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; $P < 0.05$).

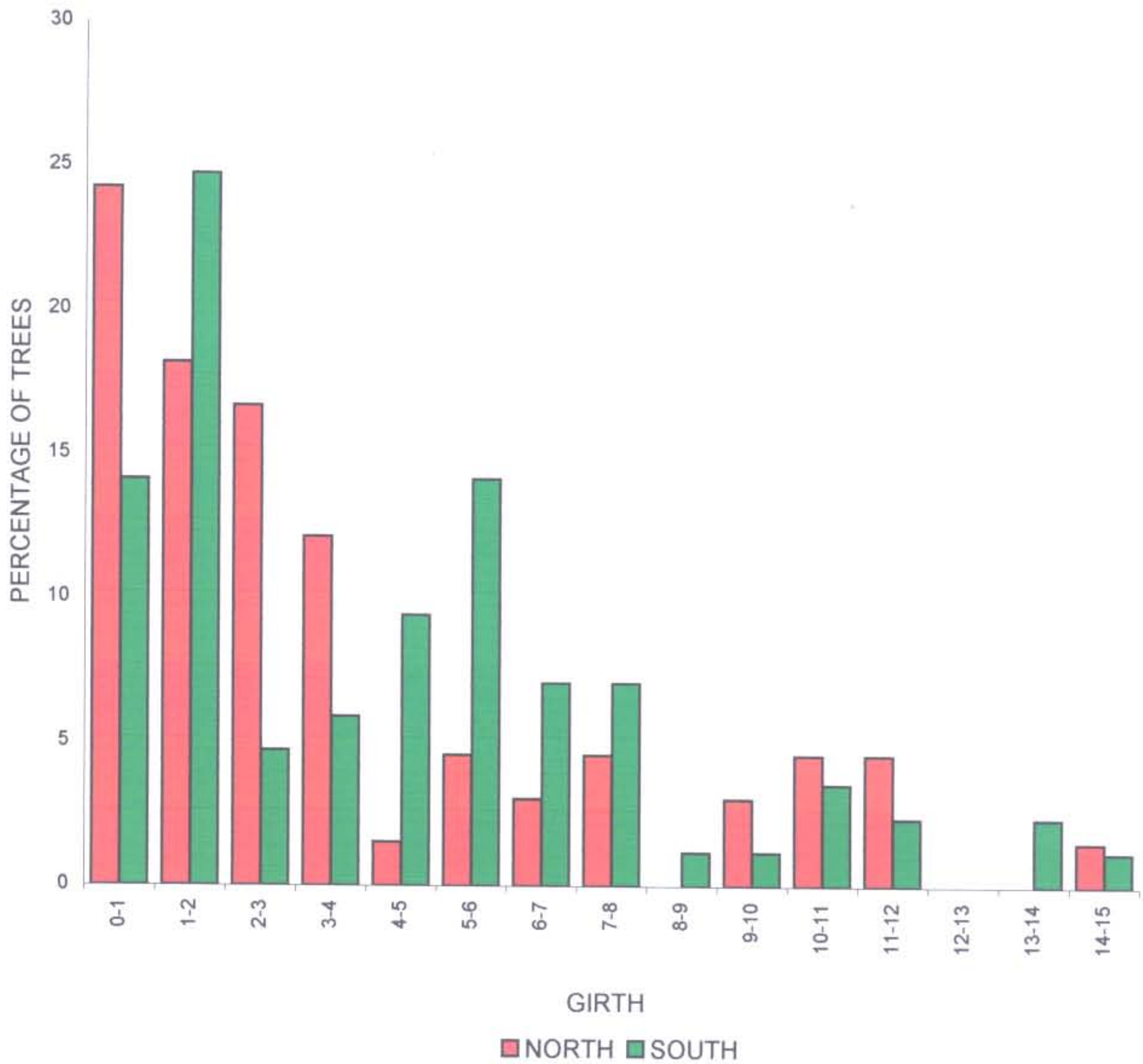

Fig. 7: Size class distribution (based on girth at breast height (m)) of *Adansonia digitata* in the Kruger National Park, north and south of the Luvuvhu River.

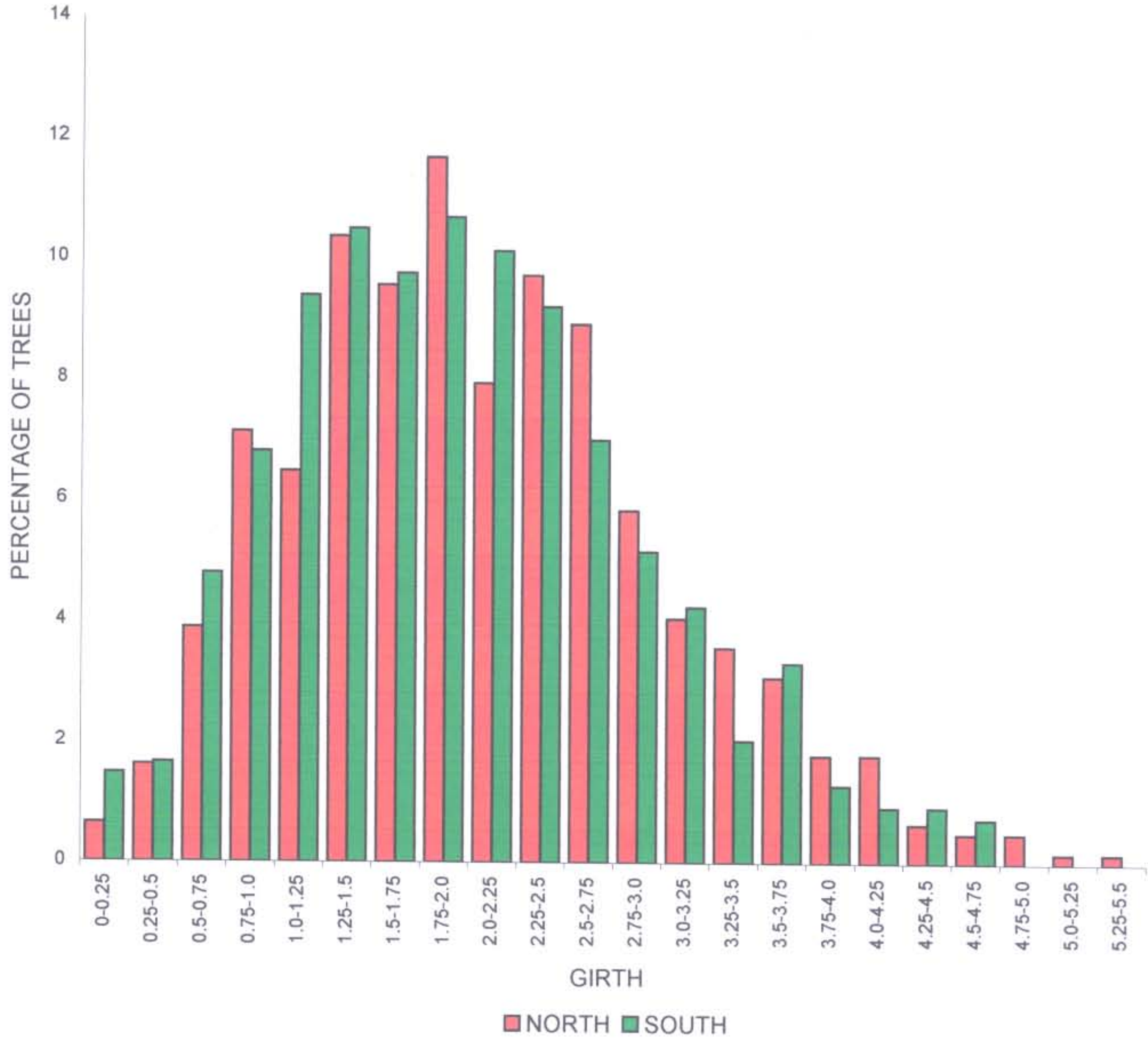

Fig. 8: Size class distribution (based on girth size at ground level (m)) of *Sterculia rogersii* in the Kruger National Park, north and south of the Luvuvhu River.

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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[2] Mr. R. Sowry. Wilderness Trails. Kruger National Park Private Bag X402 Skukuza 1350.

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.