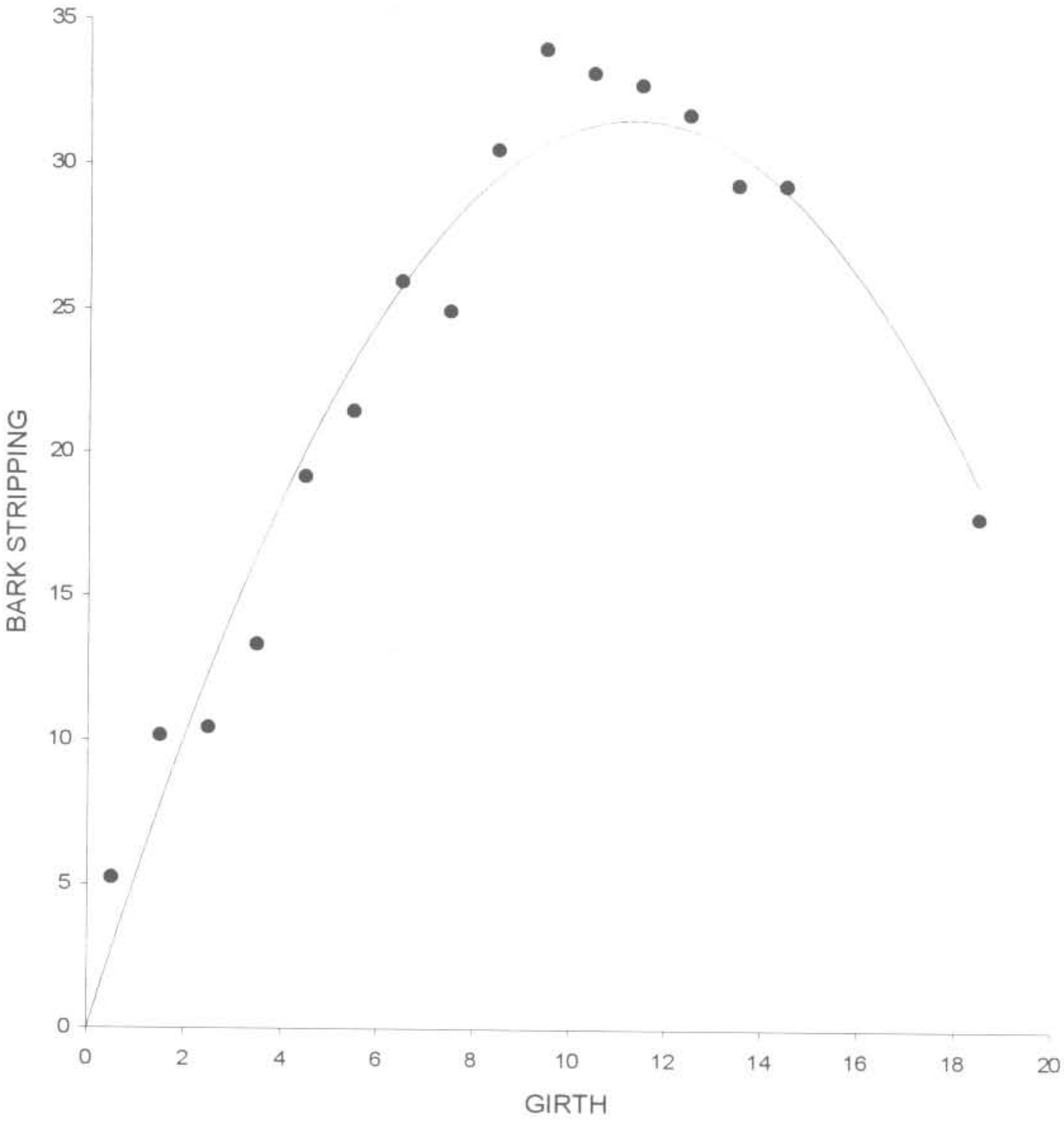


Fig. 10: Bark stripping (%) of *Adansonia digitata* in the Kruger National Park as a function of girth (m). Data for trees with a girth larger than 15 m have been pooled due to the small sample. $y = -0.25x^2 + 5.58x - 0.04$; ($r^2 = 0.96$; $X^2 = 5.15$; $P < 0.05$).

and baobab girth is described by the polynomial regression $y = -0.25x^2 + 5.58x - 0.04$ ($r^2 = 0.96$; $X^2 = 5.15$; $P < 0.05$).

The proportion of freshly debarked trees is 22 % in the northern section, which is considerably higher than the 7 % which have recently been debarked in the south (difference of proportions on freshly debarked trees, $z = 7.92$; $P < 0.001$).

Depth of utilisation

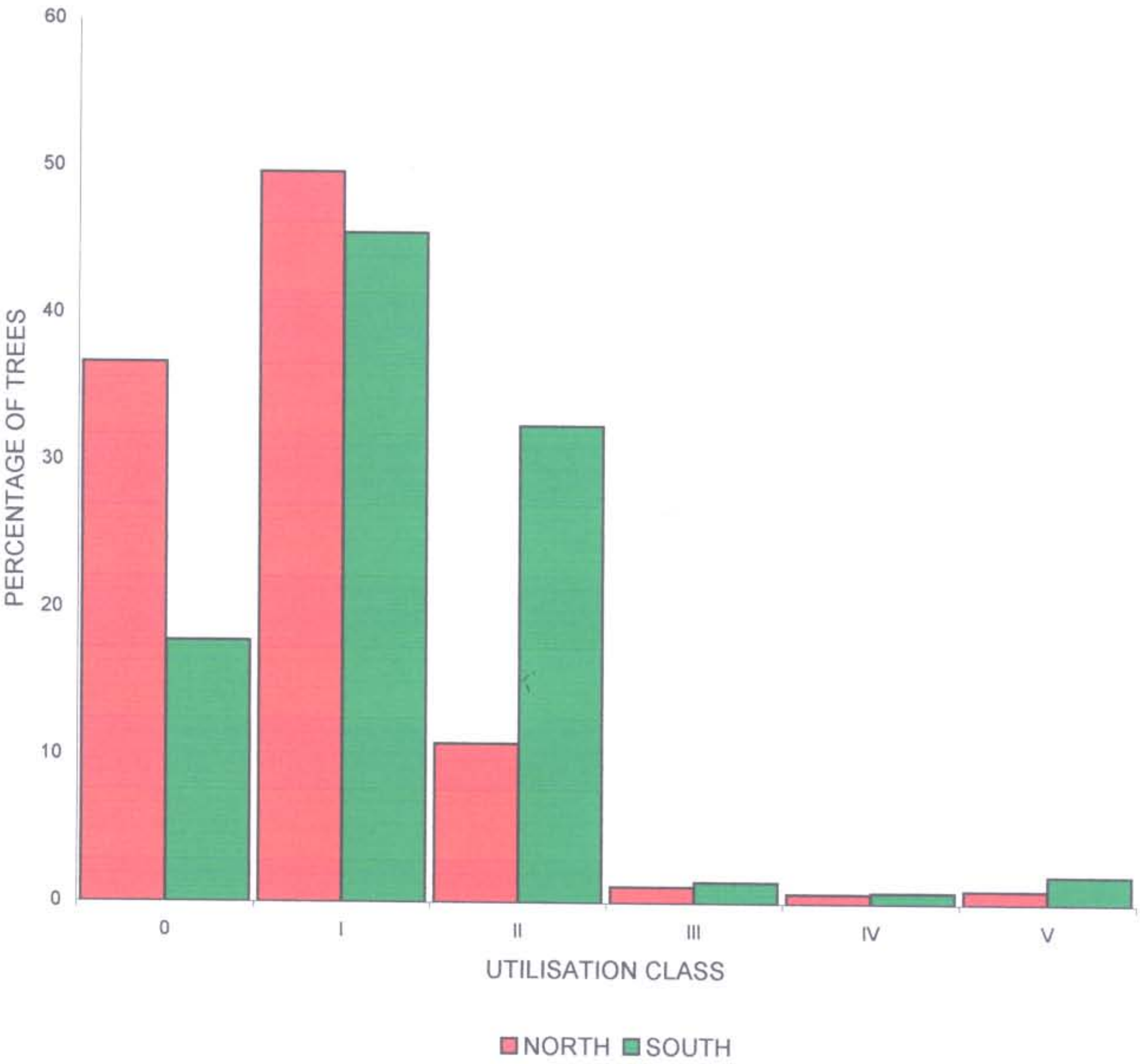
The depth of utilisation classification shows that the highest proportion of trees have been slightly scarred (Type I), with the intensity of utilisation dropping drastically into the more severe categories (Fig. 11). Utilisation is significantly different in the two study sections (Kolmogorov-Smirnov two-sample test, $D_{\max} = 0.23$; $P < 0.001$).

In the northern section, 37 % of baobab trees show no signs of utilisation, but far fewer trees (18 %) in the south are unutilised (difference of proportions on the percent undamaged, $z = 7.53$; $P < 0.001$).

This depth of utilisation scale has also been used to express the total amount of damage incurred by baobab trees in each region by using a damage score system (Swanepoel 1993). Each tree has been allocated a score from 0 (undamaged) to 5 (tree dead) based on utilisation. A damage score has then been calculated for each region and expressed as a percentage of the maximum possible score which could be attained in that region. Damage scores have been calculated using the following equation:

$$\text{Damage score} = (\text{sum of individual damage scores} \div \text{total possible damage score}) \times 100$$

The damage score for the baobab population in the entire study area is 22.54, with 16.44 and 25.54 the scores for the northern and southern section respectively. The damage score for the southern section is significantly higher than the score for the northern section (difference of proportions, $z = -8.29$; $P < 0.001$).



0: TREE UNDAMAGED.
I: TREE SLIGHTLY SCARRED.
II: TREE RINGBARKED, BUT DAMAGE SUPERFICIAL.
III: TREE DEEPLY SCARRED.
IV: TREE SHAPE RADICALLY ALTERED BY UTILISATION.
V: TREE DEAD.

Fig. 11: Depth of utilisation of *Adansonia digitata* in the northern and southern study sections of the Kruger National Park.

The severity of utilisation as a function of girth at breast height has also been determined using the damage score system described above. Due to the small number of trees in the data set with a girth larger than 15 m, these trees have all been placed in one size class. As no size data is available for dead trees, these trees have been excluded from these calculations. The scale therefore only has five points and thus the maximum score allocated to any tree is four. The damage scores for the various size classes are given in Table 2.

Regression analysis was used to determine if the degree of utilisation is affected by tree size (Fig. 12). The regression of the midpoint of each size class on the damage score of the size class has been calculated and shows that the relationship between baobab circumference and the severity of utilisation can be described by the polynomial regression: $y = -0.20x^2 + 4.86x + 10.01$ ($r^2 = 0.94$; $X^2 = 2.22$; $P < 0.05$).

Sterculia rogersii

Biomass removal

Biomass removal of *Sterculia rogersii* has been classified based on five percent increments of the percentage of biomass which had been removed from each tree. There are also categories for unutilised trees and dead or recumbent trees (Fig. 13).

In the northern section, the largest proportion of trees (21.65 %) has had less than five percent of the biomass removed. In the south, the largest proportion of trees (17.83 %) show no signs of utilisation. Only 13.25 % of trees in the north are unutilised. The distributions of utilisation of these two populations does however not differ significantly (Kolmogorov-Smirnov two-sample test, $D_{\max} = 0.057$; $P > 0.05$).

In the northern section, the amount of biomass which has been removed from trees has a mean of 18.54 % and in the southern section 21.05 %. The difference between these two means is not significant (two-sample t-test assuming unequal variances, $t = -1.91$; df = 1112; $P > 0.05$)

Table 2

Damage scores of tree size classes

ADANSONIA DIGITATA		*STERCULIA ROGERSII*	
GIRTH(m)	DAMAGE SCORE	GIRTH (m)	DAMAGE SCORE
0-1	10.76	0.00-0.25	2.08
1-2	19.42	0.25-0.50	15.79
2-3	20.57	0.50-0.75	22.50
3-4	24.19	0.75-1.00	24.38
4-5	27.68	1.00-1.25	29.12
5-6	28.71	1.25-1.50	34.92
6-7	34.14	1.50-1.75	33.71
7-8	34.64	1.75-2.00	36.15
8-9	35.92	2.00-2.25	34.13
9-10	42.31	2.25-2.50	30.23
10-11	41.95	2.50-2.75	32.53
11-12	38.75	2.75-3.00	42.18
12-13	38.16	3.00-3.25	35.42
13-14	34.38	3.25-3.50	34.09
14-15	38.64	3.50-3.75	35.14
>15	32.69	3.75-4.00	41.67
		>4	32.24

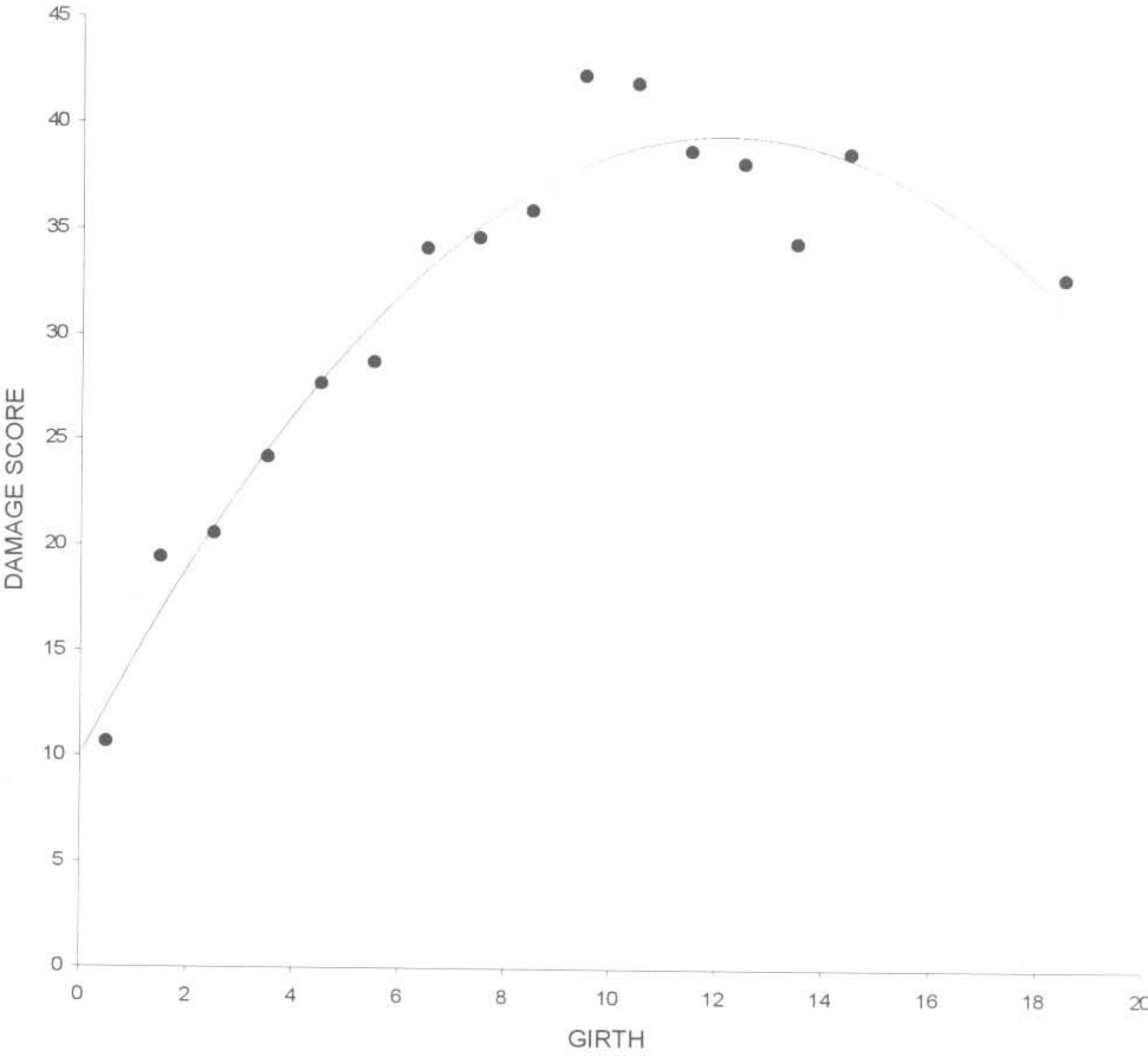


Fig. 12: Damage scores of *Adansonia digitata* in the Kruger National Park as a function of girth (m). Data for trees with a girth larger than 15 m have been pooled due to the small sample. $y = -0.20x^2 + 4.86x + 10.01$; ($r^2 = 0.94$; $X^2 = 2.22$; $P < 0.05$).

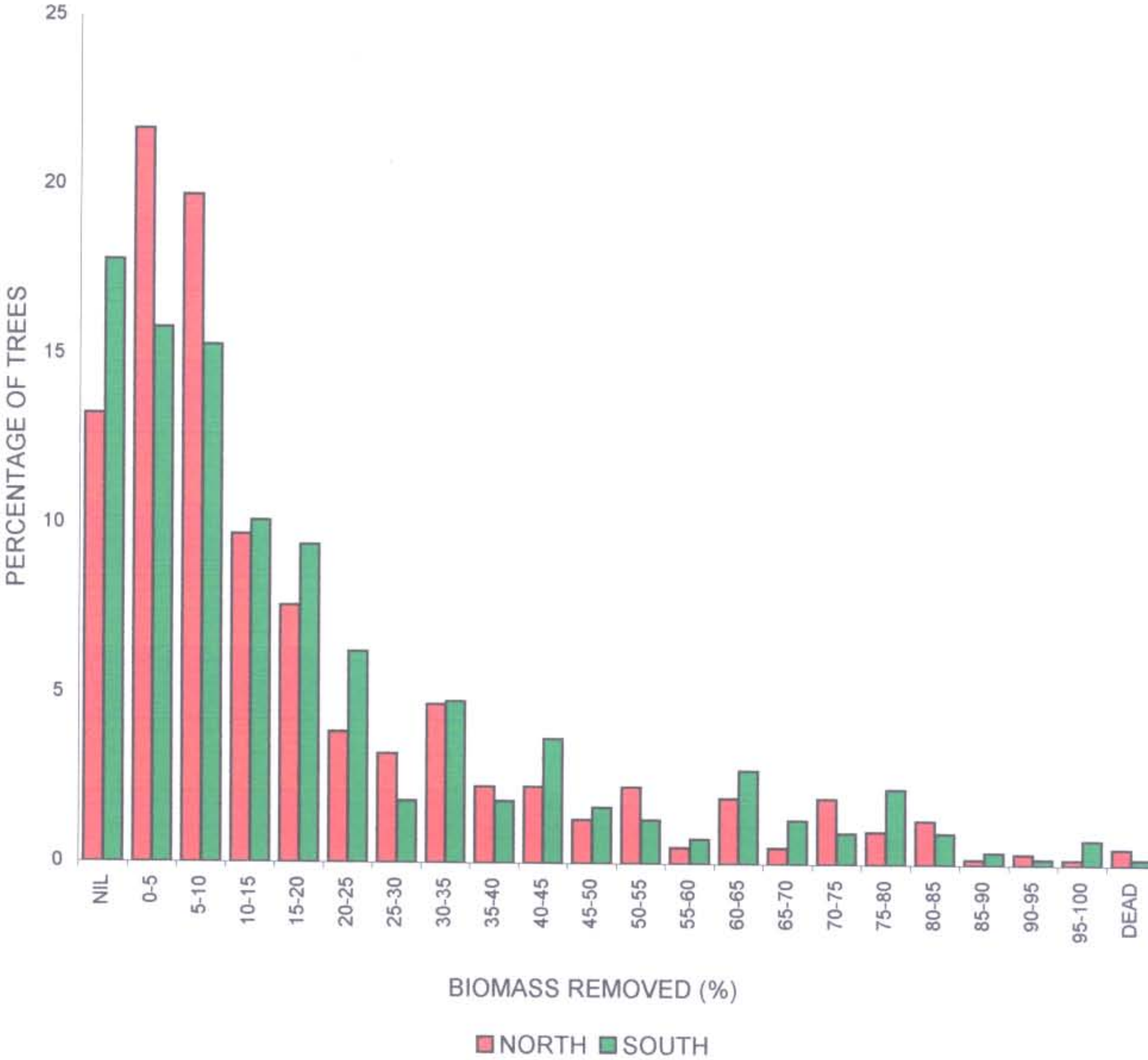


Fig. 13: Utilisation of *Sterculia rogersii* in the northern and southern study sections of the Kruger National Park.

The mean percentage of biomass removed per tree in each size class has been plotted against the mean girth of tree in the size class in Figure 14. Trees with a girth larger than 4 m have been lumped together due to the small size of the sample in this size category. The regression analysis of mean percentage biomass removed on mean girth shows that a logarithmic relationship exists between tree size and amount of browsing ($r^2 = 0.69$; $X^2 = 12.69$; $P < 0.05$).

The proportion of freshly utilised trees is 8.56 in the northern section, but only 2.76 in the south (difference of proportions on freshly utilised trees, $z = 4.21$; $P < 0.001$).

Depth of utilisation

Classification according to the depth of utilisation scale shows that the majority of star-chestnuts have been lightly browsed (Type I utilisation), while only a small proportion of trees fit the heavier utilisation categories (Fig. 15). The severity of utilisation shows significant differences in the two regions (Kolmogorov-Smirnov two-sample test, $D_{\max} = 0.106$; $P < 0.005$).

In the southern section, 18 % of trees show no signs of utilisation, but only 13 % in the north are unutilised (difference of proportions on the percent undamaged, $z = -2.16$; $P < 0.05$).

Each tree has been allocated a score from 0 (undamaged) to 5 (tree dead or uprooted) based on this scale. The damage score system which has already been described has then been used to compare the severity of utilisation in the various regions.

The damage score for the entire study area is 25.95. Trees in the northern section (24.75) are not as severely damaged as those in the southern section (27.32) (difference of proportions, $z = -2.23$; $P < 0.05$).

The depth of utilisation as a function of girth has also been determined using the damage score system. Due to the small number of trees in the data set with a girth larger than 4 m,

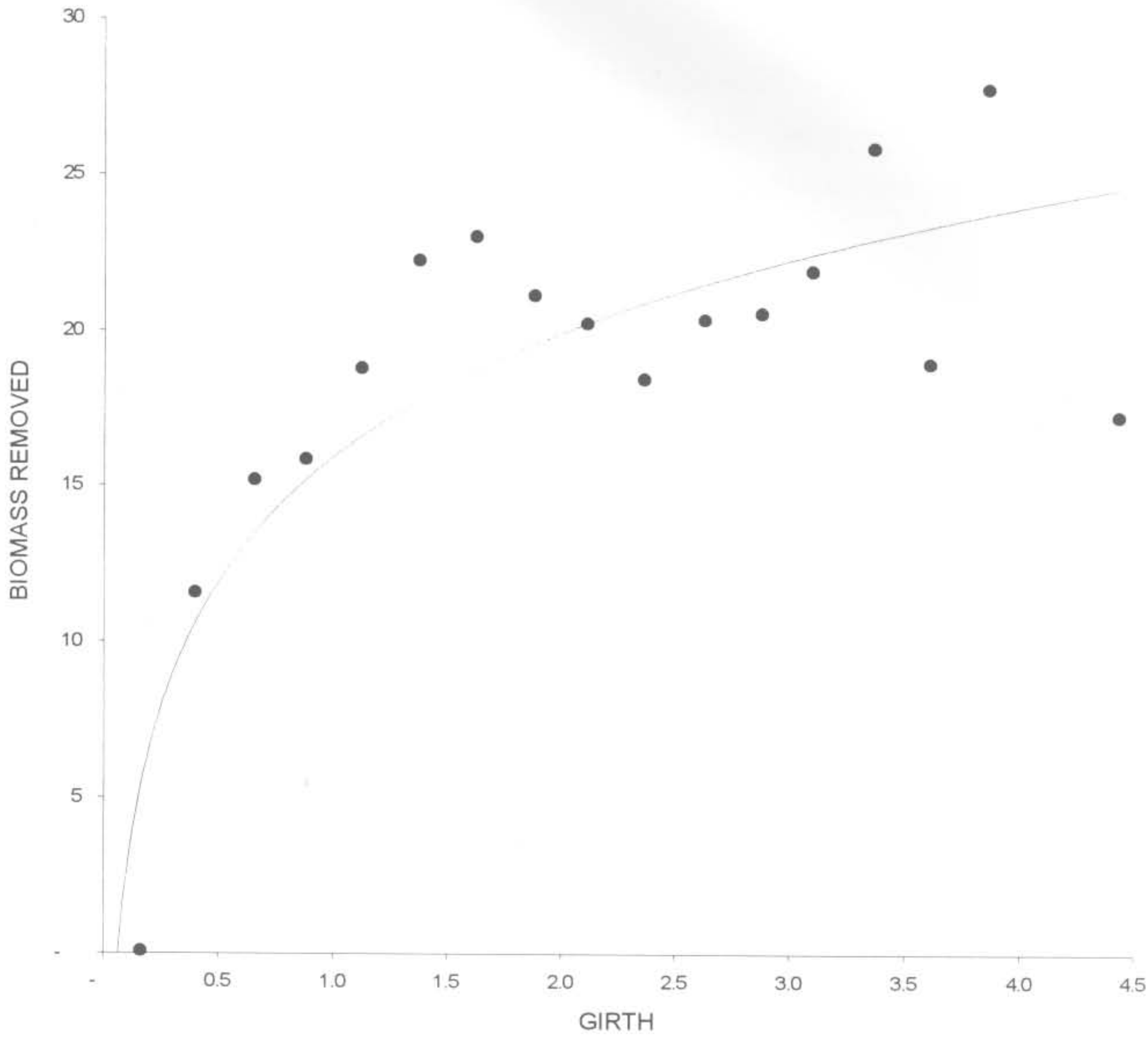
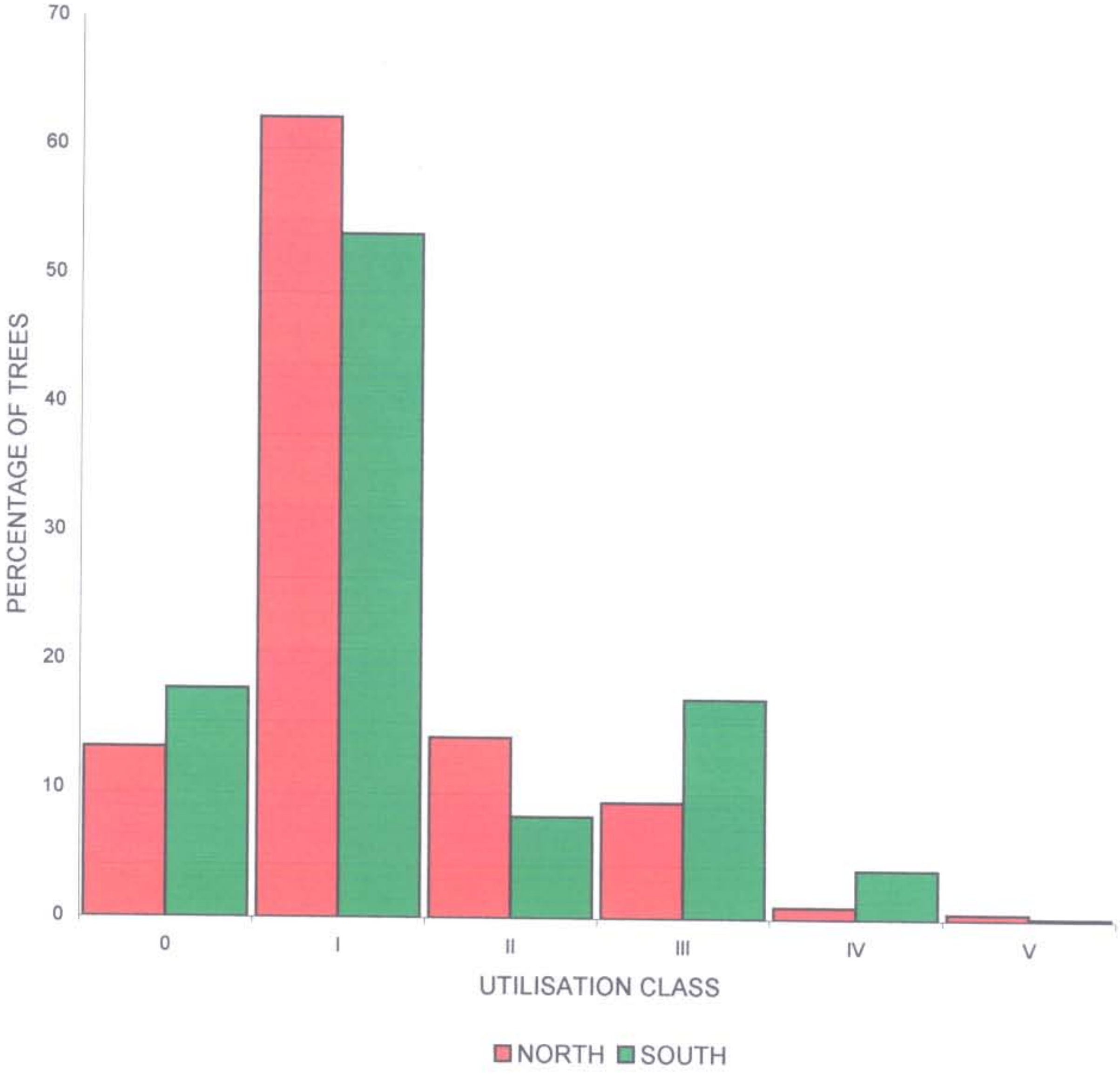


Fig. 14: Utilisation (%) of *Sterculia rogersii* in the Kruger National Park as a function of girth (m). Data for trees with a girth larger than 4 m have been pooled due to the small sample. $y = 5.76\text{Ln}(x) + 15.92$; ($r^2 = 0.69$; $X^2 = 12.69$; $P < 0.05$).



0: TREE UNDAMAGED.
I: TREE LIGHTLY BROWSED.
II: TREE WITH BRANCHES REMOVED BY BROWSING.
III: TREE WITH SOME STEMS BROKEN OFF.
IV: TREE WITH ALL STEMS BROKEN OFF.
V: TREE DEAD OR UPROOTED.

Fig. 15: Depth of utilisation of *Sterculia rogersii* in the northern and southern study sections of the Kruger National Park.

these trees have all been placed into one size class. As no size data are available for dead trees, dead trees have been excluded from these calculations. Therefore, the scale once again only has five points and thus the maximum score allocated to any tree is four. The damage scores for the various size classes are given in Table 2.

The regression of the midpoint of each size class on the damage score of the size class has been calculated (Fig. 16). This regression analysis shows that a logarithmic relationship exists between the size of *Sterculia rogersii* trees and the severity of utilisation ($r^2 = 0.84$; $X^2 = 9.35$; $P < 0.05$).

DISCUSSION

Adansonia digitata

Bark stripping is greater in the southern section than in the north. Most trees in the northern section have had either none or only small amounts of bark stripped from them, while trees in the south have generally been more heavily utilised. Between the early 1930's, when elephant elephant first began to recolonise the area, until 1969, when the northern section was proclaimed as part of the Kruger National Park, elephant numbers were greater in the south. The trees in the southern section have thus been exposed to elephant utilisation for a longer period than those in the north. It is therefore to be expected that trees in the southern section would have been more heavily utilised. Utilisation of baobabs such as debarking results in scarring of the trees. The scars are noticeable even after new bark has covered the damaged area. These scars persist for a long time, and in many if not all cases outlive the trees themselves. Much of the scarring which has been recorded occurred when elephant densities were greater south of the Luvuvhu River. The evidence of utilisation during this era is still present on the baobab trees today.

The average amount of bark stripped from baobabs is almost 20 %. Although some trees appear to have had their stems completely stripped of bark, in many cases, these trees have been regularly used over time, with the trees of similar size around them, not being utilised at all. Elephants tend to concentrate their foraging on particular trees (Swanepoel 1993).

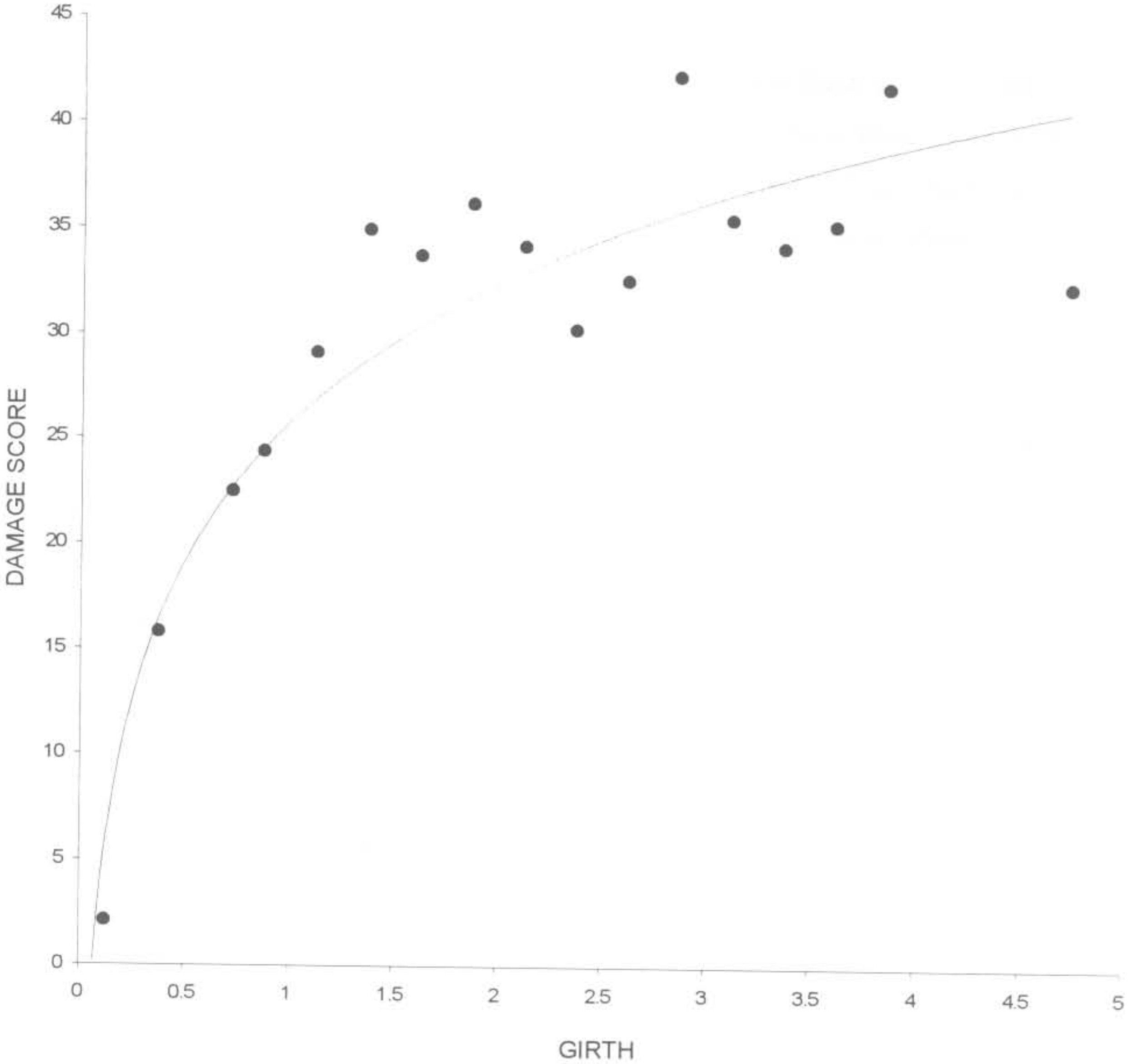


Fig. 16: Damage scores of *Sterculia rogersii* in the Kruger National Park as a function of girth (m). Data for trees with a girth larger than 4 m have been pooled due to the small sample. $y = 9.48\text{Ln}(x) + 25.78$; ($r^2 = 0.84$; $X^2 = 9.35$; $P < 0.05$).

This phenomenon may be linked to genetic differences present in these trees (Wickens 1982). Although some trees show signs of heavy utilisation, the large number of unutilised or slightly utilised trees results in a mean bark stripping value of 18.37 %. Although this seems a substantial amount, much of this is damage from which the trees appear to have recovered.

The age of utilisation of trees has been recorded in four categories based on the current appearance of the damaged plant parts. The oldest category (Class D) consists of scars on the tree, where damage has been completely covered by new bark. The tree has thus recovered fully from this damage. In a study of elephant impact on *Sclerocarya caffra* trees, Coetzee *et al.* (1979) recorded trees with old debarked areas which had been completely covered by new bark, as unscarred. Many baobabs which occur outside of game reserves, in areas where elephant are absent also show class D utilisation. This indicates that these scars are vestiges of a bygone era when elephant still occupied these regions. Elephant have probably been absent from some of these areas for more than 100 years, providing some indication of the length of time these scars persist on the trees. More than two-thirds of bark stripping is classified as class D utilisation.

For these reasons, class D utilisation has been omitted and the calculations repeated. The mean percentage of bark stripped from baobabs is then only 6.06. The southern study section (6.55 %) is still more heavily utilised than the north (5.07 %) (two-sample t-test assuming equal variances, $t = -2.87$; df = 1291; $P < 0.005$). The difference in the amount of bark stripping in the two sections is not as great. This is further evidence to indicate that these differences are due mainly to utilisation in the past when elephant densities in the two sections differed. Bark stripping of baobabs is therefore not very severe, even less so when their ability to recover from this utilisation is taken into consideration.

Baobabs have a remarkable ability to recover from damage (Wickens 1982), quickly replacing lost bark (Coates Palgrave 1956). Their robustness and vitality is legendary (Coates Palgrave 1956; Piearce *et al.* 1994). Baobabs readily withstand mechanical injury inflicted by the carving of inscriptions or harvesting of their bark (Piearce *et al.* 1994). Trees do not die even when ring-barked (Barnes 1980). While some baobabs are able to survive considerable damage, the resources required for recovery could have a negative effect on the long-term survival of these trees (Swanepoel 1993). Trees from which large amounts of bark have been removed are more noticeable than unutilised trees and thus, to the casual observer, the population may appear to be subjected to more utilisation than is actually the case. This perception may also stem from observations being made from roads, where elephant damage is perceived to be greater (Coetzee *et al.* 1979).

The proportion of freshly debarked (class A) trees in these two regions indicates that in recent times, the situation has changed drastically. Bark stripping of these trees, would have occurred not more than a year prior to the study, as extended exposure of scar tissue to sun and rain causes a loss in colour, making older damage discernible from new damage. The amount of bark which has recently been removed from trees in the northern section is significantly higher than in the southern section. This indicates that elephant foraging is now concentrated in the northern section of the study area.

Elephants tend to congregate around permanent water during the dry season (Van Wyk & Fairall 1969). The northern section is flanked by both the Luvuvhu and the Limpopo Rivers, and most of this section is therefore, relatively close to perennial water. In contrast, much of the larger southern section is a considerable distance from water, and during the dry season, elephants foraging in these parts will have to travel long distances to obtain water. This resultant higher elephant density is the likely explanation for the higher incidence of fresh bark stripping in the northern section. Swanepoel (1993) found that elephant foraging on baobabs is related to the position of the trees relative to perennial water, with trees further from water being less affected. The utilisation of baobabs relative to water is discussed in Chapter 8.

Independent studies in Lake Manyara and Ruaha National Parks, Tanzania both found an increase in bark damage with increasing baobab circumference (Weyerhauser 1985). Weyerhauser (1985) does not indicate whether older scars were included in the studies or not. The damage , which is expressed as a percentage of circumference, may or may not therefore, be cumulative. Swanepoel (1993) could not find any indication that elephants in Mana Pools National Park, Zimbabwe concentrate on any particular size of tree. The results of this study indicate that elephants in the Kruger National Park concentrate their foraging on the larger baobab trees. The severity of elephant damage and the amount of bark stripping both increase with an increase in the girth of trees. This trend is similar to that shown in the Tanzanian parks mentioned.

The top parts of the larger baobabs are not available to elephants as they are out of reach. Therefore, once a baobab reaches a certain height, the amount of bark an elephant can strip from it, in proportion to its size, reaches a limit. Any further growth of the tree thus results in a decrease of the proportion of bark which has been removed from the tree. This relationship causes the curve which plots bark stripping as a function of girth to dip after peaking at the 9 - 10 m size class. The presence of plant material on the larger trees which is unavailable to elephants causes the curve to dip. The relationship between bark stripping and size could therefore, be different to that indicated by the regression analysis. A repeat of the regression analysis of the mean percentage of bark stripping on baobab girth has therefore been carried out, this time only using data from trees with a girth of 10 m or less. Trees in the 9-10 m size class have the greatest percentage of bark removed and this is where the curve peaks. As expected, this regression shows a strong linear relationship between girth and bark stripping ($r^2 = 0.98$; $n = 10$; $P < 0.001$), and indicates a trend shown by elephants of selecting larger trees.

The more severe utilisation of the larger trees could be as a result of these trees providing an opportunity for more than one elephant to forage simultaneously (Swanepoel 1993). During the hottest part of the day, elephants often stand under shady trees to escape the heat (Smithers 1983). Baobabs, although deciduous, provide good shade in summer, and thus provide elephants with a resting place. While escaping the heat, these animals also have ample opportunity to forage on the trees. Only the large baobabs provide this opportunity, thus resulting in a trend of increased bark stripping of and more severe damage to larger trees.

By concentrating their foraging activities on the larger baobab trees, elephant are having a smaller influence on the regeneration class. This situation is less damaging to the long-term survival of the baobab population in the Kruger National Park which is dependant on regeneration.

The assessment of utilisation depth shows that utilisation of baobabs by elephants in the Kruger National Park is generally superficial with very few trees being severely damaged. Damage to most baobabs therefore, consists only of bark stripping, which is not severe enough as to threaten the survival of either individual plants or the population. Baobabs are generally able to recover well from this superficial damage. As with bark stripping, the damage scores of baobabs also indicate that trees in the southern section have been more severely damaged than those in the north. Here again, the land use history of the two sections provides a plausible explanation. For this reason, utilisation depth in the two sections have been compared, omitting the oldest (class D) utilisation. The utilisation of baobabs does not differ significantly in the two regions (Kolmogorov-Smirnov two-sample test, $D_{max} = 0.06$; $P > 0.05$).

Baobab trees which have been very severely damaged often show a remarkable ability to survive. Fallen trees have the ability to form new growth from the prostrate plant, and even felled trees are able to grow bark which covers the exposed stump and new shoots then arise from the periphery and centre of the stump (Wickens 1982). The comparison between the two study sections is therefore, affected by the scars left by utilisation which occurred when elephants only inhabited the area south of the Luvuvhu River. The results of the scoring system also show that fresh damage is higher in the northern section, once again indicating that this area was, at the time of the study supporting a higher concentration of elephants.

Sterculia rogersii

This plant species is known as an important source of nourishment for elephants (Van Wyk 1974), but in both sections of the study area, the majority of common star chestnut trees are either undamaged, or have only been lightly browsed. Of the entire population, 34 % of trees have had less than five percent of the biomass removed from them. There is also a very small proportion of trees with more than 50 % of their biomass removed. The differences in utilisation in the two sections are not significant, indicating that utilisation has been the same in these two areas. Observations of star-chestnuts which, have been made in Messina Nature Reserve, an area which is not inhabited by elephant, indicate that these trees are a favoured browse item for other large herbivores such as kudu (*Tragelaphus strepsiceros*), giraffe (*Giraffa camelopardalis*) and eland (*Tragelaphus oryx*). While no trees were seen in this reserve which had not been utilised at all, the vast majority of trees had only been lightly browsed, with 76 % of trees having had less than 10 % and 96 % of trees having had less than 15 % of their biomass browsed. This compares with figures of 52 % and 62 % in the Kruger National Park respectively. Much of the browsing of this tree species can therefore, be attributed to herbivores other than elephant, although the more destructive utilisation is almost certainly due to elephant. The absence of unutilised trees and the higher proportion of trees fulfilling the smaller utilisation categories in the Messina Nature Reserve are as a result of higher stocking rates of non-elephant browsers in this reserve. Clearly, browsers other than elephant are responsible for consuming a considerable amount of *Sterculia rogersii* browse.

The differences in the numbers of unutilised trees in the northern and southern study sections is not necessarily due to elephants. Where only small amounts of the tree have been browsed, no differentiation can be made between elephant utilisation and the utilisation by other herbivores. These trees can therefore, not be classed as unutilised. Other herbivores also browse on star-chestnuts and their foraging, affects the number of unutilised trees in the area.

The depth of utilisation scale shows that the majority of *Sterculia rogersii* trees in the study area have only been lightly browsed (Type I utilisation), and that trees with Type I and Type 0 utilisation constitute 73 % of the population. Type I utilisation can probably be attributed to browsers other than elephant and is unlikely to have any long term effect on the tree. Differences in the depth of utilisation in the two study sections are due to the larger proportion of trees in the south with Type III utilisation. Observations on trees in Messina Nature Reserve showed that 14 % of trees had Type III utilisation. There are two possible reasons why some trees in this area have had stems broken off. The first is that the stems have broken off during strong winds, or die due to infection or as a result of consumption by arthropods and not as a result of browsing. The second explanation is that this damage is extremely old and was inflicted on the trees sometime in the past when elephant still inhabited the area. When the oldest (class D) utilisation is omitted, less than three percent of the trees have Type III utilisation. This indicates that the more severe damage to these trees in Messina Nature Reserve occurred a number of years back. Although elephant have probably not been resident in the area since the mid 1800's, elephants were known to pass through the area now occupied by the reserve until the 1970's when it was proclaimed and fenced. The damage to *Sterculia rogersii* trees could thus be attributed to elephant presence in the reserve during this period.

The breaking of large branches and stems and the uprooting of trees can be attributed to the elephant population. The historic distribution and density of elephant in the two study sections in the Kruger National Park can be used to explain the higher proportion of trees which have Type III and IV utilisation in the southern section. The southern section also has a higher damage score than the north. The system used to determine these scores allocates a different number of points to different types of damage. A greater number of points are allocated to severely damaged trees and thus the south study section has a high total. Here again, omitting the utilisation data from the oldest (class D) utilisation category presents a very different scenario. In both the northern and southern sections, each category of the utilisation scale is occupied by similar proportions of trees and the damage scores for the two sections of 14.60 (north) and 16.14 (south) are no longer significantly different (difference of proportions $z = -1.62$; $P > 0.05$). The difference in utilisation of these two areas can therefore, be attributed to elephant with the higher damage score in the south a result of the higher elephant density in that section between 1931 and 1969. Utilisation of these trees has however been more intense in the northern section in recent times as is shown by the damage score (2.46) for the most recent (class A) utilisation which is considerably larger than the score for the southern section (0.92) (difference of proportions $z = 4.47$; $P < 0.001$). Once again this can be attributed to the higher herbivore density and increased utilisation of browse, due to the proximity of permanent water.

Both the proportion of biomass removed from and the damage score of *Sterculia rogersii* trees shows an increase with an increase in girth, indicating that browsers concentrate their foraging on the larger trees. The seedlings and regeneration class of trees are therefore, not as likely to be affected by browsing as are the older trees. This is a favourable situation with regards to long term survival of the population, especially when considering that for the same foraging effort, a smaller tree would suffer more injury than a larger one. The resources which are required for a smaller tree to recover are greater and the risk of the tree not surviving is consequently greater.

As with baobabs, the star-chestnuts possess a remarkable ability to recover from browsing induced damage. New bark covers areas which have been exposed by browsing and where branches or stems have been broken off. Some trees have been so severely damaged that all their stems had been broken off at ground level, leaving only the subterranean parts of the plant. These trees are still able to survive and coppice from the remaining parts of the tree, effectively forming a new plant. Many plants can be seen growing from the prostrate stem of a tree which had been pushed over in the past and from which new shoots emerged. Despite being severely injured, these trees still manage to survive.

The remarkable survival ability of these trees even under heavy herbivore pressure would indicate that, to determine the sustainability of the population, the causes and rates of mortality of the trees should be investigated. The amount and intensity of utilisation does not provide any clues in this regard. Browsers have been concentrating their foraging efforts on the larger trees which tend to recover from browsing and not the regeneration classes and so, although there is a lack of smaller trees in the Kruger National Park, it is most likely from the evidence presented here that elephant are not solely to blame if at all for the poor number of trees being recruited into the Kruger National Park population.

Unfortunately the effect of fire on *Sterculia rogersii* trees did not form part of this study as it is likely that an increase in the frequency of fire has hampered recruitment and regeneration of this species. The susceptibility of small trees to fire may be the cause of the poor recruitment of trees into the population. The effect of fire on the population structure of this species has been discussed in more detail in Chapter 4.

CONCLUSION

Utilsation of both tree species (*Adansonia digitata* and *Sterculia rogersii*) has taken place in the Kruger National Park. This has been greater in the southern study section as a result of higher elephant densities being present in this area for most of this century. In all cases, utilisation increases with an increase in girth. However, both species show an ability to recover from even severe damage and utilisation is therefore, unlikely to kill trees. Utilisation may, however, lower the resistance of plants to drought-induced or other forms of stress. This could not be determined during this study. Monitoring of mortality rates would be a better indicator of the potential of these populations to survive than monitoring utilisation. A reduction in the utilisation of common star-chestnuts will only be achieved if the stocking rates of all the larger herbivores are reduced.

CHAPTER 6

AGE OF ELEPHANT UTILISATION OF *ADANSONIA DIGITATA* AND *STERCULIA ROGERSII* IN THE KRUGER NATIONAL PARK

INTRODUCTION

Due to the age which trees can attain, they often bear scars from incidents which may have injured them hundreds of years previously. Baobabs have long been a popular target for vandals, who often carved names and dates on them. In some instances these inscriptions have remained on the trees for many years. Inscriptions carved by sailors on trees on the Magdalene Islands in the 15th and 16th centuries were still present when Adanson travelled there in 1749 (Wickens 1982). In the Kruger National Park, a number of trees have been defaced, but one of the more famous inscriptions was made by a hunter named Briscoe, who in 1890 carved his name and the year on the tree. This inscription is still visible more than 100 years later. Similarly, and of relevance to this study are the scars left on trees by browsing animals which, are also still visible a number of years later and can provide an indication of the history of utilisation of each tree.

This part of the study was intended to compare the amount of utilisation of the two plant species in the two study sections over time. It was intended that the utilisation over different periods could be compared with past elephant densities to evaluate trends in the utilisation of these tree species by elephant. If elephants had been consistent in their diet, signs of new and old elephant feeding damage would be associated (Ben-Shahar 1993).

METHODS

Damage to trees was classified into four age categories based on the colour and texture of the damaged plant tissue. This damage was distinguished in the field, as bark and branches which had been damaged recently were a bright yellow colour. With age, this faded and became greyish and later white as a result of extended exposure of the inner plant parts to sun and rain (Ben-Shahar 1993; Engelbrecht 1979; Kabigumila 1993). Four age categories were identified and trees were classified according to the following criteria:

A: The damaged parts of these trees were a deep orange-yellow colour.
B: The colour of the damaged parts had faded, but was still yellow.
C: Damaged areas were greyish-white in colour and new bark was beginning to form.
D: A new layer of bark had completely covered the damaged parts of these trees and damage was only indicated by scars

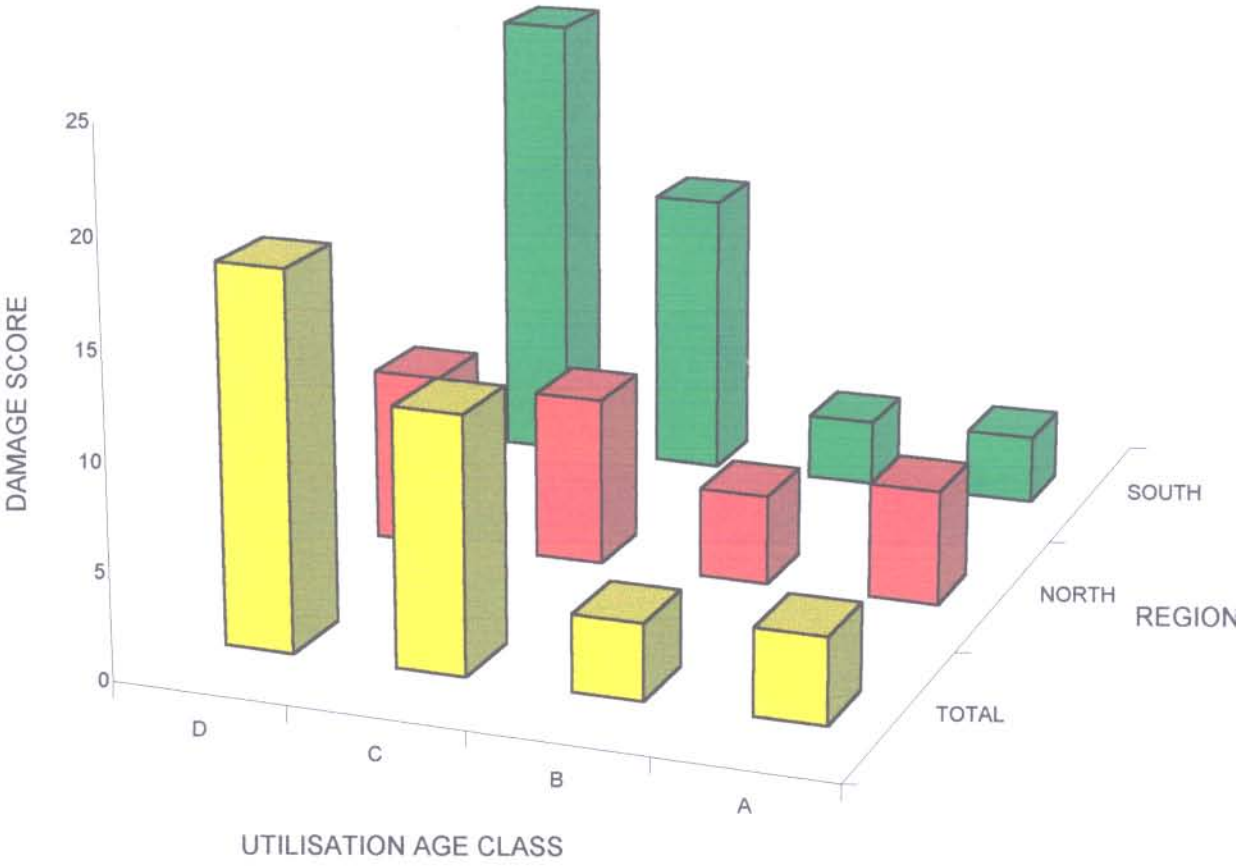
RESULTS

Adansonia digitata

The damage score of baobabs as a function of the age of utilisation is shown in Figure 17 for the two sections and the study area as a whole. This has been based on the system described above. Damage scores for class A and class B utilisation are highest in the northern section ($z = 4.17$; $P < 0.001$ and $z = 2.20$; $P < 0.05$ respectively). The southern section however has significantly higher class C and D scores ($z = -6.93$; $P < 0.001$ and $z = -14.07$; $P < 0.001$ respectively).

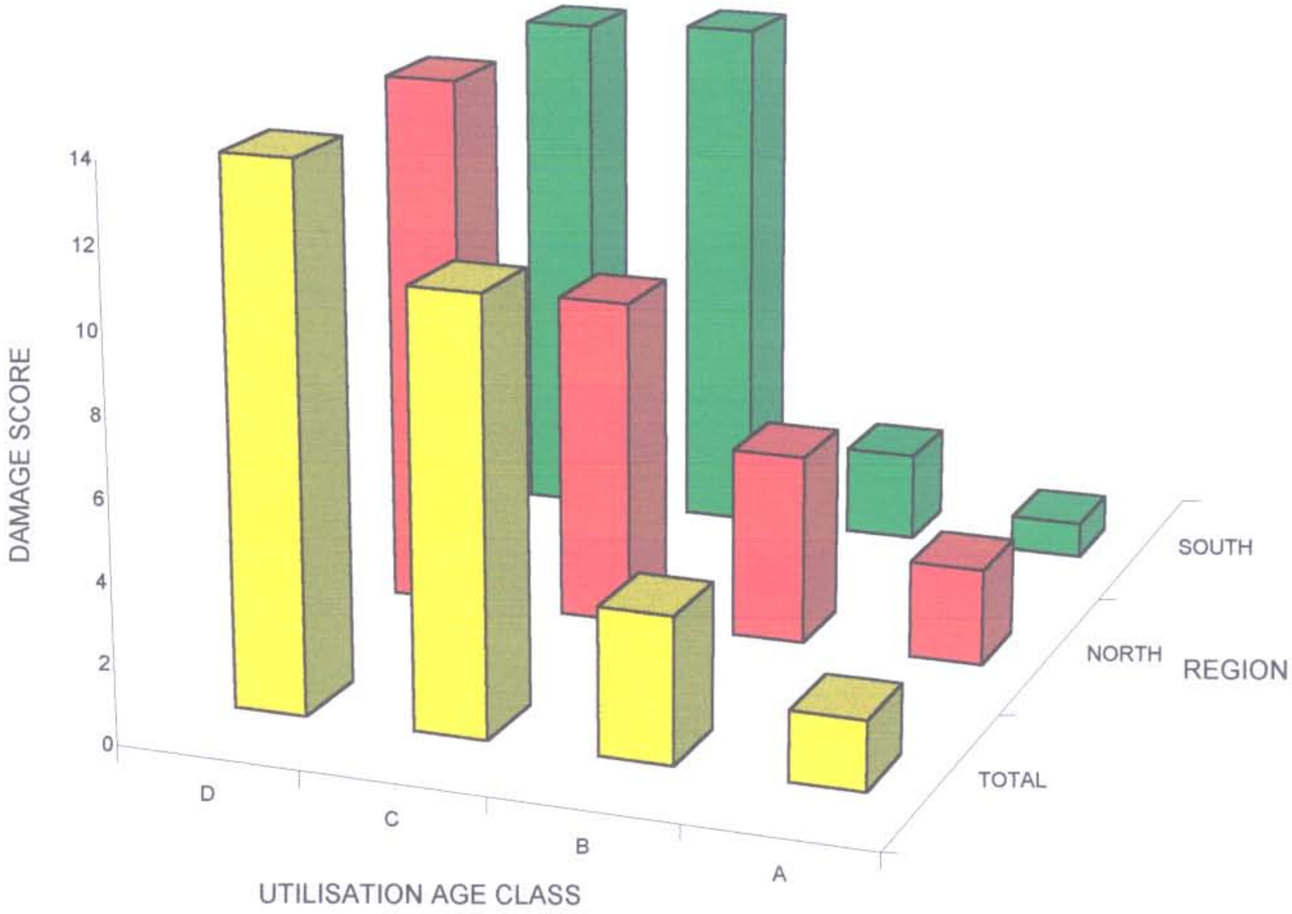
Sterculia rogersii

The damage score as a function of the age of utilisation for the two sections and the entire study area is shown in Figure 18. As with baobabs damage scores are higher in the northern section for class A and B utilisation ($z = 4.47$; $P < 0.001$ and $z = 5.13$; $P < 0.001$ respectively). Trees in the southern section have a greater class C utilisation score ($z = -6.45$; $P < 0.001$), while damage in class D is not significantly different in the two regions ($z = 0.27$; $P > 0.05$).



A: FRESHLY SCARRED TREE.
B: SCARS BEGINNING TO FADE DUE TO EXPOSURE.
C: NEW BARK GROWING OVER THE FADED SCAR.
D: DAMAGED PARTS COMPLETELY COVERED BY NEW BARK.

Fig. 17: Damage scores of *Adansonia digitata* in the northern and southern study sections of the Kruger National Park as a function of utilisation age. Utilisation age class is based on the colour of the damaged plant tissue and presence of new bark.



A: FRESHLY SCARRED TREE.
B: SCARS BEGINNING TO FADE DUE TO EXPOSURE.
C: NEW BARK GROWING OVER THE FADED SCAR.
D: DAMAGED PARTS COMPLETELY COVERED BY NEW BARK.

Fig. 18: Damage score of *Sterculia rogersii* in the northern and southern study sections of the Kruger National Park as a function of utilisation age. Utilisation age class is based on the colour of the damaged plant tissue and presence of new bark.

DISCUSSION

Adansonia digitata

The age categories which have been used are based on the current appearance of damaged plant tissue. Each category therefore, does not represent the same period of time. When damage is first inflicted on a plant, it is brightly coloured, but soon fades. The first age category is only applicable to damage which is less than one year old. The second category also only applies to damage which occurred over a one to two year period, while damage in the third category covers utilisation over a much longer period. Photographs of baobabs show that this damage changes little if at all over four years and probably even more. The final damage type is in the form of very old scars. These scars persist on baobab trees for extremely long periods, and the timespan over which this damage could have occurred is undoubtedly far greater than any of the other utilisation age classes.

Some trees may be damaged, recover from the damage, and then be damaged again in the same place. The result of this is that the newer damage obscures the older damage, which can therefore, not be recorded. The values of the older damage classes are thus not accurate. The consequences of this are that the ageing system introduces bias into the results of utilisation age and comparisons made between ages are therefore inaccurate and have not been attempted.

The ageing system has, however, allowed for utilisation in the two study sections to be compared. In classes C and D, utilisation is much greater in the southern section. These discrepancies are as a result of the period during the middle of this century when the elephant density was much greater in this section. In the last one to two years, utilisation has, however, been more intense in the northern section. This is due to this section currently supporting a higher concentration of elephant.

Sterculia rogersii

Utilisation by elephants of baobabs usually takes the form of bark stripping, but utilisation of star chestnuts results in branches being broken off. If the branch or stem is broken from the tree at it's base, a small scar results. This scar is visible on the tree, but if new branches grow from the same point, they obscure the scar. In many cases, evidence of the damage to these trees does not persist for as long as in baobab trees as it is obscured by growth of new branches. Trees which are severely damaged and only have the trunk remaining often coppice from this trunk and after some years growth, no evidence of the damage remains.

As with the ageing of damage to baobab trees, no consistency exists in the timespan over which damage in each of the categories could have occurred, and the data can only be used for comparisons between the northern and southern sections. The ages also differ in the two tree species. It is clear that for a period in the past, the southern tree populations were subjected to greater utilisation than trees in the northern section. The bulk of class C utilisation probably occurred during the period when only the southern section was a wildlife sanctuary. This resulted in the large difference in utilisation of trees in the two sections. Class D utilisation took place prior to either section forming part of a wildlife sanctuary, while class A and class B damage has been inflicted since 1969, once recolonisation of the northern section by elephant and other game had taken place.

CONCLUSION

Comparisons between ages could not be made as each age class represents a different time period. Comparisons between the two study sections showed that damage of both tree species is proportional to elephant density.

CHAPTER 7

MORTALITY OF *ADANSONIA DIGITATA* AND *STERCULIA ROGERSII* IN THE KRUGER NATIONAL PARK

INTRODUCTION

The age of death of individuals in a population is known as longevity. There are two types of longevity, potential longevity and realised longevity (Krebs 1994). Potential longevity is the maximum lifespan an individual can attain and is limited by the physiology of the organism. This lifespan can only be achieved when living under optimum conditions. Under natural conditions, most plants and animals die due to disease, predation or herbivory, and realised longevity is therefore, shorter than potential longevity (Krebs 1994).

Along with natality, immigration and emigration, mortality is one of the four primary population parameters (Krebs 1994). The pattern of mortality in populations has been described using three hypothetical curves (Fig. 19). Type I mortality is exhibited by species which suffer very few losses for most of their lifespan, but suffer high losses of older organisms. Type II mortality is of a constant rate of mortality, irrespective of age, while type III mortality is a pattern of high loss early in life, followed by a period of much lower and relatively constant losses. These patterns are hypothetical and real situations are usually a composite of these idealised situations (Krebs 1994).

Mortality of a number of tree species has been linked to elephant utilisation (Swanepoel 1993; Tchamba 1995). In areas where elephant densities have increased, they have been responsible for mortalities of as much as 40 % and 67 % of certain tree species (Barnes 1985). Some authors feel that it is unlikely that elephants are playing a critical role in baobab mortality, except in certain specific cases (Wilson 1988), while others believe that mortality in some baobab populations is only apparent and is due to declining recruitment over a long period (Caughley 1976).

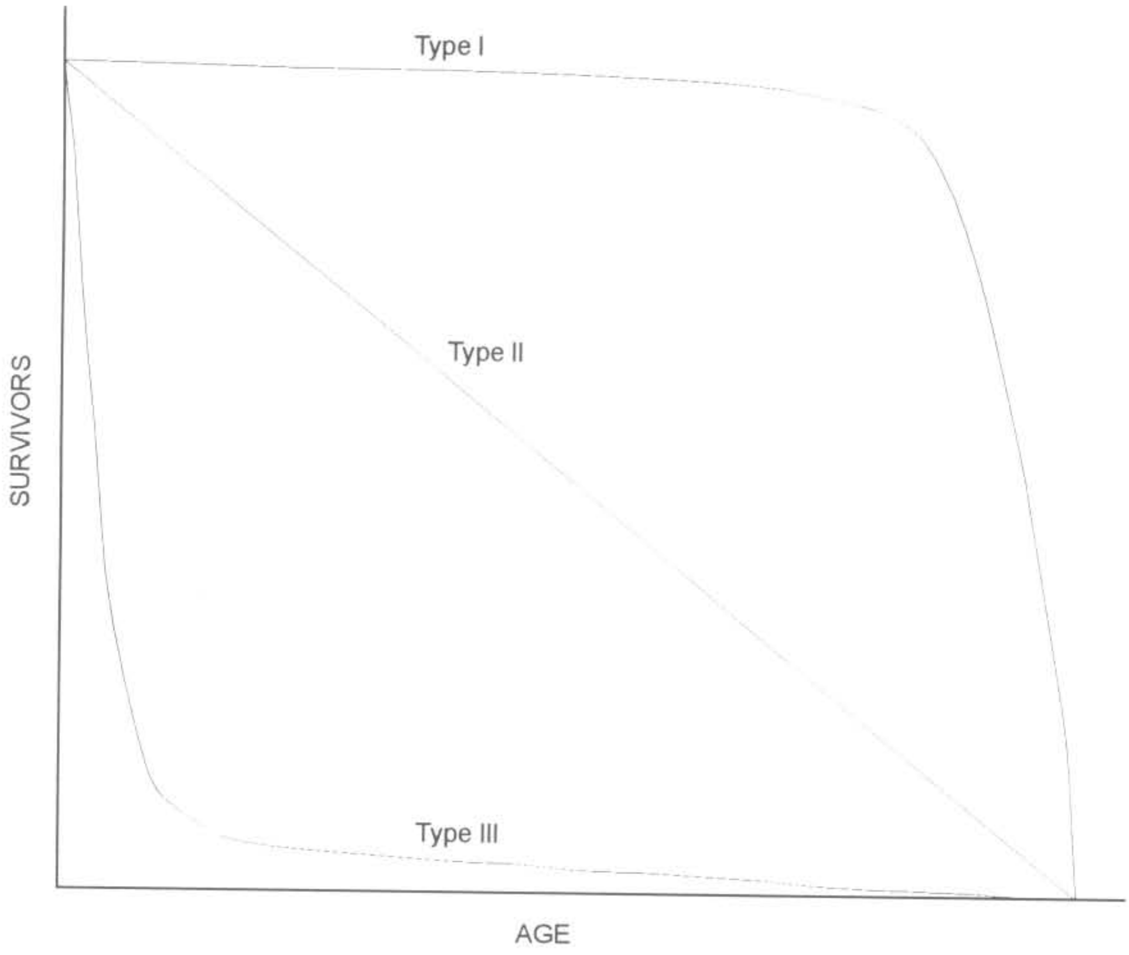


Fig. 19: Hypothetical survivorship curves.

Mortality can be measured directly or indirectly (Krebs 1994). Direct measurement is achieved by marking certain individuals and observing how many survive through time. Indirect measurement can be achieved by determining the abundance of successive age groups in the population (Krebs 1994). Due to the timescale required for direct measurement of mortality in tree populations, mortality has been measured indirectly in this study.

METHODS

Both tree species being studied have soft wood and after dying, the trees decompose relatively quickly. An indication of mortality over a short period can therefore be obtained by observation and enumeration of dead trees. In this study mortality has been assessed by determining the proportion of dead trees in each of the samples. Survivorship curves have also been calculated for each of the species based on the size class distributions.

RESULTS

Adansonia digitata

Of the baobabs sampled, 21 out of 1314 (1.60 %) were dead. At least nine of these trees had been recorded as dead by the beginning of the 1995-1996 summer season, 2 years before this study commenced. Remains of these trees were, however, still present during this study period. Therefore a maximum of 12 out of 1305 sampled trees (0.92 %) had died since this time. This figure should probably be lower considering the amount of time it takes for the plant material to decompose completely. This figure of 0.92 % is for mortality over a period of at least 2 years. Mortality is the same (0.92 %) in both the northern and southern sections. A total of two baobab trees out of the 151 trees (1.32%) which occurred within the sampling transects were dead. Of these, 1.5 % of the northern sample and 1.2 % of the southern sample were dead The proportion of dead trees in the transects does not differ significantly from the proportion in the total sample ($z = -0.48$; $P > 0.05$).

Sterculia rogersii

Of the 1163 star-chestnuts sampled, four (0.34 %) were dead. Of these trees, three were from the northern section. The proportion of dead trees sampled in the north was 0.49 % and in the south was 0.18 %. A total of two trees out of the 461 trees (0.43 %) which occurred within the sampling transects were dead. In the northern transects, 0.54 % of sampled trees were dead and 0.36 % were dead in the south. The difference in proportions of dead trees in the transects and in the total sample are not significantly different ($z = -0.27$; $P > 0.05$).

DISCUSSION

Adansonia digitata

A maximum of 12 out of 1305 sampled baobabs (0.92%) had died after July 1995. Swanepoel (1993) found that it takes 2 years for baobabs to disintegrate completely, and a number of trees in this study had been dead for longer than this, but traces of plant material could still be located. All the baobab trees which had died within the preceding year would have been accounted for in this figure. With time the amount of decaying plant material present on the ground is reduced, and the chance of spotting trees which have been dead for a long time therefore, also declines. While larger trees are visible for a long time after they die, the smaller ones disintegrate faster. It is probable that only a portion of the baobabs which have been dead for more than a year would have been spotted, and this portion would be inversely proportional to the amount of time the tree has been dead. The estimated mortality of 0.92 % is therefore, too large to be the annual mortality figure, but is for mortality over a period of at least two years. The annual mortality could be as little as 50 % of this, but if it is accepted that a portion of the trees dead for more than a year were missed and it is estimated that 75 % of these trees had died within the year, then the annual rate of mortality is only 0.69 %.

Barnes *et al.* (1994) have demonstrated the problems associated with spotting dead trees with increasing distance from the transect midline. The estimate which only includes trees from the sampling transects is more accurate, as the chance of dead trees being overlooked in this sample is reduced considerably. The 1.32 % of baobabs which were dead in the transects is, again a figure for mortality for more than one year, considering the amount of time it takes for the remains of trees to disintegrate. The annual mortality rate in this case is thus less than 1.32 %, but, taking Swanepoel's (1993) findings into consideration, probably greater than 0.66 %. If the assumption is made that 75 % of the dead baobabs had died within the year, the observed annual mortality rate is 0.99 %.

For discussion, ages have been assigned to the various size classes. These ages are based on the growth rate of baobabs as discussed in Chapter 1. The ages for each size class have been calculated using the midpoint of the size class. Data from trees with a girth larger than 15 m have been grouped due to the small dataset. Two survivorship curves have been calculated and superimposed on the age distribution (Fig. 20). The first (A) is a linear curve which derives the regression of the percentage of trees in each age class on age ($r^2 = 0.84$; $n = 16$; $P < 0.001$). The regression equation is $y = 12.723 - 0.0532x$. This curve assumes mortality of a constant number of trees. The expected mortality for this curve would be 0.53 % of the original number of trees per year (Weyerhaeuser 1985). The second curve (B) is negative exponential and derives the regression of the natural logarithm of the percentage of trees in each age class on age. This curve is defined by: $\ln y = 2.92 - 0.0117x$ ($r^2 = 0.897$) and assumes the mortality of a constant percentage of trees. The mortality rate of this curve is 1.2 % of the population per year.

The instantaneous mortality rate of trees in the area prior to elephant recolonisation in 1931 has been obtained by deriving the regression of the natural logarithm of the percentage of trees in each age class on age (Barnes 1980; Krebs 1994; Wilson 1988). Only trees with a girth larger than 5 m have been included. The regression equation is: $\ln y = 3.49 - 0.0147x$ ($r^2 = 0.91$). The estimated mortality rate in the absence of elephants was therefore 1.5 % per annum. This estimated mortality rate is higher than the mortality rate when elephants are present, but does rely on a few assumptions:

i) The age distribution of trees with a girth of more than 5 m is the result of a long period of constant mortality and regeneration rates;

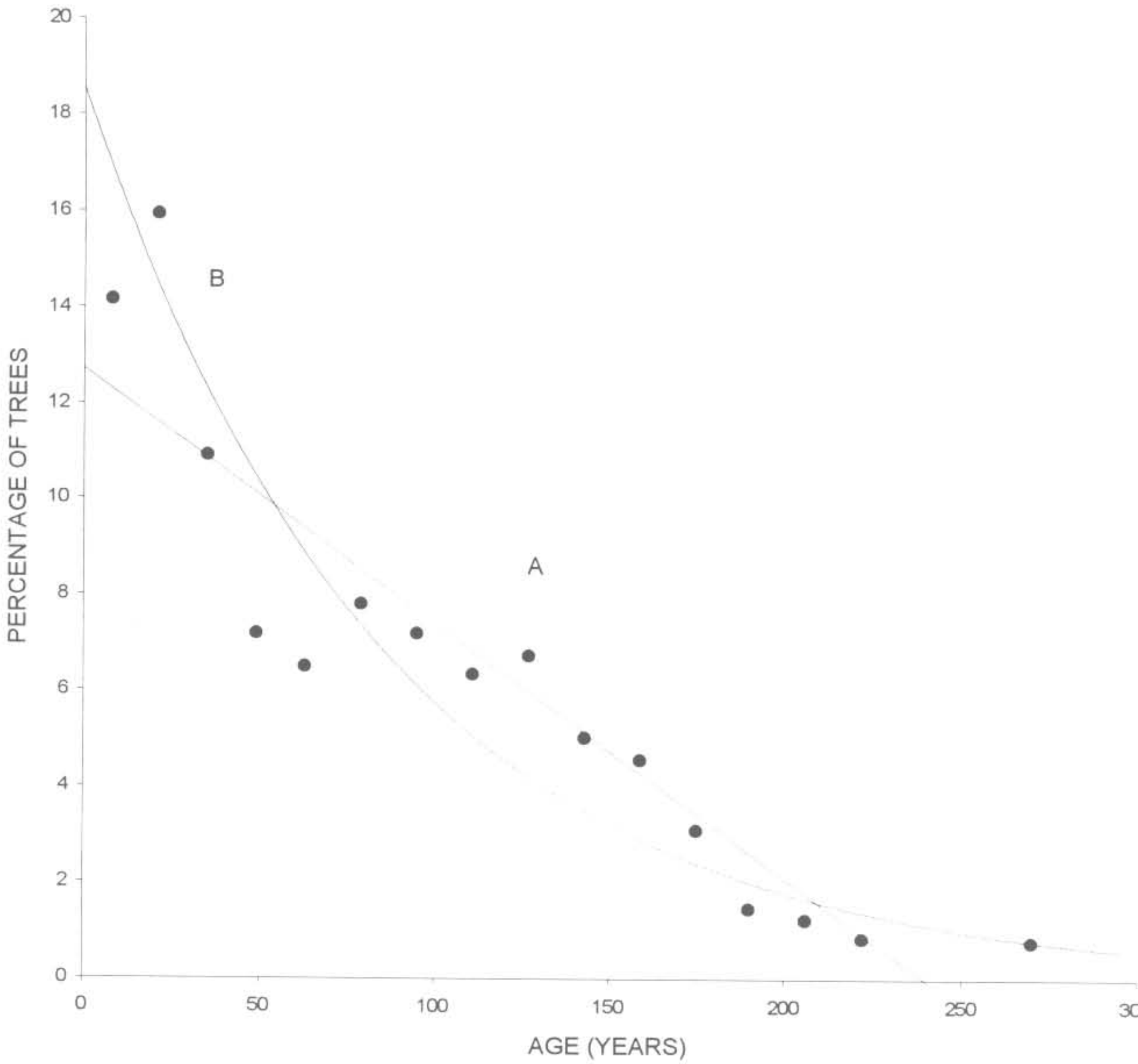


Fig. 20: Estimated age distribution and calculated survivorship curves of *Adansonia digitata* in the Kruger National Park.

A: $y = 12.72 - 0.053x$; ($r^2 = 0.84$; $n = 16$; $P < 0.001$).
B: $\ln y = 2.92 - 0.012x$; ($r^2 = 0.90$; $n = 16$; $P < 0.005$).

ii) The rate of increase of the population was zero before this time;
iii) The natural mortality rate is the same for all age classes.

It can be concluded that the annual mortality rate of the sampled baobabs in the study area lies somewhere between 0.69 % and 0.99 %, while the curves superimposed on the age class distribution give mortality estimates of 0.53 % and 1.2 %. This, however, is the total mortality for the area, and if elephant are causing mortality of baobabs, they are only responsible for a portion of this. Barnes (1980) found that although elephant were killing baobabs in Tanzania, they were only responsible for 75 % of mortality.

A number of baobabs have died in the study area for which notes had been made of their condition prior to dying. Of the four baobabs noted, two had no elephant damage at all. One of these trees had died after it had been damaged by another tree falling on it. The other two trees had been utilised by elephant. The one, which had a girth of 1.16 m, had been deformed by utilisation, but the other (girth of 5.95 m), although ringbarked, had only been damaged superficially. The damage to both of these trees was a number of years old before the trees died. Therefore, the deaths of only two out of these four trees could have been due to elephant. This deduction is, however, based on the assumption that the trees were not damaged by elephant in the period between these observations and the time the trees collapsed. Trees would need to be monitored constantly to be certain they have not been damaged by elephant, due to the short time it takes a baobab tree to collapse after dying. Three of these baobabs died in the three years prior to July 1998 and formed part of a sample of 198 trees. Therefore, 1.5 % of this sample died during these three years, with an annual average of 0.5 %.

One baobab located during this study had fallen over very recently and was still whole. This was a large tree with a girth of approximately 15 m. Although this tree had at some stage been extensively utilised by elephant, by the time it collapsed, complete regrowth of bark had occurred and old scars were the only remaining evidence to indicate that elephant had once utilised the trees. The damaged areas gave the appearance of not having been utilised in more than ten years and due to the complete regrowth of bark, this utilisation would not have contributed to the trees' demise. The possibility does exist that the side of the tree which was lying against the ground had been recently damaged by elephant, but attempts at finding signs of recent elephant damage proved fruitless. The reason for the death of this tree is almost certainly not related to elephant utilisation.

Estimates of the annual mortality rate of baobabs are therefore 1.2 % (regression equation), 1.5 % (regression equation prior to elephant), 0.7 % (total sample), 1.0 % (transect sample) and 0.5 % (sample of known trees)

Wilson (1988) calculated the mortality rates for baobab populations which he studied in five countries. The annual mortality rates for these populations have been estimated at 1.1 % in Tanzania, 1.4 % in Zambia, 1.9 % in Sudan, 3.4 % in Mali and 3.7 % in Kenya. In Zimbabwe, a sample of baobabs had an average mortality of 4.9 % with rates as high as 15.5 % in some areas (Swanepoel & Swanepoel 1986). In Ruaha National Park, Barnes (1980) found that the mortality rate of baobabs was 2.7 %, but felt that it could be higher as a number of trees had been overlooked.

Although baobab populations in some of these places were studied as there was a perceived threat to survival of the population, and high mortality rates would be expected, these mortality rates are generally greater than estimates of current mortality in the Kruger National Park. Even in Mali where baobabs are grown as a crop (Wilson 1988) and elephant are probably kept away from the trees, the mortality rate is much greater than in the Kruger National Park. It would therefore, appear that the mortality of baobabs in the Kruger National Park has not yet reached a level at which the baobab population is threatened with extinction.

The annual mortality rates of baobabs in the Kruger National Park have been determined, but not the pattern of mortality. If mortality is not affected by herbivore utilisation, the rate will not be affected by tree density, but will remain constant, unless influenced by environmental or other factors. Mortality due to elephants can result in one of three patterns. The first would be caused by elephants destroying the same percentage of the population each year, the second by elephant killing the same number of trees each year and the third by a completely random effect (Barnes 1980). In the first case the population will be reduced constantly, but the number of trees which die will become smaller each year and the rate at which the population nears extinction will slow down as it gets smaller. In the second scenario, elephant actively seek out baobab trees and the mortality will therefore, remain constant until the tree population is driven to extinction. As the third scenario is random, no predictions of its impact can be made.

The effects of the first two types of mortality on the Kruger National Park baobab population have been predicted in Figure 21 at the observed mortality rate of one percent, based on the following assumptions:

(i) There is no regeneration, and
(ii) The population is subjected to a constant mortality rate.

As can be seen from this figure, even without regeneration, at the current mortality rate, the baobab population will halve itself in 69 years if it follows curve A, but after two hundred years the population will still consist of more than 2000 trees. The population will only be completely eliminated after 959 years. The second scenario (curve B) is more drastic, in which case it will only take 100 years before the population is extirpated.

The assumption of no regeneration is a worse case scenario, and is not true for the Kruger National Park at this stage, as a relatively large proportion of the population consists of trees in the smallest (regeneration) size class. Provided the mortality rate does not increase, the baobab population is in no immediate danger of extinction. Irrespective of which of these patterns is followed, it is still unlikely that the Kruger National Park elephant population will ever be able to drive the baobab population to extinction due to the large number of trees which are growing in areas which are inaccessible to elephants.

Sterculia rogersii

Common star-chestnuts, like baobabs have soft wood which decomposes quickly, but unlike baobabs they are relatively small trees and the remains of dead trees will therefore, be overlooked more easily than the remains of dead baobabs. Evidence of this comes from one

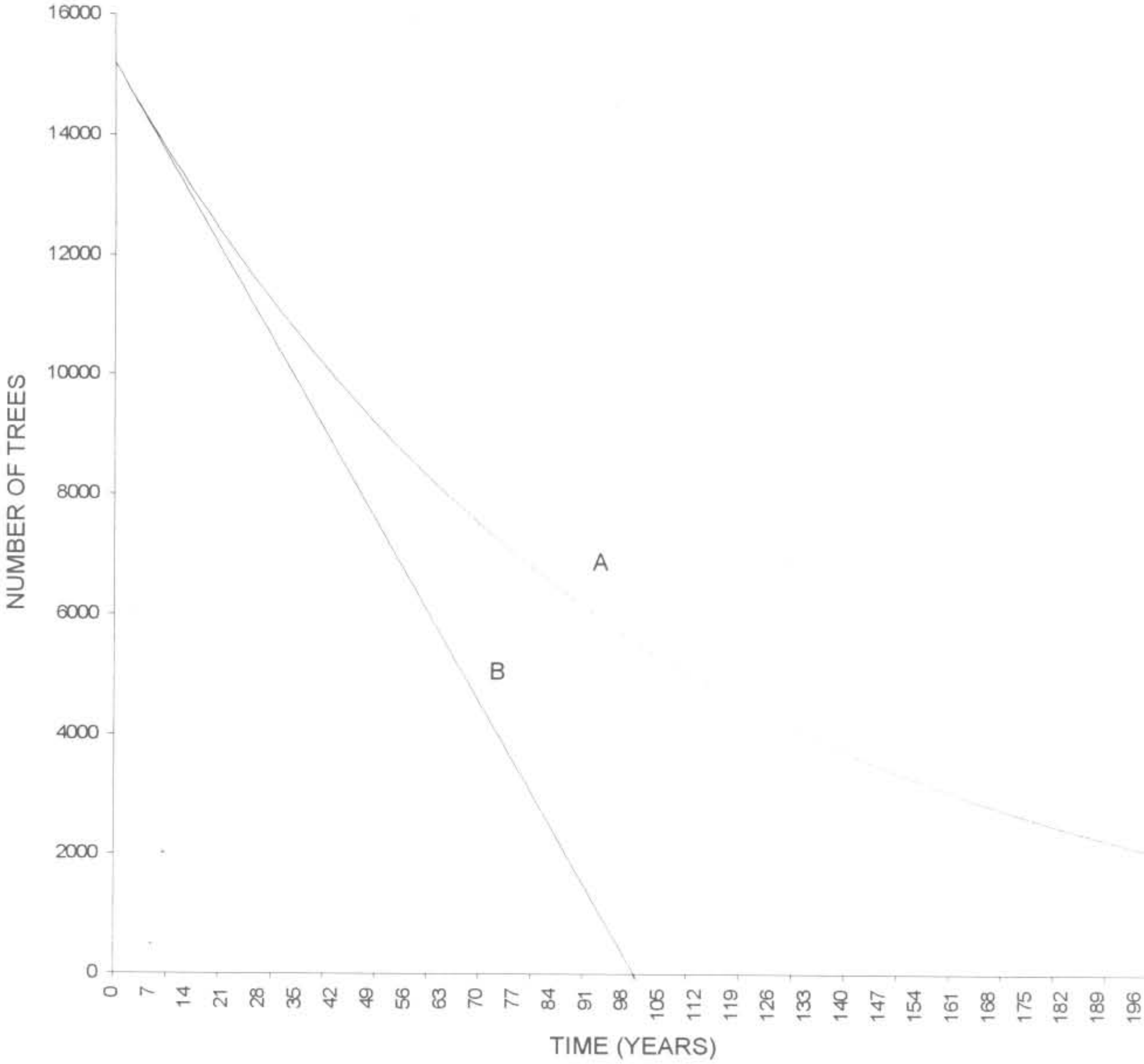


Fig. 21: Calculated future decline in the Kruger National Park *Adansonia digitata* population.

A: A constant percentage of the tree population is destroyed annually.
B: A constant number of trees is killed annually.

tree in the study which had been dead for less than a year, and was already in an advanced stage of decomposition. The increased chance of missing trees with increasing distance from the transect midline (Barnes *et al*. 1994) has already been discussed. The observed mortality of 0.43 % of the sample is therefore, likely to be near the annual mortality rate as dead trees which are located are unlikely to have been dead for more than one year.

Due to the extremely small number of young *Sterculia rogersii* trees present in the study area, survivorship curves superimposed on the age distribution data had an extremely poor fit and have not been included here.

The regression of the natural logarithm of the percentage of trees in each age class on age has been derived to determine the natural mortality of the *Sterculia rogersii* population in the absence of elephant. Younger trees were thus omitted from the calculation. This calculation is reliant on three assumptions:

i) The age distribution of trees older than 67 years (the period for which elephant have been present in the area is the result of a long period of constant mortality and regeneration rates);
ii) The rate of increase of the population was zero before this time;
iii) The natural mortality rate is the same for all age classes.

The curve estimates that the annual mortality rate of *Sterculia rogersii* trees in the study area has not changed from 0.11 % since 1903 when the Shingwedzi Game Reserve was proclaimed. Repeating the regression, using the faster growth rate suggests that the mortality rate has decreased from 2.5 % ($r^2 = 0.931$) before 1903 to 2.2 % ($r^2 = 0.897$) before 1931 (the year in which elephant recolonised the study area). According to this evidence, the proclamation of the study area as a wildlife sanctuary has not resulted in an increase in mortality rates of *Sterculia rogersii* in the Kruger National Park.

A number of estimates of instantaneous mortality have been made for different time periods and growth rates. These estimates have been used to compare mortality in the northern and southern study sections. Due to the structure of the population, the curves generally do not fit the data well, except where calculations exclude the younger trees. This is due to the regeneration of trees not being constant and therefore, one of the assumptions remains unfulfilled. Although the accuracy of these estimates is questionable, they are discussed here for interest.

If the rate of growth is slow, mortality in the northern section is estimated at 0.09 % per annum ($r^2 = 0.384$). This area has formed part of the Kruger National Park since 1969, but the sample did not contain any trees younger than 29 years, so any changes to the mortality rate which may have occurred with the recolonisation of the area by elephant cannot be determined.

In the southern section, the estimated annual mortality rate of *Sterculia rogersii* is 0.06 % ($r^2 = 0.254$). Prior to 1931 it was also 0.06 % ($r^2 = 0.220$) in this area but before 1903 it was only 0.05 % ($r^2 = 0.175$). These estimates suggest a very small increase in the annual mortality rate of this species in this section.

When using the faster growth rate in the regression, estimates of the mortality rate are proportionally higher. In the northern study section , the estimated mortality is 0.93 % per annum. Prior to 1969, *Sterculia rogersii* trees had an estimated rate of mortality of 1.46 % per year. In the southern section, the annual mortality rate of *Sterculia rogersii* is 0.61 %. Prior to 1931 it was 1.68 % in this area and before 1903 it was 1.95 %.

Trees with a girth greater than 1.75 m show a pattern consistent with constant regeneration and satisfy the assumptions necessary for estimating instant mortality. The instantaneous mortality rate for these trees is 0.255 % ($r^2 = 0.931$); (0.228 % in the north and 0.195 % in the south); ($r^2 = 0.945$ and 0.949 respectively). The faster growth rate gives estimates of instantaneous mortality of 2.55 % (2.28 % in the north and 1.95 % in the south).

If elephant are responsible for mortality of *Sterculia rogersii*, there would have been an increase in instantaneous mortality rates concomitant with an increase in elephant densities. This has not happened, as mortality rates have decreased in all instances except for one case in which mortality has increased by 0.01 % in the period since 1903. Therefore if elephant are having any effect on the mortality of the *Sterculia rogersii* population, this effect is negligible. The increase in densities of other browsers in this area during this century has also not increased mortality rates of *Sterculia rogersii*.

Methods used to determine the annual mortality rates of *Sterculia rogersii* in the Kruger National Park, give estimates ranging from 0.11 % to 0.43 %. The actual annual mortality rate is probably close to the observed rate of 0.43 %. It does not appear that mortality of this species is cause for concern, however, the survival of the species in the Kruger National Park may be in jeopardy as a result of poor recruitment rates as shown by the population structure data. This study does not provide evidence to indicate that elephant are responsible for a decline in the population. More information on the effect of factors such as fire on the population needs to be obtained.

As with the baobab population, the decline in the *Sterculia rogersii* population has been predicted in Figure 22 using the observed annual mortality rate of 0.43 % and based on the assumption of no regeneration. Both the scenario of mortality of a constant proportion of trees (curve A) and a constant number of trees (curve B) have been investigated. In the first scenario, the population will halve itself after 161 years, but will only reach extinction in 2490 years. In the second situation, the population will halve in 116 years, and it will take 233 years for the population to disappear completely.

These curves predict a hypothetical situation and the real situation may therefore, differ somewhat. As curve A moves further from the *y* axis, it becomes less accurate as with no regeneration the population will age progressively, causing an increase in the total mortality rate. Therefore, in the absence of regeneration, it is likely that the population will become extinct sooner than predicted.

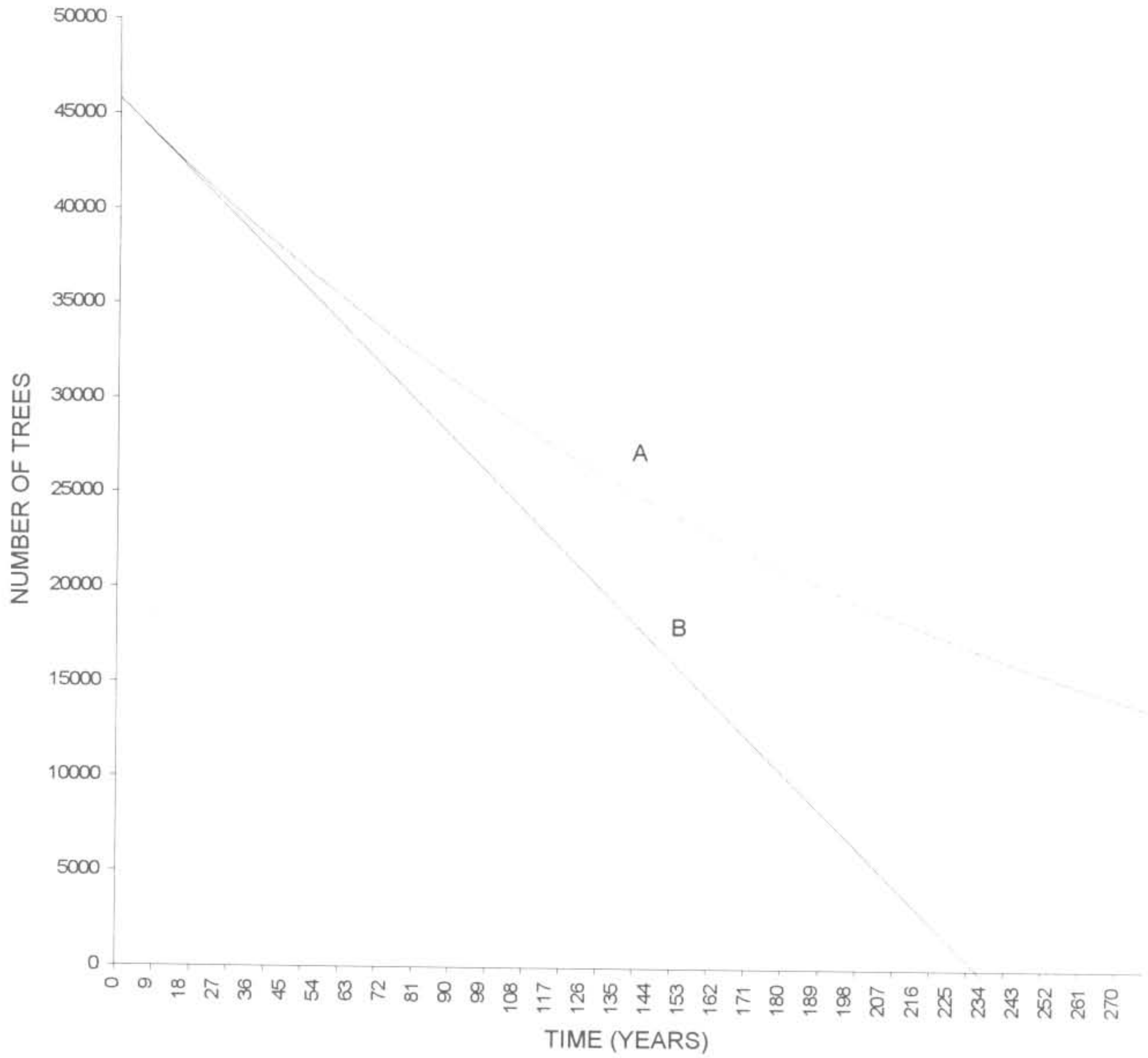


Fig. 22: Calculated future decline in the Kruger National Park *Sterculia rogersii* population.

A: A constant percentage of the tree population is destroyed annually.
B: A constant number of trees is killed annually.

CHAPTER 8

EFFECT OF THE DISTANCE FROM WATER ON THE POPULATION STRUCTURE AND UTILISATION OF *ADANSONIA DIGITATA* AND *STERCULIA ROGERSII* IN THE KRUGER NATIONAL PARK

INTRODUCTION

The increased elephant damage to trees near water is well known (Ben-Shahar 1993). During the wet season, elephants tend to be widely dispersed, but concentrate near permanent water during the dry season. Increases in elephant density around the water result in increased pressure on the vegetation (Swanepoel & Swanepoel 1986).

In the Kruger National Park, this trend was established during early research projects on the utilisation of vegetation by elephant (Van Wyk & Fairall 1969). During winter, elephant in the far north of the Kruger National Park concentrate around the river systems, as areas without permanent water are unsuitable as winter range for them. Because of this, they exhibit highly destructive behaviour in the areas surrounding permanent water (Van Wyk & Fairall 1969).

This section of the study was therefore to determine if any relationship exists between the amount of utilisation of *Sterculia rogersii* and *Adansonia digitata* and their distance from the perennial rivers.

METHODS

The position of all sampled trees was recorded relative to the starting point of the transect. It was thus possible to isolate trees which were growing more than 10 km from the Limpopo and Luvuvhu Rivers, and other permanent water sources (Group 1). The population structure and utilisation data from these trees were then compared with data from trees growing within a 10 km distance from permanent water (Group 2).

RESULTS

Adansonia digitata

The size class distribution of baobabs growing within 10 km of permanent water (Group 2) is significantly different from that of baobabs growing further from water (Group 1); (Fig. 23); (Kolmogorov-Smirnov two-sample test, $D_{\max} = 0.12$; $P < 0.005$). In Group 2, the smallest size class is best represented, with generally decreasing proportions into the larger size classes. Trees with a girth of 1 to 2 m are, however, most common in Group 1, while very few trees have a girth of 3 to 5 m.

The two populations have been compared using the depth of utilisation scale and the differences are highly significant (Kolmogorov-Smirnov two-sample test, $D_{\max} = 0.17$; $P < 0.001$). More than half (55 %) of trees further than 10 km from water are unutilised, but only 37 % of baobabs within closer proximity to water have not been foraged on (difference of proportions of unutilised trees $z = 5.42$; $P < 0.001$); (Fig. 24). Although only a few trees close to water have been severely damaged, no trees more than 10 km from these water sources showed signs of Type III or IV damage.

The damage scores of the two groups of baobabs have also been calculated, and show that trees closer to water have been more heavily utilised than trees further away. The damage score of baobabs close to the water sources (15.57) is substantially greater than the damage score of baobabs further away (9.66); (difference of proportions $z = -5.90$; $P < 0.001$).

Sterculia rogersii

The size class distribution of *Sterculia rogersii* trees is also very different in the two groups (Kolmogorov-Smirnov two-sample test, $D_{\max} = 0.22$; $P < 0.001$). The smaller size classes

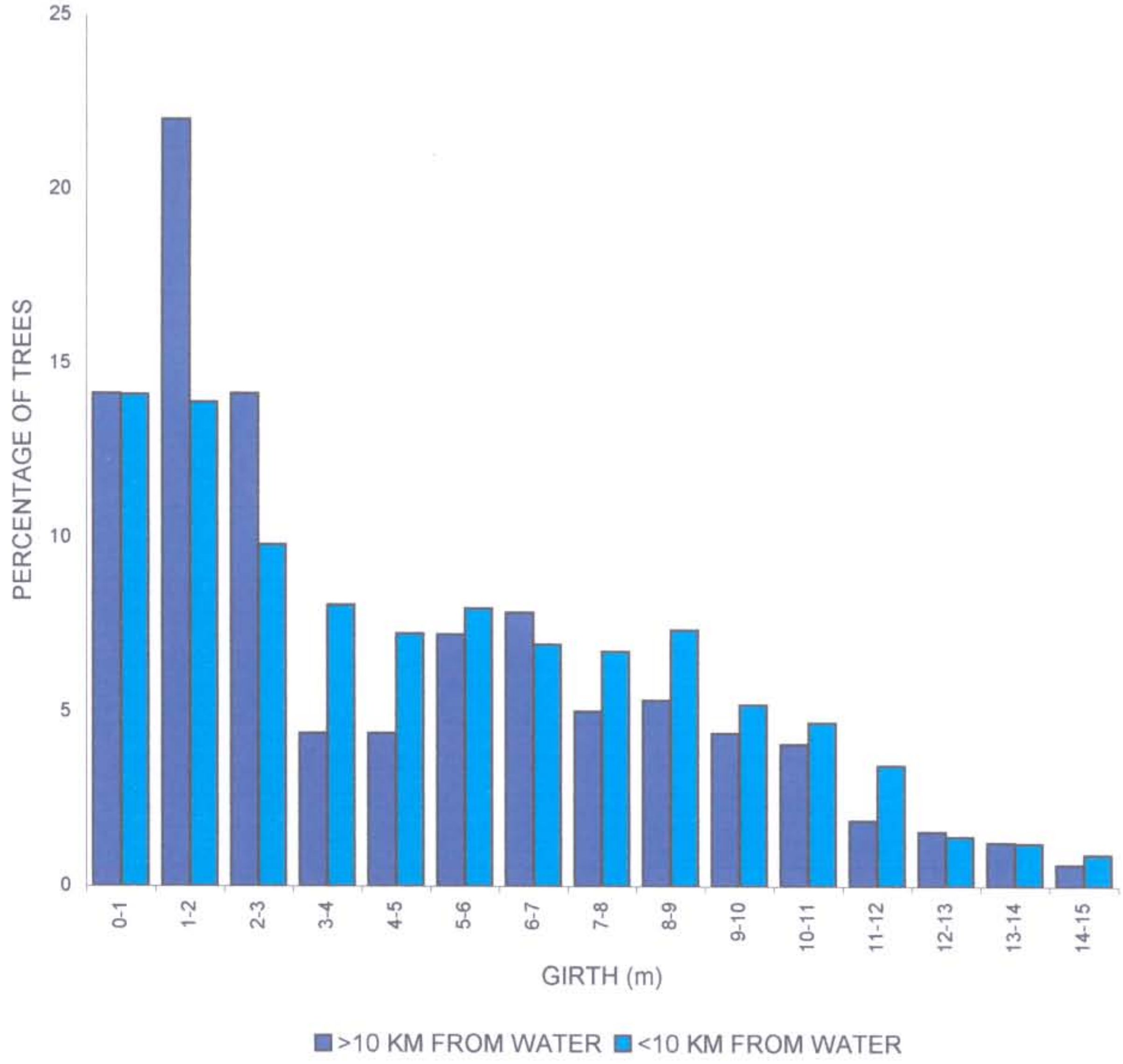
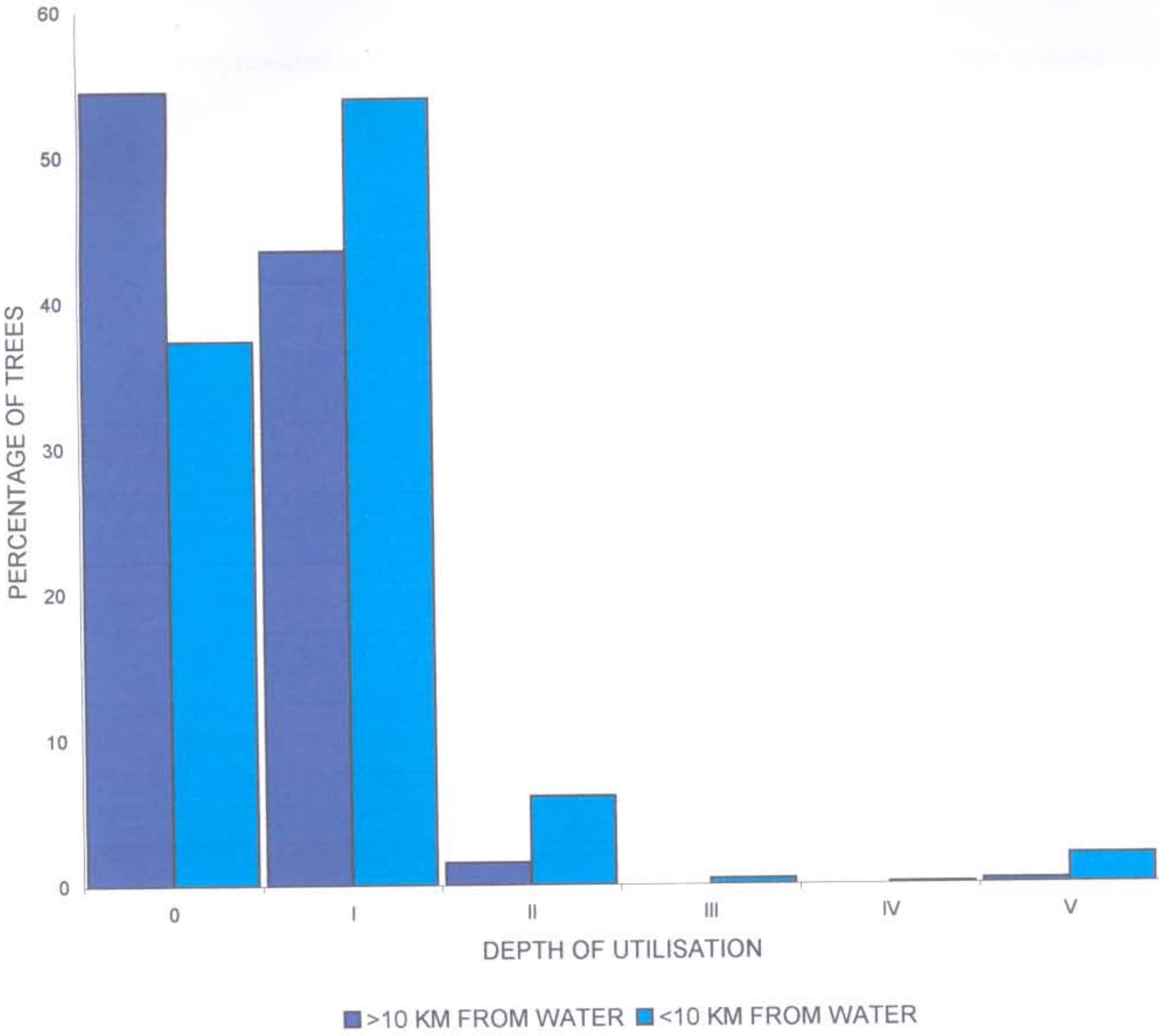


Fig. 23: Size class distribution of *Adansonia digitata* in the Kruger National Park in relation to the distance from permanent water.



0: TREE UNDAMAGED.
I: TREE SLIGHTLY SCARRED.
II: TREE RINGBARKED, BUT DAMAGE SUPERFICIAL.
III: TREE DEEPLY SCARRED.
IV: TREE SHAPE RADICALLY ALTERED BY UTILISATION.
V: TREE DEAD.

Fig. 24: Depth of utilisation of *Adansonia digitata* in the Kruger National Park in relation to the distance from permanent water.

are all better represented in the sample of trees further away from water than close to water (Fig. 25).

Utilisation of *Sterculia rogersii* trees is also greater near to water (Fig. 26). The distribution of the two populations on the depth of utilisation scale is significantly different (Kolmogorov-Smirnov two-sample test, $D_{\max} = 0.19$; $P < 0.001$), as are the damage scores (difference of proportions $z = -2.93$; $P < 0.005$). *Sterculia rogersii* trees within 10 km of permanent water have a damage score of 26.74, compared with a score of 22.19 for trees further away. The proportion of unutilised trees close to water is 12.06 %, compared with 31.34 % of trees further away (difference of proportions of the percent unutilised $z = 6.89$; $P < 0.001$).

DISCUSSION

To assess elephant utilisation, Swanepoel (1993) compared trees 20-30 km away from water with those closer to it. The study area in the Kruger National Park is bordered on two sides by perennial rivers. As a result of this, most areas are within a distance of 20-30 km from permanent water. In the Kruger National Park, vegetation utilisation becomes fatuous at a distance of more than 10 km from water. This smaller distance (10 km) was therefore chosen for this study, but was considered sufficient enough to yield significant results. Utilisation of both *Adansonia digitata* and *Sterculia rogersii* was far greater close to the river systems and waterholes than away from them.

In Mana Pools National Park, Zimbabwe, damage inflicted on baobab trees away from perennial water has been found to be significantly lower than damage inflicted on trees closer to water (Swanepoel 1993). It has also been found that the mortality of baobab trees near the Zambezi River is considerably higher than that of trees 20-30 km from perennial water.

In the Kruger Park, Van Wyk and Fairall (1969) have found that the utilisation of woody plants by elephant is inversely proportional to distance from water as well as the state of the

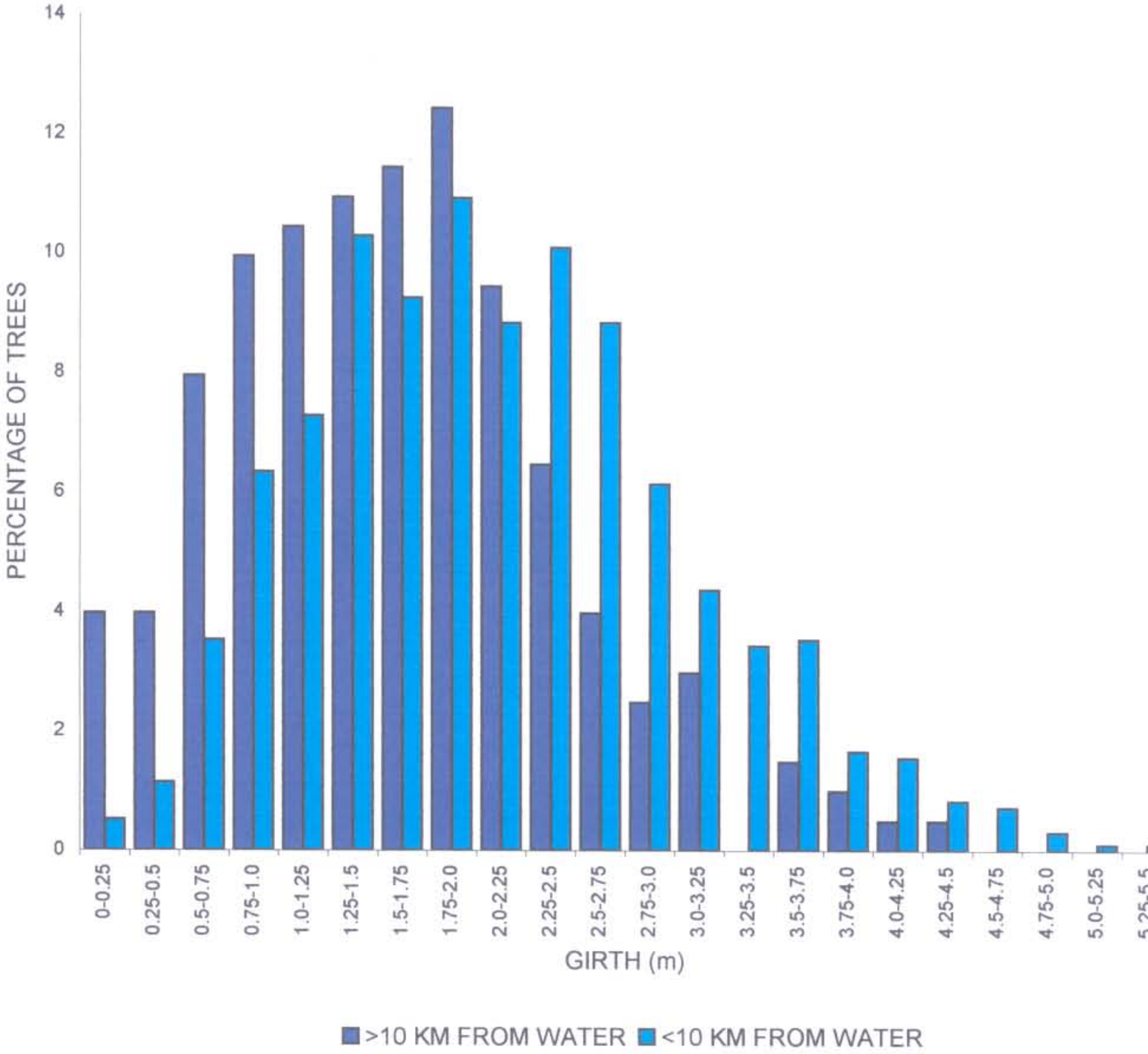
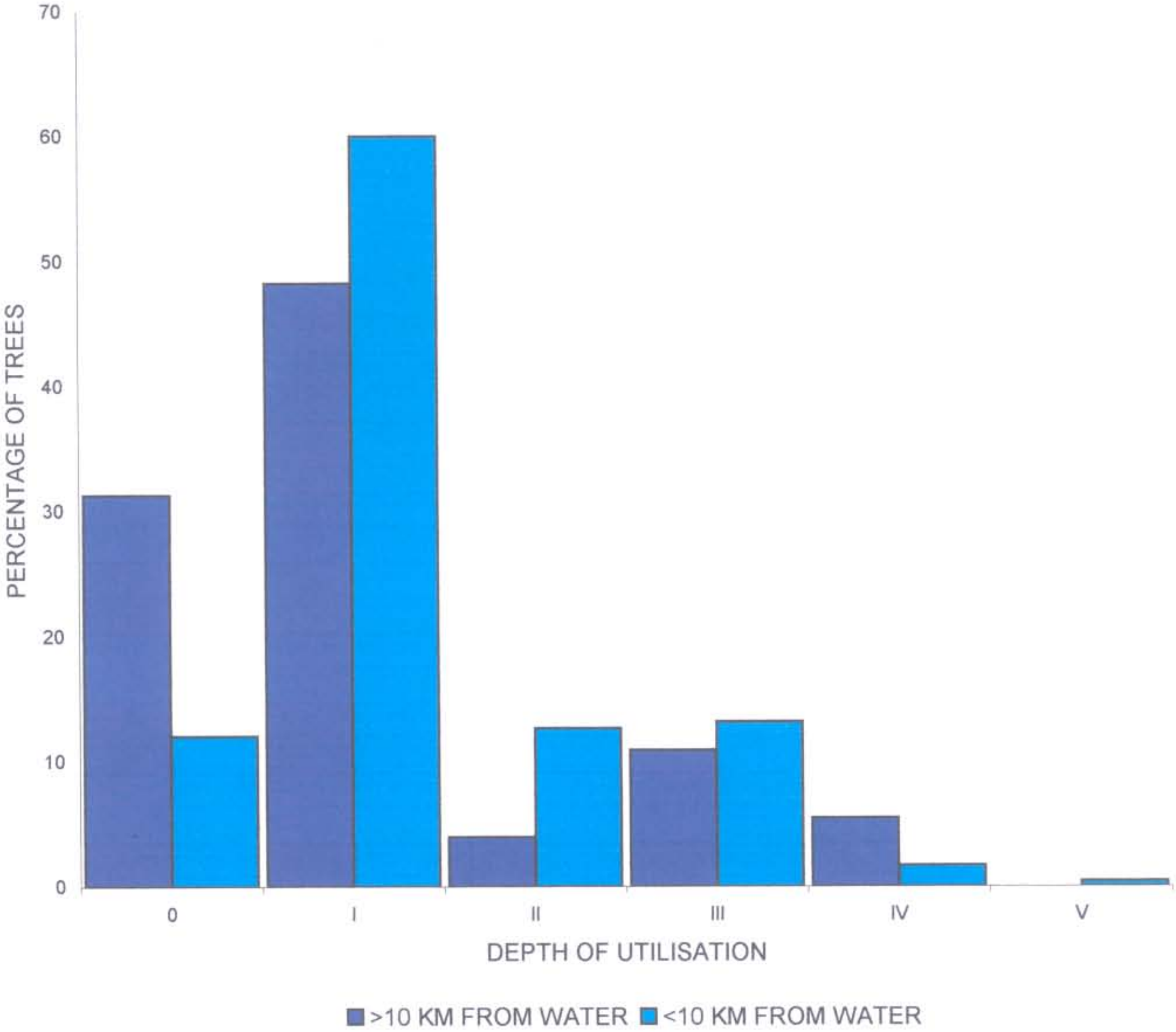


Fig. 25: Size class distribution of *Sterculia rogersii* in the Kruger National Park in relation to the distance from permanent water.



0: TREE UNDAMAGED.
I: TREE LIGHTLY BROWSED.
II: TREE WITH BRANCHES REMOVED BY BROWSING.
III: TREE WITH SOME STEMS BROKEN OFF.
IV: TREE WITH ALL STEMS BROKEN OFF.
V: TREE DEAD OR UPROOTED.

Fig. 26: Depth of utilisation of *Sterculia rogersii* in the Kruger National Park in relation to the distance from permanent water.

grass cover. The number of trees which died from causes other than elephant utilisation, however, shows an increase with distance from water which has been attributed to the fact that elephants remove some plants in the areas near water which would have died anyway.

This increase in utilisation close to water can be attributed to the distribution patterns of animals relative to water. A number of animals concentrate in the areas surrounding water. These include impala (*Aepyceros melampus*), zebra (*Equus burchelli*), blue wildebeest (*Connochaetes taurinus*) and buffalo (*Syncerus caffer*). Even during the winter months in the Kruger National Park, impala will usually only venture up to 2.2 km from water, zebras 7.2 km, blue wildebeest 7.4 km, and buffalo 7.8 km from water (Trollope 1990).

Although the distribution pattern of elephants is seasonal, during the dry season, they concentrate near permanent water points (Ben-Shahar 1993; Swanepoel & Swanepoel 1986; Van Wyk & Fairall 1969). During the August (dry season) of their study in the Kruger National Park, Van Wyk and Fairall (1969) found that all the larger elephant herds were either in the vicinity of the larger watercourses which had permanent waterholes or along perennial rivers. Only bachelor bulls, either solitary or in small herds were in areas where the water supply was meagre. Greater pressure on the vegetation surrounding permanent water results from this seasonal distribution patterns of elephants.

Swanepoel (1993) found that elephant feeding on baobabs occurred during the dry season, becoming more intense as the season progressed and then stopping abruptly with the first rains of the new season. This behavioural pattern of elephants, can further explain the increased utilisation of baobabs near water. During the dry season, when elephants feed on baobabs, the herds are in the vicinity of the water, and baobabs close to water are therefore utilised. With the onset of the rains, when the elephants move away from the rivers, they have ceased feeding on baobabs, with the result that the trees at a distance from water are not utilised to the same extent.

During dry periods, and especially drought years, the browsing by other large herbivores such as kudu and eland, causes considerable damage to fleshy stemmed plants such as

Sesamothamnus lugardii and *Sterculia rogersii*. Species other than elephant may therefore also be responsible for the increase in pressure on vegetation close to water.

CHAPTER 9

CONCLUSION

Insufficient evidence is available from the population structure of either tree species studied to indicate that elephant have had an effect on structuring the populations. The forces acting on the populations to determine this structure are not the same in the two species. There is overwhelming evidence to indicate that elephant do utilise the trees as a source of nourishment. This however is well known, but of greater relevance is the effect of this utilisation on the tree populations.

The utilisation of both tree species generally differs in the two study sections, mainly as a result of the older utilisation which is due to elephant only being present to the south of the Luvuvhu River for a number of years. The southern trees have therefore been utilised for a longer period and bear scars as evidence of this. Recently however, utilisation has been more intense in the north, a result of the increased elephant numbers in the area. Elephants are feeding on and injuring the trees, but do not appear to be affecting the long term survival of either the *Sterculia rogersii* or *Adansonia digitata* population. There is a possibility that utilisation lowers the resistance of trees to stress inducing factors such as drought, but this could not be determined in the time available for this study. Other than this, no evidence could be found to suggest that elephant are causing mortality of either tree species in the Kruger National Park. The death of baobabs is most likely due to a lack of soil water or simply extreme old age taking its toll (Piearce *et al.* 1994). The perception that increasing numbers of baobabs have perished in recent times is probably a result of the dry 1980s and early 1990s. A pertinent comment made by a Zimbabwean when questioned about the death of baobabs in that area was "it's not only the trees which are dying; people are dying of starvation and so are our livestock" (Piearce *et al.* 1994). During 1997, sooty mould was present on a number of baobabs in the study area. This syndrome is a manifestation of systemic stress related to lengthy periods of below average rainfall (Piearce *et al.* 1994), which lends further weight to the theory that drought and not elephant utilisation is currently the main cause of death of baobabs in the Kruger National Park.

It is risky to base conclusions about vegetation dynamics on single locations and short-term periods. It is also risky to base the management of protected areas in Africa on observations over short-term periods or single locations only (Prins & Van der Jeugd 1993). The impact of this utilisation therefore needs to be determined by means of a study over a number of years. It is recommended that a long-term monitoring programme is implemented in order to determine the correct management strategy regarding the utilisation of *Sterculia rogersii* and *Adansonia digitata* by elephant.

Long term monitoring is necessary to evaluate the impact of elephants and ensure correct management (Hoft & Hoft 1995; Kabigumila 1993; Tchamba 1995). Further research could most profitably concentrate on obtaining a better understanding of the conditions necessary for pollination and viable seed production by these two tree species. The conditions necessary for regeneration of baobabs and common star-chestnuts as well as the effect of other herbivores, fire and changes in climate on the tree populations could also be investigated further. This knowledge will also assist in isolating factors which may threaten the survival of these tree species in the Kruger National Park.

A long term monitoring programme should include trees of all ages from the full range of habitats. Although trees should be selected for monitoring which are easily accessible, care should be taken to ensure that these trees are representative of the entire population. If all monitoring takes place too close to roads, the data may be affected by the apparent affinity of elephant to use roads as routes of movement (Coetzee *et al.* 1979; Van Wyk & Fairall 1969). Similarly , the distance of trees from water needs to be taken into consideration as the utilisation of woody material has been shown to be higher close to watering points. Provision should also be made to allow for the incorporation of seedlings into the monitoring programme. Without this, no new information on regeneration can be gleaned and the monitored populations will simply appear to be ageing and will eventually die out.

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