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).

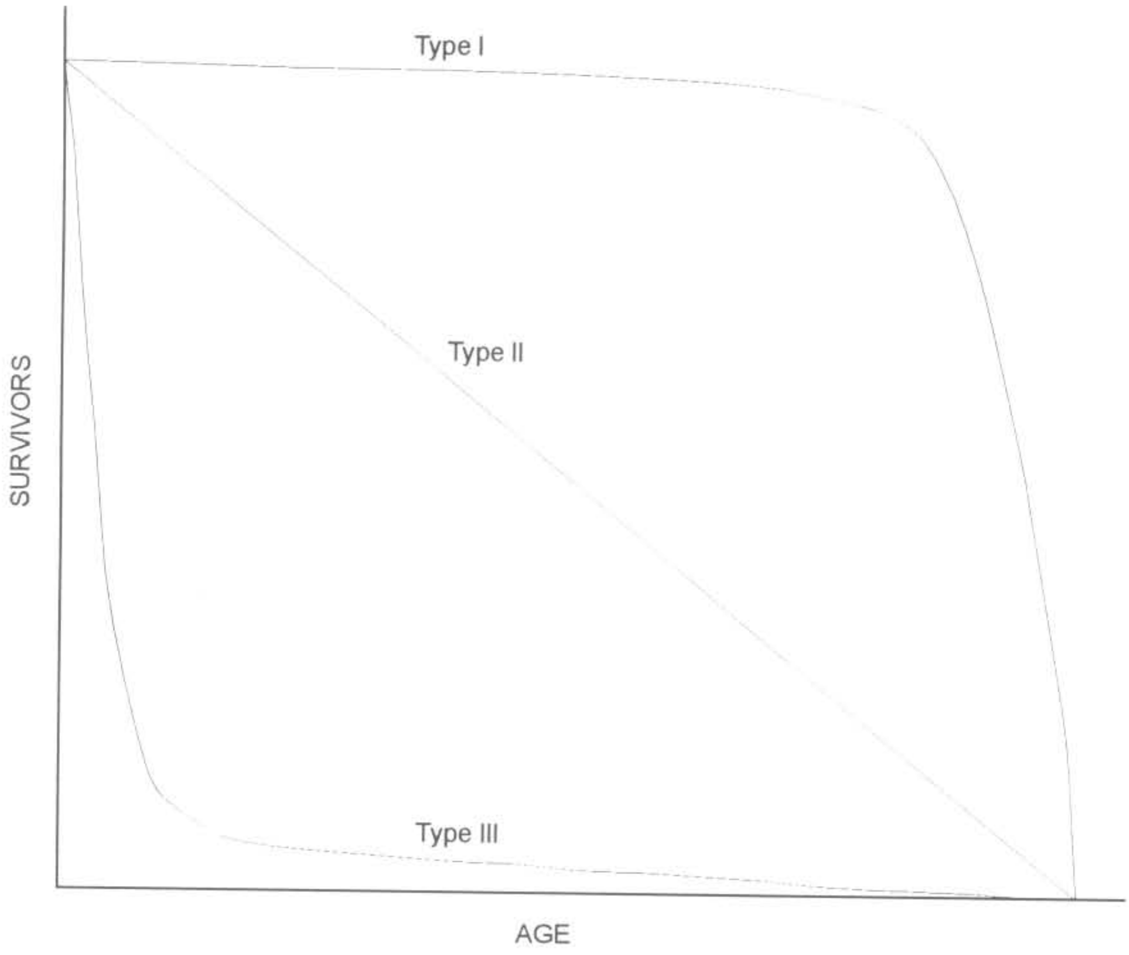

Fig. 19: Hypothetical survivorship curves.

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;

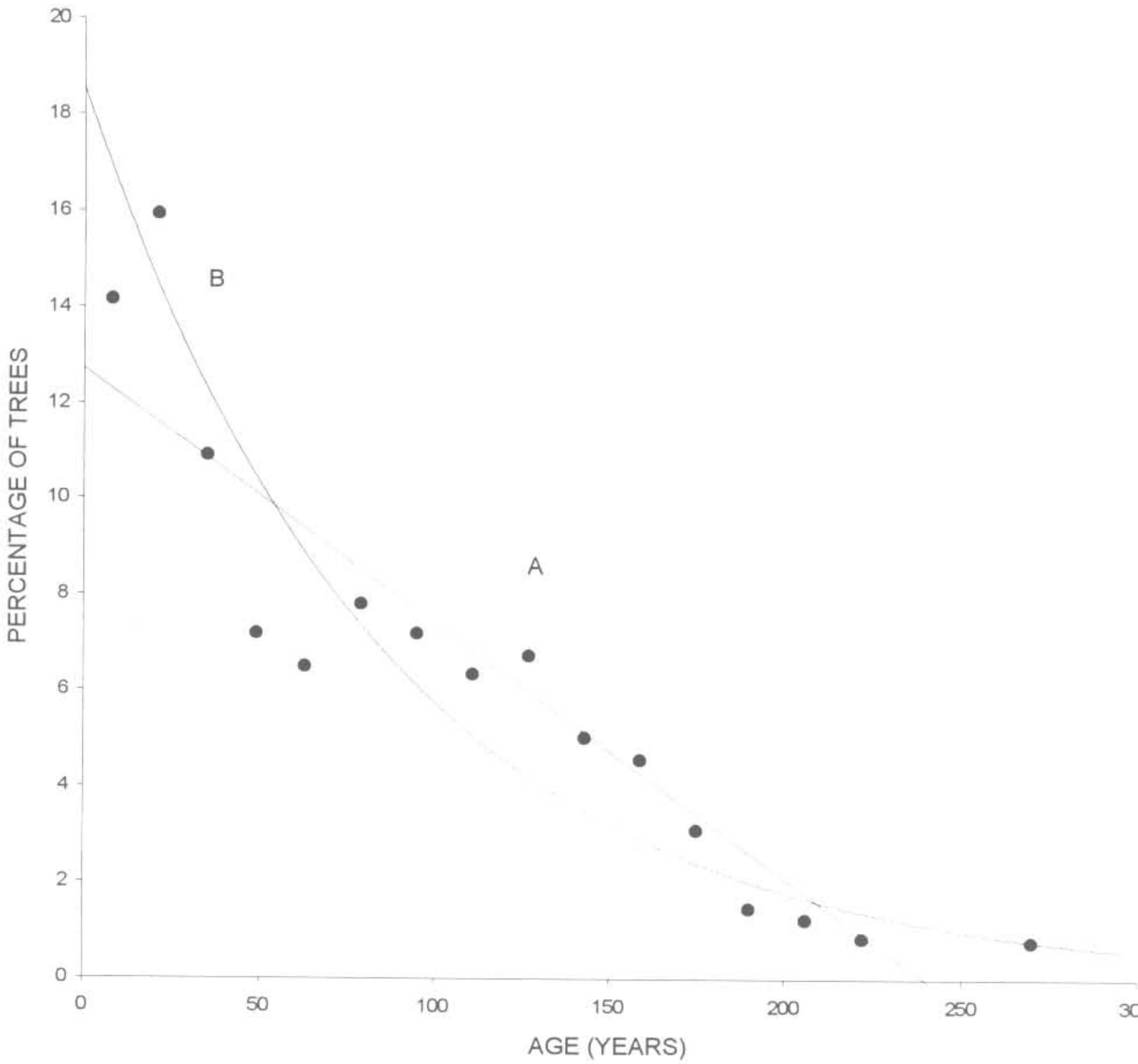

Fig. 20: Estimated age distribution and calculated survivorship curves of *Adansonia digitata* in the Kruger National Park.

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

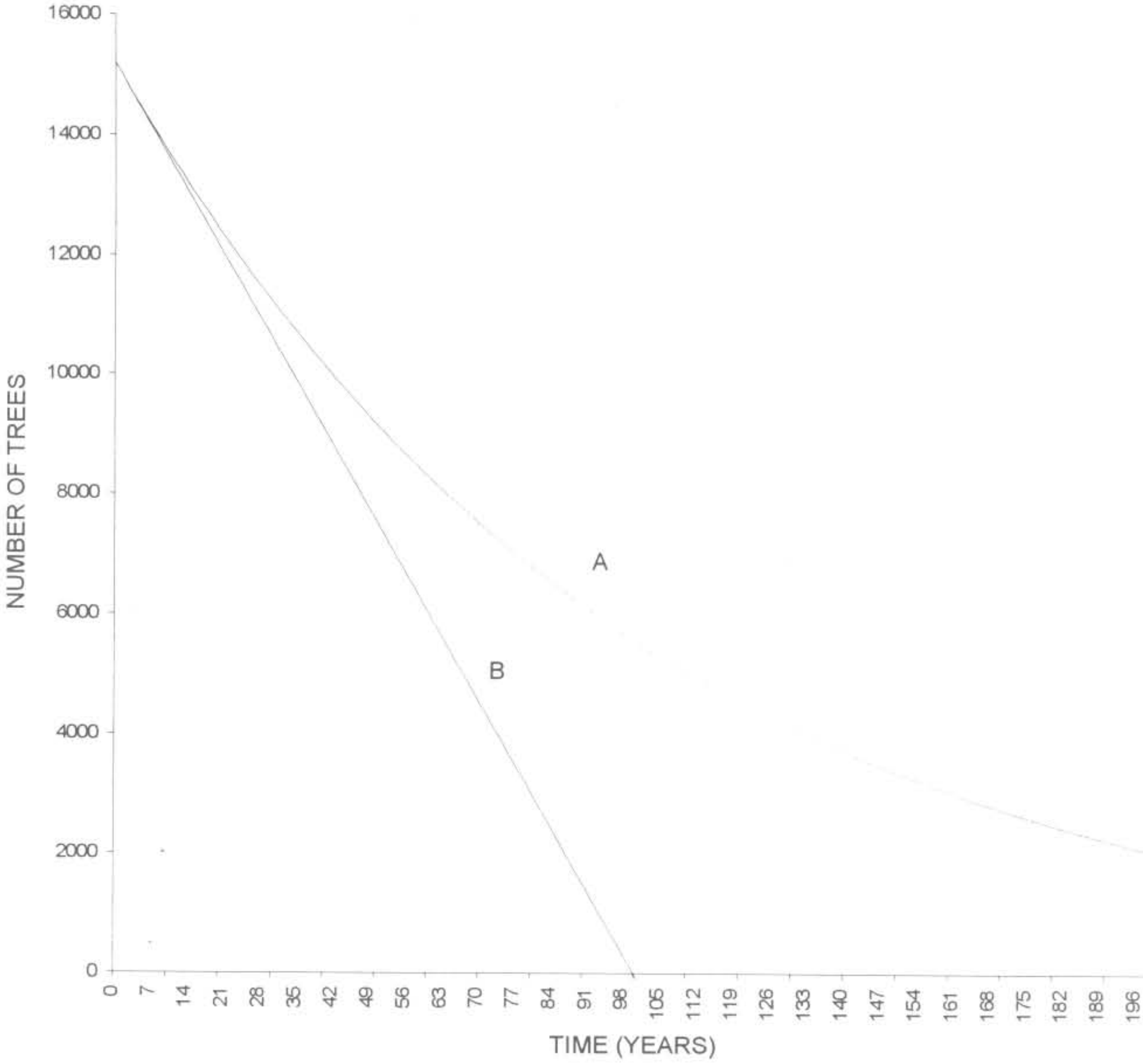

Fig. 21: Calculated future decline in the Kruger National Park *Adansonia digitata* population.

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.

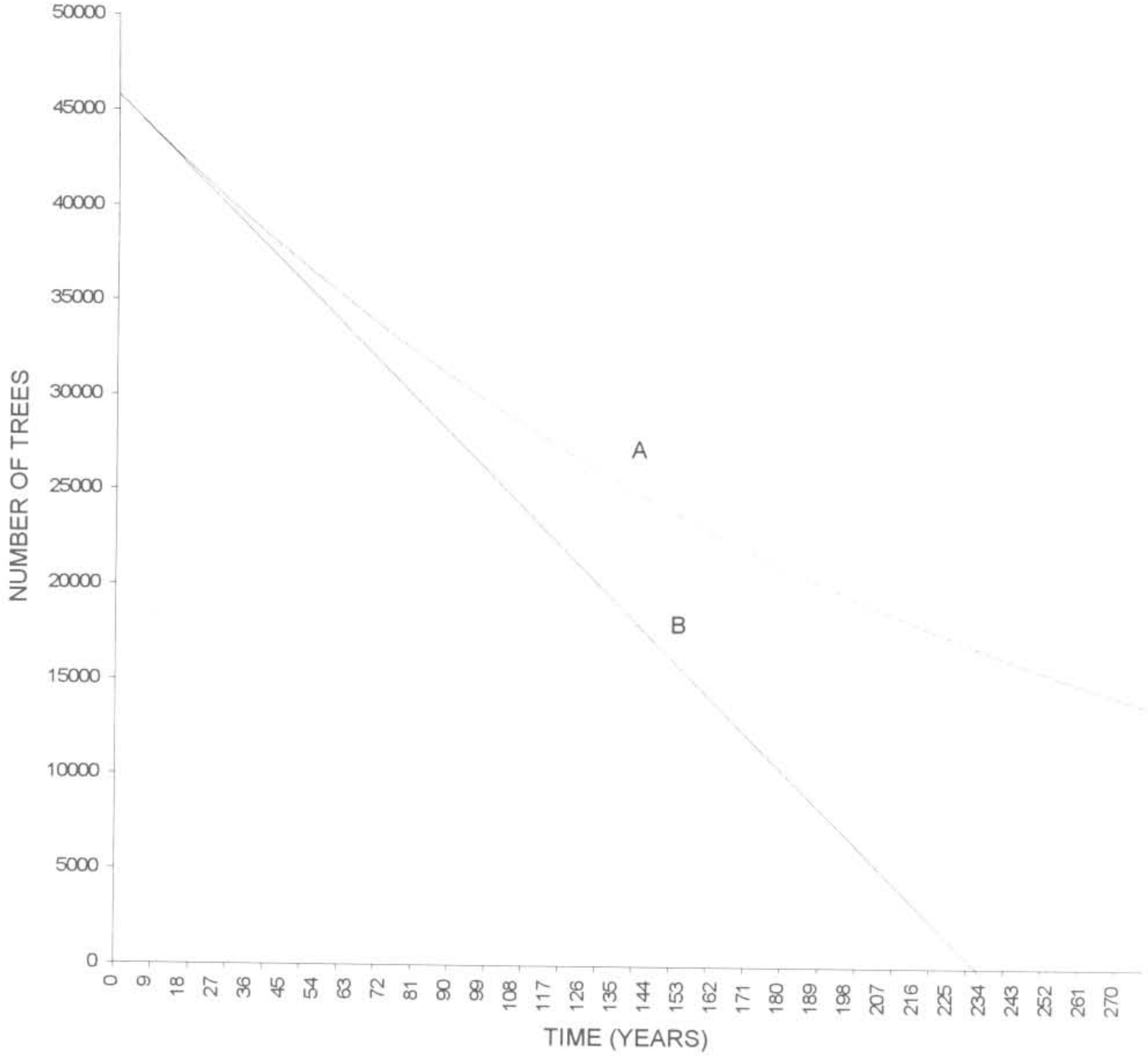

Fig. 22: Calculated future decline in the Kruger National Park *Sterculia rogersii* population.

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