TEMPORAL AND SPATIAL VARIATION IN POPULATION STRUCTURE OF THE AFRICAN BAOBAB (*Adansonia digitata*) IN THE KRUGER NATIONAL PARK, SOUTH AFRICA

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A dissertation submitted in fulfilment of the academic requirements for the degree
of Master of Science in the School of Animal, Plant and Environmental Sciences,
University of the Witwatersrand, Johannesburg.

June 2016

DECLARATION

I declare that this dissertation is my own, unaided work. It is being submitted for the Degree of Master of Science at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination at any other University.

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Signed on the 1st day of June 2016 in Hilton

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July 1995 | September 2013

ABSTRACT

The African baobab (*Adansonia digitata*) is a charismatic and iconic tree. This keystone species has highly specific moisture requirements for recruitment, a very slow life history, low dispersal capabilities, and is exposed to heavy, often destructive utilization by baboons, elephants and humans. These characteristics result in the reduced ability for baobabs to accommodate and respond to changing environmental conditions. During periods of unfavourable conditions, baobabs rely on the persistence of established individuals for the survival of the population.

The Kruger National Park (KNP), South Africa falls within the southern-most distribution of the baobab. A perceived lack of recruitment together with high numbers of dead large baobabs recorded in aerial surveys prompted concern over local population decline in the early 1990s. Long-term monitoring is necessary in order to quantify changes occurring within the KNP baobab population. For this reason Dr Ian Whyte sampled 424 baobab trees in northern KNP in 1995/1996 to describe population size-class distributions and elephant damage. Nearly all of these baobabs, with the addition of 486 individuals were resampled in 2001 by Michele Hofmeyr. This study resampled the majority of these 910 baobabs plus 126 individuals within 50m of those previously sampled, culminated in a data set spanning 18 years and most of the dominant vegetation and climatic zones within the baobab's KNP range. Photographs taken in 1995/6 and repeated in 2013 allowed for simultaneous direct visual comparisons of elephant damage to baobab stems. This study aimed to record the temporal and spatial changes in the demographics of, and damage to, this sample of 1036 baobabs in order to define and evaluate the factors threatening KNP baobab persistence.

The overall population stem diameter structure of baobabs in the KNP showed a healthy inverse J-shaped distribution, with a high proportion of smaller trees and a decreasing proportion of larger trees at each sampling snapshot. However no seedling recruitment was observed during intensive searches within 50m of sampled trees, accumulating in a total area of 4km^2. Growth was only noticeable in sub-adult trees >0.15m and <1m in stem diameter. Annualised mortality increased three-fold between the periods 1995/6-2001 (0.25%) and 2001-2013 (0.79%). It is speculated that this increase in mortality is due to the cumulative effect of increased elephant damage, together with below average rainfall years of 2002 to 2013. Trees that had previously sustained severe and very severe damage contributed the highest proportion (32%) of mortality. When comparing size-classes, the majority of mortality (61%) was recorded within the <1m stem diameter size-class. However, a high proportion of very large trees (21% of the 4-4.5m and 29% of the 5-5.5m stem-diameter baobabs sampled) had died from unknown causes. With no recruitment of seedlings evident and little recruitment between size classes, mortality alone was not enough to significantly change the baobab population structure between 1995/6, 2001 and 2013. This might change should more very large (>4m stem-diameter) trees die, as these size classes make up less than 2% of the population.

At a spatial scale, maximum fire return interval, level of elephant damage and mean annual temperature all had significant impacts on the size-class distribution of baobabs. Longer (>30 years) maximum fire return intervals and higher mean annual temperatures (23°C) supported an inverse J-shaped baobab population structure whilst shorter (<30 years) maximum fire return intervals and lower mean annual temperatures (21-22°C) supported a bell-shaped population structure. Increases in bark damage over time correlated with increased elephant density (primarily attributed to mature male elephant density). Smaller baobabs – those less than <1m in stem diameter, generally escaped elephant utilization altogether, or suffered very severe damage by elephants.

Despite a 3-fold increase in mortality and no recruitment over the 18 year study period, the KNP baobab population has maintained its inverse J-shaped population structure. The high proportion of mortality in the >4m stem diameter is however concerning as the persistence of these large baobabs is essential for the survival of the population during unfavourable conditions for recruitment.

ACKNOWLEDGEMENTS

My sincere thanks goes to my supervisors Prof. Ed Witkowski and Dr Dave Thompson whose academic and financial support made this study possible. Their continued guidance, comments and suggestions were valuable in all aspects of this study. Their encouragement and patience for a student whose love for fieldwork often kept him from his computer was much appreciated.

I thank Dr Ian Whyte, who initiated the measurement of baobabs in KNP in1995, and Michele Hofmeyr, who repeated and added to the sampling in 2001. Both gave their data freely, without which this project would not have been possible.

I would like to thank my post graduate research committee; Prof. Stuart Sym (Chairman), Prof. Ed Witkowski, Dr Dave Thompson, Prof Barend Erasmus, Michele Hofmeyr and Dr Sarah Venter for valued advice at the commencement of this study.

I thank South African National Parks Scientific Services Sharon Thompson, Sandra MacFadyen, Jacques Venter, and Chenay Simms, section rangers Sandra Visagie and Thomas Mbokota, field rangers Corporal Solomon, Carlos, Amos, Vusi, Jackson, Simon, Rirhandzu, and Pieter and game guards Isaac, Thomas, and Jacob for providing logistical support, geographical data, access, and protection in Kruger National Park. EcoTraining is thanked for accommodation in Pafuri.

I further thank Janet Taylor, Dr Ricky Taylor and Simon Smit for assistance in the field, Melissa Whitecross for advice with R-code, and Dr Izak Smit, Dr Ricky Taylor, Dr Tony Swemmer, Dr Daryl Codron and Tracey Johnson for advice and discussions relating to the study.

This research was made possible through funding provided by the Botanical Education Trust, the University of the Witwatersrand, Johannesburg, the South African Environmental Observation Network (SAEON), and the South African

National Research Foundation (NRF) Innovation fund (SFH12082710827). Opinions expressed and conclusions arrived at, are those of the author and are not necessarily to be attributed to the NRF or SAEON.

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LIST OF ABBREVIATIONS

KNP	Kruger National Park
LNP	Limpopo National Park
MAP	Mean Annual Precipitation
NRF	National Research Foundation
SAEON	South African Environmental Observation Network
SANParks	South African National Parks
SCD	Size Class Distribution

PREFACE

The work described in this dissertation was carried out in the Kruger National Park, South Africa, and combines archived data collected by Dr Ian Whyte in 1995/6 and Michele Hofmeyr in 2001 with current data collected in 2013. This 2013 data was collected by the author whilst registered with the School of Animal, Plant & Environmental Sciences at the University of the Witwatersrand, Johannesburg under the supervision of Professor Ed Witkowski and Dr Dave Thompson.

This dissertation is comprised of four chapters; a general introduction, two chapters forming the main body of work and a synthesis chapter to conclude the study. Chapters 2 and 3 have been structured as papers to facilitate publication. Hence there will unavoidably be some repetition in part for the sections such as the study site description, sampling methodology and the biology of baobabs, but this has been minimised as much as possible.

This dissertation, submitted for the degree of Master of Science at the University of the Witwatersrand, Johannesburg, represents the original work of the author. Where use has been made of the work of others, it has been duly acknowledged in the text.

CHAPTER ONE

General introduction

1.1 Baobabs and Global Change

Global climate change is expected to affect the distribution and abundance of most species (Thuiller *et al.* 2008). Changes in land use and habitat fragmentation decrease species abilities to adapt to change, thus compounding these effects. Tropical and subtropical Africa are expected to experience increases in average annual temperatures of up to 6°C with an increased frequency of extreme rainfall events combined with prolonged periods of drought by the end of the 21st century (Christensen *et al.* 2007; McClean *et al.* 2005; Engelbrecht *et al.* 2011). In a study of over 5000 African plant species, McClean *et al.* (2005) predicted that 25-42% of species would completely lose their climatically suitable habitat niche by 2085, whilst 81-97% would suffer from a reduction or shift in the area comprising suitable climate.

Taxa considered most vulnerable to habitat loss due to large-scale environmental changes are those with highly specialized habitats; delayed maturation and low reproductive rates; low dispersal capabilities or rates; and which are under pressure from intensive utilization (Hughes 2003; Araujo *et al.* 2006; Foden *et al.* 2007; Penman 2010; Cuni Sanchez *et al.* 2011). The African baobab *Adansonia digitata L.* (Malvaceae) meets most of these criteria, rendering it vulnerable to suffer habitat loss through environmental change. The baobab has a broad distribution, with trees surviving in the humid (1000-1500mm mean annual precipitation (MAP)) to very arid (50-100mm MAP) regions of Africa. However the geographic extremes of its distribution are thought to be relic populations established under past climates. Baobabs are typical of tropical and subtropical savannas, where a MAP of 400-800mm is considered ideal for their establishment and growth (Wickens & Lowe 2008). In order to survive a seedling cannot desiccate during its initial growing season and survival is micro-site limited

(Venter & Witkowski 2013a). Baobabs occur where the mean monthly maximum temperatures range from 23-38°C and the mean minimum temperature ranges from 5-15°C (Wickens & Lowe 2008; Cuni Sanchez 2010). Although its range rarely overlaps with frost occurrence, the species appears to be resilient to frost and can withstand night-time temperatures down to -7°C (Leger 1977 cited in Wickens & Lowe 2008). Baobabs are intolerant of deep unconsolidated soils, which are unable to provide sufficient soil moisture and anchorage, as well as frequently waterlogged soils, in which they rot (Wickens & Lowe 2008).

Baobabs are long-lived and Patrut *et al.* (2013) used radio carbon dating to age a very large individual in Limpopo province, South Africa at 1835 ± 40 years old. The species also has a very slow life history. First flowering can occur after approximately 20 years (Pardy 1953; Wickens & Lowe 2008) however some studies suggest that, where water is limiting, trees take much longer to mature with some trees only flowering after 246 years (Venter & Witkowski 2013c). Whilst seed production ranges from 30-400 seeds per pod (Rashford 1991), and up to 299 pods per adult tree, there is high inter-annual variation in seed production and a high proportion (up to 41%) of poor-producers, consistently producing less than 5 fruit per year (Venter & Witkowski 2011). Seeds are dispersed by baboons, within local home ranges, elephants, now often confined within parks and protected areas (Wickens 1982; Wickens & Lowe 2008) and humans. Germination success has been shown to increase with the physical scarification of seeds or soaking of seeds in water for several days or acid for several hours (Esenowo 1991; Hines & Eckman 1993; Wickens & Lowe 2008). The successful recruitment of seedlings through to maturity is very low (Wickens & Lowe 2008). Observations in north-eastern Zimbabwe found that no seedlings in the vicinity of adults survived for more than one season due to heavy herbivory (Schutte 1954). Venter and Witkowski (2013a) showed that within communal lands in northern South Africa, infrequent rainfall resulted in the mortality of almost all the seedlings and those that managed to persist, within suitable micro-sites, were eaten by livestock. The baobab is a favoured resource among both humans and elephants and, as such, endures heavy, often destructive, utilization which further threatens the species (Wickens & Lowe 2008). Extensive bark and stem damage is expected to decrease an individual's ability to survive extended periods of drought (Whyte 2001b).

The highly specific moisture requirements for recruitment and the intolerance of waterlogged or deep unconsolidated soils, the very slow life history, the low dispersal capabilities reliant on baboons, elephants and humans, and the heavy often destructive utilization by these same species, result in the reduced ability of baobabs to adapt or disperse. Unable to accommodate changing environmental conditions, the baobab is vulnerable to range retraction (Cuni Sanchez 2010).

1.2 Baobab Ecology

The baobab, with adult height and stem girth measurements in excess of 20m, is a charismatic and iconic large tree of tropical and subtropical African savanna (Wickens 1982; Kelly 2000; Venter & Witkowski 2010). On mainland Africa, there is currently only one naturally occurring species of baobab. A recent study suggested a split in this species based on differences in chromosome numbers, into tetraploid *A. digitata* and diploid *A. kilima* (Pettigrew *et al.* 2012). This spilt has since been rejected and the *A. kilima* type specimen has been shown to be tetraploid (Cron *et al.* 2016). There have been several previous suggestions regarding the taxonomic status of other *Adansonia* species and varieties on mainland Africa, but none are widely accepted (Pettigrew *et al.* 2012).

The African baobab plays a keystone role in ecosystem functioning providing habitat and food for many animals (Kelly 2000). Baboons, elephants, and a variety of antelope utilize various parts of the tree for forage whilst moths and fruit bats utilize nectar and pollen (Wickens 1982). Large trees especially provide important nesting sites for many birds, including several rare and locally threatened species *viz.* grey-headed parrots, southern ground-hornbills, white-headed vultures and two species of spinetail (Kelly 2000; Whyte 2001a; 2001b; Edkins *et al.* 2008; Venter & Witkowski 2011). The species is also highly valued by humans for the many services it provides. Important sources of food, fodder, building material, water, medicine, shelter, and spiritual and cultural services are examples of the over 300 human-related services attributed to this species across its range (Wickens 1982; Sidibe *et al.* 2002; Wickens & Lowe 2008; Cuni Sanchez *et al*. 2011; Venter & Witkowski 2013b).

Observed natural recruitment of baobabs is very low throughout Africa and it is thought to be confined to the current higher rainfall regions of its distribution (Wickens and Lowe 2008). Recruitment is non-existent in the very arid regions of its range, where large baobabs are considered relics of more humid climates that are reliant largely on ground water for survival (Wickens and Lowe 2008). While seedlings are less resilient to droughts and have difficulty establishing in the absence of rain, long-lived adults are likely to survive for a period as a relict population before extirpation (Wickens & Lowe 2008; Cuni Sanchez *et al*. 2011). Wickens & Lowe (2008) suggest that the baobab distribution will inevitably retreat from the dryer regions of Africa through adult mortality. There is however very little certainty as to the extent to which the current population will retreat (Cuni Sanchez *et al*. 2011). Models of eastern and southern African baobab distribution predict that between 27% - 91% of the current range is likely to remain suitable for them in the future (Cuni Sanchez *et al.* 2011). Mean temperature of the coldest 4 months and temperature seasonality were the most important variables for predicting baobab distribution (Cuni Sanchez *et al*. 2011).

As a long-lived species, a mature baobab may have several opportunities to successfully recruit during its lifetime. Indeed, due to individual longevity, a low recruitment rate is sufficient to sustain existing populations (Wickens & Lowe 2008; Venter & Witkowski 2010). In the absence of continuous recruitment, the survival of reproductive adults is important for the long-term survival and conservation of the species.

1.3 Baobabs and Elephants

Many studies in Africa have shown the negative effects of elephants on established baobab populations (Robertson-Bullock 1960; Caughley 1976; Barnes 1980; Swanepoel 1993; Edkins *et al*. 2007). In 1975 baobab mortality of 3% was recorded in Ruaha National Park, Tanzania, attributed to elephant densities of 4 elephant/km^2 (Barnes 1980). Further Barns (1980) suggested that bull elephants were most likely responsible for the destruction of mature baobabs. An annualised mortality of 2.9% was recorded for baobabs in Mana Pools National Park, Zimbabwe, for the period 1984 to 2005 (Swanepoel & Swanepoel 1984; Ndoro *et al.* 2014a), correlating with elephant densities of between 1.6 and 2.7 elephant/km^2. Baobab mortality of 1.1% was recorded at Lake Manyara National Park, Tanzania in 1981, where elephant densities were as high as 4.9 elephants/km^2. However, the baobab population structure showed no significant changes over an 11-year (1969 to 1981) comparison (Weyer-Haeuser 1985). Weyer-Haeuser (1985) suggested that steep slopes and rough terrain reduced elephant impact on baobabs growing on the escarpment. Edkins *et al.* (2005) labelled these less accessible areas as baobab 'refugia' from elephants. Elephants spend a large portion of their time near water sources and habitat-use generally increases with proximity to water (Harris 2008). In a comparison of baobab densities and elephant damage at different distances from the Zambezi River in Mana Pools National Park, Zimbabwe, Ndoro *et al.* (2014b) found that baobab densities were highest ~50km from the Zambezi (22.4 baobabs/km^2 as opposed to <5 baobabs/km^2 at sites closer to the Zambezi). Baobabs located ~50km from the Zambezi also had the lowest level of recorded bark damage, suggesting that increased distance from water does afford baobabs greater protection from elephant damage, and indeed, of survival.

1.4 Baobabs in the Kruger National Park

The Kruger National Park (KNP), South Africa, is listed as one of only nineteen protected areas in Africa that currently has suitable habitat for baobabs that will remain suitable in the future under all models and scenarios tested by Cuni Sanchez *et al.* (2011). The southernmost limit of the baobab's natural distribution is approximately 24.5°S, with KNP spanning this southernmost boundary. Due to its importance as a keystone species, its cultural and spiritual value and the potential threat of over-utilization by humans, baobabs are formally protected under South African legislation in the National Forests Act of 1998 and in the revised Act of 2012. Furthermore, the listing of the baobab as a species of special concern, a functionally important and locally threatened species, by SANParks highlights the significance of this species and provides motivation for on-going monitoring and where necessary, conservation action (McGeoch *et al.* 2010).

Between ~20 000 (Nel 1988) and ~15 000 (Kelly 2000) baobab trees are thought to occur in northern KNP. Calculated densities range from 32.2 baobabs/km^2 along the flood plains of the Luvuvhu and Limpopo rivers in the north of the park to 5.3 baobabs/km^2 in the vicinity of Punda Maria rest camp (Kelly 2000). However, as reported elsewhere in Africa (Assogbadjo *et al.* 2005; Wilson 1988; Caughley 1976; Barnes 1980), there has been growing concern among local conservationists over a perceived lack of recruitment of baobabs in KNP (Edkins *et al*. 2007). With very low recruitment rates, long-lived baobabs are reliant on the survival of established trees in order for the population to persist (Venter & Witkowski 2010). These established baobabs were however declining in number and during the 1980's and early 1990's aerial surveys, mortality of more than 1000 large baobabs in northern KNP were recorded (Whyte 2001).

Whyte (2001) and Hofmeyr *et al*. (2004) considered extended periods of drought to be the predominant cause of mortality in mature baobab trees, and although both studies recorded the widespread occurrence of elephant impacts, few trees were extensively damaged. Whyte (2001) warned that an increased density of elephants may have a negative effect on the baobab population and increase individual's vulnerability to droughts. However, transects conducted in 1999 by Kelly (2000) provided no evidence that elephants played a significant role in the mortality of adult baobabs in northern KNP.

In his study, Kelly (2000) compared two sub-populations of baobabs in KNP, one north of the Luvuvhu River which had previously been managed for very low elephant densities and one south of the Luvuvhu River, which had relatively higher elephant densities. Kelly (2000) found that, while elephant impact – as seen from the level and severity of bark utilization - was greater in the southern population, there was no substantial difference between the size structures of the two populations. Both displayed an inverse-J shaped size-class distribution with many small and fewer large individuals. In 2004 Edkins *et al.* (2007) compared a small subset of the baobab population sampled by Kelly (2000) in northern KNP with a population in the adjoining Limpopo National Park (LNP), Mozambique, with substantially relatively lower elephant densities. While the LNP population showed an inverse J-shaped size class distribution, the KNP population displayed a bell-shaped population size structure, with a decreased number of smaller and larger trees. Edkins *et al.* (2007) attributed this to heavy elephant utilization that resulted in increased mortality of smaller individuals as the expected inverse J-shaped population size structure was only found on steep rocky slopes that were considered largely inaccessible to elephants. These authors further suggested that the limited distribution of suitable baobab 'refugia' within the landscape was not sufficient to sustain the KNP baobab population. There are however a multitude of other variables that could possibly affect the demographics of baobabs in the region including the effects of fire, rainfall and temperature. In addition several changes have occurred in the management of KNP in recent decades, including changes in fire regime, elephant management, and water availability (Table 1). Kelly (2000) suggested that further studies were needed to critically asses changes occurring within the KNP baobab population and evaluate those factors threatening their survival.

Table 1. The history of fire management, elephant management, artificial water provision and human habitation in KNP, from Carruthers (1995), Pienaar (2005), van Wilgen *et al.* (2003), Whyte (2007) and SANParks (2013).

Year	**Fire**	**Elephants**	**Artificial Water**	**Human Habitation**
1900		No elephants due to hunting.		The expansion of the Sabi Game reserve incorporated many African communities. Approximately 3000 residents were permitted to live within the park.
1905		First sign of elephants in the KNP.		
1910				
1915				
1920				
1925	Occasional and limited burning.			
1930			Initial phase of artificial water point provision.	The eviction of the Makuleke community from the north of the park was the start of major relocation of African residents out of KNP
1935				
1940				
1945				
1950	Management burns were stopped and wild fires were suppressed.			
1955				
1960	Blocks burnt every 3 years, in spring.		Rapid increase in the development of artificial water points.	
1965				
1970		Aerial census estimates population to be 6586.		
1975		Culling program maintains population at around 7000.		
1980	Variable periods between burns depending on rainfall, time since last burn, and management objectives		No. of artificial water points reached its peak with 35 dams and over 200 active boreholes.	
1985				
1990	Lightning fires only, anthropogenic fires were suppressed.			
1995		Culling program stopped.	Selected artificial water points are closed to relieve pressure on vegetation and rare antelope.	
2000	Utilization of an integrated fire approach using point ignition and unplanned fires. Once a pre-set target is reached only lightning ignitions are tolerated.	Population reaches 10000.		
2005				
2010		Population estimated at 13750.		

1.5 Rationale

Elephants, desertification, climate change, fire, and modern management practices have all been blamed for the reduction in baobab densities and distribution, yet all these factors require critical assessment over time-periods appropriate to this long-lived species (Wickens & Lowe 2008). Seventeen trees in Skelmswater near Messina, South Africa, have been monitored for growth in relation to rainfall since 1931 (Wickens & Lowe 2008). This 76-year dataset provides a relevant temporal scale and useful information on tree growth in response to rainfall; alone it is of limited use for the purpose of comparing population demographics and assessing factors that limit survivorship within various landscape contexts. Long-term monitoring is necessary in order to quantify changes occurring within the KNP baobab population and to define and evaluate those factors threatening local baobab survival (Kelly 2000). This monitoring should be inclusive of all the habitats and environmental conditions experienced by baobabs within KNP (Kelly 2000).

In July 1995 and January 1996, Dr Ian Whyte sampled 424 baobab trees in northern KNP in order to compare differences in their population structure and degree of elephant damage north and south of the Luvuvhu River in Pafuri (Whyte 2001). In a comparative study, Michele Hofmeyr resampled nearly all (413) of these 424 individuals between April and September 2001 (unpublished). She included an additional 486 trees to increase the range of habitats sampled. Together the 1995/6 efforts of Whyte and the 2001 sampling of Hofmeyr provided a 5/6-year data set reflecting recruitment, adult mortality and survivorship, and elephant damage for 892 baobab individuals in northern KNP. These trees are distributed over several Mucina and Rutherford (2006) vegetation units, and across broad rainfall, temperature and fire frequency gradients.

1.6 Aim and objectives

During this study the majority of previously sampled baobabs, 418 of the initial (1995/6) 424 individuals and 340 of the additional (2001) 486 individuals, were resampled between July and November 2013. This study could not include all of the previously sampled trees due to access constraints imposed by security concerns relating to poaching. An additional 126 individuals occurring within a 50m radius of previously measured trees (a total of about 4 km^2 searched, including seedlings and saplings) was added to the data-set. The resulting data-set spanned 18 years and the dominant vegetation and climatic zones within the baobabs KNP range.

The aim of this study was to record temporal and spatial changes in the demographics of, and levels of damage to, a sample of 1036 baobabs in northern KNP in order to define and evaluate those factors threatening local survival. In addition, in order to assess baobab regeneration, a 50 m radius search around previously sampled baobabs was undertaken for seedlings and saplings.

This study compares changes in the population structure of baobabs over time across multiple environmental and climatic conditions to better understand the drivers of recruitment, growth and mortality in KNP (Chapter 2).

In addition, this study focuses on levels of elephant utilisation and the resultant damage to baobabs, and relates damage, and individual fates across different size classes and landscapes of variable accessibility to elephants (Chapter 3).

CHAPTER TWO

Fire, utilization by elephants and temperature shape the population structure of baobabs in the Kruger National Park, South Africa

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Target journal: *Forest Ecology and Management*

2.1 Abstract

The African baobab is an iconic species throughout subtropical and tropical African savannas. Concern for this keystone species is mounting in the northern Kruger National Park (KNP) where little to no recruitment and perceived high mortality levels are considered to be leading towards population decline of these long-lived trees. This study builds on the foundation of previous efforts conducted in 1995/6 and 2001 and compared changes in baobab population structure over ~18 years (1995-2013) and across multiple environmental and climatic conditions, to better understand factors driving recruitment, growth and mortality. The overall population structure of baobabs in KNP showed an inverse J-shaped distribution, with a high proportion of smaller trees and a decreasing proportion of larger trees at each sampling snapshot. Population structure did not change significantly during ~18 years. At a spatial scale, maximum fire return interval, level of elephant damage and mean annual temperature all had significant impacts on the size-class distribution of baobabs. However, rainfall showed no significant effect on the population structure of baobab. The northern-most parts of KNP, which has longer (>30 years) maximum fire return intervals and higher mean annual temperatures (23°C) supported a negatively skewed and theoretically healthy baobab population structure whilst further south, the area around Punda Maria rest camp has shorter (<30 years) maximum fire return intervals and lower mean annual temperatures (21-22°C) supported populations dominated by intermediately sized individuals. Elephant damage affected smaller sized trees more than large trees, where trees <0.5m in stem-diameter either escaped elephant utilization or suffered severe or worse damage. Increased levels of elephant damage is likely to decrease the ability of baobabs to persist under unfavourable climatic conditions.

2.2 Keywords

Adansonia digitata, demographics, elephant utilisation, rainfall, size-class distribution, temperature, vegetation units

2.3 Introduction

The African baobab, *Adansonia digitata* L. (Malvaceae), plays a keystone role in ecosystem functioning providing habitat and food for many animals (Kelly 2000). Baboons, elephants, and a variety of antelope utilize various parts of the tree for forage whilst moths and fruit bats utilize nectar and pollen (Wickens 1982). Large trees especially provide important nesting sites for many birds, including several rare and locally threatened species *viz*. grey-headed parrots, southern ground-hornbills, white-headed vultures and two species of spinetail (Kelly 2000, Whyte 2001a; 2001b, Edkins *et al*. 2008, Venter & Witkowski 2011). The species is also highly valued by humans for the many services it provides. Important sources of food, fodder, building material, water, medicine, shelter, and spiritual and cultural services are examples of the over 300 human-related services attributed to this species across its range (Wickens 1982; Sidibe *et al*. 2002; Wickens & Lowe 2008; Cuni Sanchez *et al.* 2011; Venter & Witkowski 2013b).

Whilst the baobab has a broad distribution, with relic trees surviving in both the humid (1000-1500mm mean annual precipitation (MAP)) to very arid (50-100mm MAP) regions of Africa, a MAP of 400-800mm is considered optimal for establishment and growth (Wickens & Lowe 2008). Baobabs occur where the mean monthly maximum temperatures range from 23-38°C and mean minimum temperature ranges from 5-15°C (Wickens & Lowe 2008, Cuni Sanchez 2010). Baobabs are intolerant of deep unconsolidated soils, which are unable to provide sufficient soil moisture and anchorage, as well as frequently waterlogged soils, in which they rot (Wickens & Lowe 2008). Baobabs are therefore found on a wide range of well drained soils. They also grow in shallow and stony soils and on rock outcrops where water is provided through seepage lines.

Observed natural recruitment of baobabs is very low throughout Africa (Wickens and Lowe 2008). Recruitment is non-existent in very arid regions, where large baobabs persist largely through reliance on ground water for survival; they are considered relics of previously more humid climates (Wickens and Lowe 2008).

Wickens & Lowe (2008) suggest that the contemporary distribution range will inevitably retreat from the dryer regions of Africa through adult mortality. Models of eastern and southern African baobabs predict that 27% to 91% of the current baobab distribution is likely to remain suitable for them in the future (Cuni Sanchez *et al*. 2011). Mean temperature of the coldest 4 months and temperature seasonality were the most important variables for predicting baobab distribution (Cuni Sanchez *et al*. 2011).

There have been reports of little or no recruitment and reduced proportions of smaller baobabs throughout its range, often resulting in bell-shaped size-class distributions (SCDs) for populations (Caughley 1976; Barnes 1980; Wilson 1988; Assogbadjo *et al.* 2005; Edkins *et al.* 2007). In conservation areas, heavy utilization of saplings and small trees by increasing densities of elephant is often blamed for the decreasing number of baobabs in these smaller size classes. Other probable causes of mortality of smaller baobabs are overstocking by game or livestock, changes in climate, altered fire regimes, agricultural development, or, more likely, the interactive effects of several of these factors in combination (Caughley 1976, Guy 1970; 1982, Wickens & Lowe 2008, Venter & Witkowski 2013a). An inverse J-shaped population distribution indicates a high proportion of smaller individuals and lower proportions of larger individuals and is generally accepted as an example of a healthy population (Condit *et al.* 1998; Venter & Witkowski 2013a). Deviation from this population structure indicates a population with low recruitment; Venter & Witkowski (2010) suggest that baobabs, with their long lifespans and very low adult mortality rates, do not necessarily require continuous, high levels of recruitment to maintain population sizes.

Protection offered by the establishment of the Kruger National Park (KNP), South Africa, in the early 1900’s resulted in the exponential growth of the elephant population (Whyte 2007). A culling programme was implemented in the late 1970’s to stabilise the elephant population at ~7000 individuals. Culling ceased in 1995 and the elephant population grew rapidly again, exceeded 16000 individuals by 2012 (SANParks 2013). There has been growing concern over the impacts of elephants on adult baobabs within KNP prompting several associated research projects in recent decades. Whyte (2001) and Hofmeyr *et al*. (2004) considered extended periods of drought to be the primary agent of mortality of mature baobab trees, and although they recorded widespread elephant impacts, few trees were extensively damaged. Whyte (2001) suggested that drought conditions of the 1980’s and early 1990’s, during which time the Pafuri ranger station recorded a Mean Annual Precipitation (MAP) 18% below that of the long-term MAP for the area, resulted in the increased mortality of baobabs. During this period aerial game surveys additionally recorded the mortality of more than 1000 large baobabs in northern KNP. In 1999 Kelly (2000) found no evidence that elephants played a significant role in the mortality of adult baobabs in northern KNP, and concluded that they did not alter baobab demographic patterns. However, Whyte (2001) suggested that an increased density of elephants, through increased utilization impacts, may have a negative effect on the baobab population by increasing individual vulnerability to drought. Whyte (2001) recommended that long-term monitoring is necessary to define and evaluate those factors threatening local baobab survival and quantify changes occurring within the KNP baobab population.

Whyte (2001) sampled 418 baobabs in northern KNP in 1995/6. Hofmeyr then resampled these baobabs, with an additional 340 individuals in 2001(Unpublished data). Resampling of these trees in the current study created an ~18 year data set for baobabs in northern KNP which could be used to compare changes in population structure over time and across multiple environmental and climatic conditions to gain a better understanding of the drivers of recruitment, growth and mortality in the park.

2.4 Methods

2.4.1 Study area

KNP, South Africa’s largest protected area, is situated in the north east of the country along the Mozambique border. KNP is divided into 22 managerial sections. This study falls within the 3 most northerly sections, *viz*. Pafuri, Punda Maria, and Vlakteplaas, which are collectively bordered by the Limpopo River in the north, the Luvuvhu River in the west, and the Lebombo Mountains in the east.

The study area has a north-south altitudinal gradient ranging from 200 m.a.s.l. at the Limpopo River to 540 m.a.s.l. at the Punda Maria hills; a north-eastern extension of the Soutpansberg range. A rainfall gradient follows that of altitude, ranging from 375 mm in the Limpopo valley in the north to 575 mm MAP in the vicinity of Punda Maria rest camp in the south-west (Figure 1c; SANParks, 2013). There is also a 2^{o}C decrease in mean annual temperature from 23°C in the north to 21°C in the south (Figure 1d; SANParks, 2013).

Fine fersiallitic sands and loams dominate the southern regions of the study area, with calcareous pedocutanic clays sloping northwards towards the Limpopo valley, and with calcareous alluvial soil deposits along the flood plains (SANParks, 2013). The parent material is mostly Ecca shale and mudstone, fine grained sandstone, and some Olivine-rich basalts.

The landscape varies from *Colophospermum mopane* savanna north-east of Punda Maria, to *Terminalia sericea* savanna sandveld communities to the east and west, and *Faidherbia albida* savannas on the Limpopo and Luvuvhu river alluvial plains (SANParks, 2013). Gertenbach (1983) used geomorphology, micro-climate, soils, vegetation, and fauna to describe and map 35 ‘landscape units’ within KNP, 12 of which are represented within the study area. These landscapes form the basis of Mucina and Rutherford’s (2006) vegetation units within KNP, which allow for comparison with vegetation outside of KNP. In the current study the majority of sampling took place in 5 vegetation units *viz*. Cathedral Mopane Bushveld, Makuleke Sandy Bushveld, Limpopo Ridge Bushveld, Lowveld Riverine Forest, and Subtropical Alluvial Vegetation (Figure 1a; Mucina and Rutherford, 2006).

Due to the low grass biomass in the north of KNP, both game density (Gertenbach 1983) and fire frequency (Smit *et al.* 2012; Figure 1b) is lower than the rest of the park. For this reason fire is seldom used as a management tool, but occasionally occurs through arson and lightning.

Elephants do well on the mixed diet afforded by these savannas and their population in the study area has increased from an estimated 0.381 elephants/km^2 (0.0719 elephant bulls/km^2) in 1995 to 0.664 elephants/km^2 (0.0848 elephant bulls/km^2) in 2012 (SANParks, 2013).

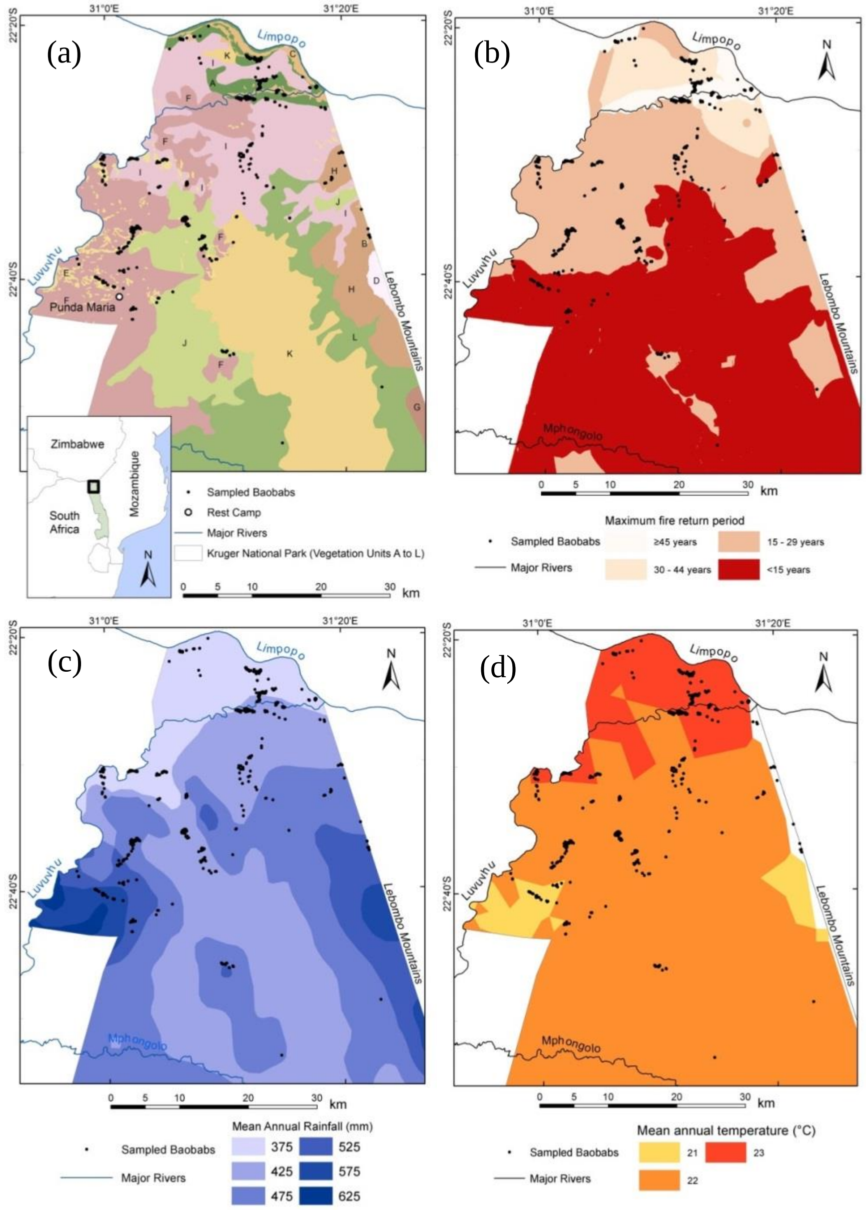

Figure 1. The regional context of the study area, including all sampled baobab trees and (a) the vegetation units as described by Mucina and Rutherford (2006); A: Subtropical Alluvial Vegetation, B: Subtropical Salt Pans, C: Lowveld Riverine Forest, D: Sand Forest, E: Ironwood Dry Forest, F: Makuleke Sandy Bushveld, G: Northern Lebombo Bushveld, H: Nwambyia-Pumbe Sandy Bushveld, I: Limpopo Ridge Bushveld, J: Cathedral Mopane Bushveld, K: Mopane Basalt Shrubland, L: Tsende Mopaneveld; (b) the maximum fire return interval calculated from 1941 to 2006 (Smit *et al.* 2012); (c) the MAP and (d) the mean annual temperature from Schulze *et al.* 1997; SANParks 2013. Many tree localities overlap due to the scale of the maps, so not all are visible.

2.4.2 Study species

The African baobab, with adult height and stem girth measurements in excess of 20m, is a charismatic and iconic large tree of the African savanna (Wickens 1982; Kelly 2000; Venter & Witkowski 2010).

Due to its importance as a keystone species, its cultural and spiritual value and the potential threat of over-utilization, baobabs are formally protected under South African legislation in the National Forests Act of 1998 and in the revised Act of 2012. Furthermore, the listing of the baobab as a species of special concern, a functionally important and locally threatened species, by SANParks (McGeoch *et al.* 2010) highlights the significance of this species and provides motivation for on-going monitoring and, where necessary, conservation action.

2.4.3 Sampling

This study builds on earlier surveys conducted by SANParks staff; in 1995/6 by Dr Ian Whyte (2001) and in 2001 by Michele Hofmeyr (unpublished). In July 1995 and January 1996, 424 baobab trees were sampled in northern KNP, initially focusing on differences in their populations north and south of the Luvuvhu River. As such, trees were sampled predominantly in the Pafuri section of KNP (Whyte, 2001). Large trees were located from tourist and management roads and, when clustered, all trees in a group were sampled (Whyte, 2001). Smaller trees were located through ‘slow movement and careful scanning’ whilst travelling in the vehicle or when moving between trees on foot (Whyte, 2001). As baobabs were sampled close to access roads, large areas of wilderness where baobabs likely occur, were not sampled.

Nearly all (413) of these 424 trees were located, using a GPS together with written directions, and resampled between April and September 2001, with the inclusion of an additional 486 trees. These additional trees were located predominantly in the Punda Maria section to increase the diversity of habitats sampled (M.V. Hofmeyr pers. comm., 2012). Methods comparable to those used in 1995/6 were used to locate and measure these additional trees.

Between July and November 2013, 418 of the initial (1995/6) 424 trees and 340 of the additional (2001) 486 trees were located and resampled (a number were un-sampled due to access constraints imposed by security concerns relating to rhino poaching within KNP). All baobab individuals within 50m of previously measured trees were included in the 2013 sampling, which also involved careful searching whilst walking in concentric circles around each tree for 20 minutes. The area thus searched accumulated to 4km^2 and added a further 126 trees across all sizes. The total number of trees sampled at least once during the ~two decade period was 1036. Of these, 345 trees (33%) were sampled twice, and 413 (40%) were sampled thrice (Table 1).

Table 1. The number of baobab trees (n) sampled a) each year and b) once, twice or thrice over the 18-year period. The spread between sampling efforts is shown.

a)

Year	n	Initial trees	Addition 1	Addition 2
1995	424	424	-	-
2001	899	413	486	-
2013	884	418	340	126

b)

Repeated	n	Initial trees	Addition 1	Addition 2
Once	278	6	146	126
Twice	345	5	340	-
Thrice	413	413	-	-
Total	1036			

In 1995/6, 2001 and 2013 the circumference of each tree was measured (in meters, to two decimal places) at 1.3m above the most elevated ground at the base of the tree (unless otherwise specified by the original observer) and perpendicular to the vertical axis of the stem using a taut, non-stretchable tape measure that did not follow the contours of the tree. Where trees were less than 2m in height, the circumference was recorded from the base of the tree. Circumference measurements were converted to diameters for better visualisation, as recommended by Wickens and Lowe (2008). Trees less than 2m tall and less than

0.15m in basal stem-diameter were categorised as saplings. Any baobabs that had germinated in the previous growing season, defined by cotyledons and green stem still being present, were categorised as seedlings. A record was made of all previously sampled baobabs that had died, including possible cause of death. The maximum fire return interval represents the longest interval that a seedling or sapling baobab has to establish in the absence of fire. Maximum fire return interval (Smit *et al.* 2012), the Mucina & Rutherford (2006) vegetation unit, MAP and mean annual temperature (Schulze *et al.* 1997) were extracted for each baobab off geographical information provided by SANParks (2013).

In addition, an estimate of elephant damage was recorded for each tree sampled. Overall elephant damage was recorded as i) none, ii) slight (some utilization, but not ring-barked), iii) moderate (utilization shallow and tree ring-barked), iv) severe (tree ring-barked and utilization affecting the shape of the stem), and v) very severe (utilization dramatically affecting the shape of the stem) following Whyte (2001).

2.4.4 Statistical analysis

Growth

Absolute growth over the study period was calculated by subtracting the initial stem-diameter recorded in 1995/6 from the stem-diameters recorded in 2013. Relative growth refers to actual growth relative to the initial stem-diameter recorded in 1995/6. Both the absolute and relative growth data differed significantly from a normal distribution. Log, arcsine, square-root and power transformations were unsuccessful in normalising these data and, as such, non-parametric Spearman’s rank correlations were run to test for relationships between these measures of growth and the initial stem-diameters recorded in 1995/6.

Comparison of Size-Class Distributions

SCDs were compared between all sampled trees and those that died, between 1995/6, 2001 and 2013, across Mucina & Rutherford’s (2006) vegetation units, maximum fire return intervals (1941-2006; Smit *et al.* 2012), 50mm mean annual rainfall isohyets and 1°C mean annual temperature isotherms (Schulze *et al.* 1997; SANParks 2013), and 5 levels of elephant damage. Two-sample Kolmogorov-Smirnov tests were used to determine if size-classes occurred in similar proportions between variables. Bin widths of 0.5m stem-diameters, up to 6m, were used for the visualisation of the SCDs. All statistics were performed in R (R Core Team, 2013).

2.5 Results

Recruitment, Growth and Mortality

No seedlings were found in the sampled 4km^2 during the course of this study. Thirteen saplings were found, of which the majority were located during the circular active searches conducted in 2013 (Table 2). By comparison, only 2 and 3 saplings were recorded in 1995/6 and 2001, respectively, but this discrepancy likely reflects sampling effort and not natural occurrence. Those saplings resampled in 2001 and 2013 showed very little or no increase in stem-diameter and all had been browsed or trampled to lower heights (Figure 2). Multiple shoots had coppiced from their bases by 2013; measurements given in Table 2 are of the largest of these shoots.

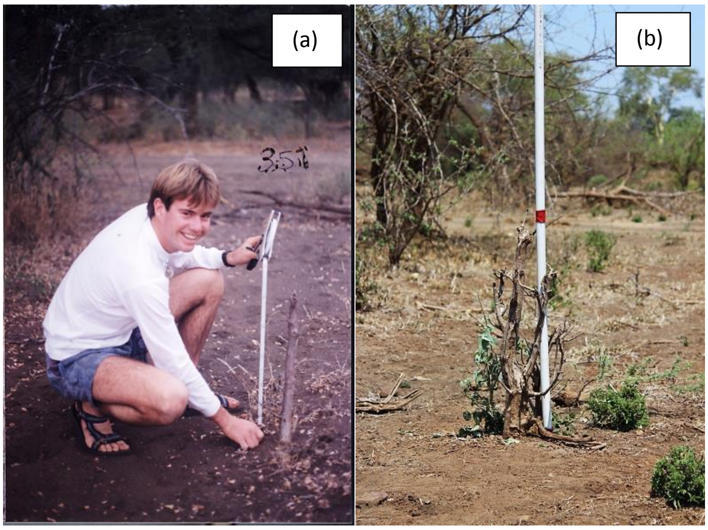

Figure 2. Sapling baobabs appear to have grown little over the study period, here a 0.04m stem-diameter, 0.53m tall sapling is pictured in (a) 1995 and (b) 2013. Browsing or trampling has resulted in coppice growth, slightly decreased height to 0.52m, and a slight increase in stem-diameter to 0.05m. Photograph (a) by Dr Ian Whyte.

Table 2. Diameters (Ø) and heights, all in meters, of sapling baobabs (defined as cotyledons absent, under 2m tall and less than 0.15m in basal stem-diameter) recorded in 1995/6, 2001 and 2013. Arrows indicate the direction of change from previous sampling event. Differences in numbers between years relate to sampling effort, and not necessarily occurrence.

	1995/6		2001		2013	
No.	Ø	Height	Ø	Height	Ø	Height
1	0.10	1.00	↑ 0.14	↓ 0.94	↓ 0.04	↓ 0.68
2	0.04	0.53	-*	-*	↑ 0.05	↓ 0.52
3			0.07	0.90	↑ 0.10	↓ 0.57
4			0.11	1.10	-**	-**
5					0.09	0.76
6					0.10	1.90
7					0.14	1.80
8					0.10	1.60
9					0.07	0.50
10					0.01	1.50
11					0.08	0.73
12					0.06	0.90
13					0.09	1.14

*missing, **dead

Change in stem-diameter between 1995/6 to 2013 was highly variable, with adult baobabs showing both positive or negative growth of up to 0.8m and -0.9m, respectively (61 and -61% relative growth; Figure 3). Overall the sampled baobabs showed very little absolute or relative growth over the study period (Absolute growth: Mean=-0.02m, S.E.=0.01m, Median=-0.02m, Mode=0m; Relative growth: Mean=0.13%, S.E.=0.81%, Median=-1.02%, Mode=0%). Positive growth was more prevalent in trees <1m in stem-diameter (Absolute growth: Mean=0.03m, S.E.=0.01m, Median=0.01m, Mode=0m; Relative growth: Mean=4.52%, S.E.=2.58%, Median=3.87%, Mode=0%). Absolute and relative growth were both correlated negatively with initial stem-diameter ($S = 8585200$, $P < 0.0001$, $r_s = -0.25444$; $S = 7669700$, $P = 0.025$, $r_s = -0.12067$, respectively) although the relationships were not strong. Larger trees showed lower relative growth than smaller trees over the 18-year period (Figure 4). Similar trends were noted for the inclusive periods 1995/6 to 2001 and 2001 to 2013 (data not shown).

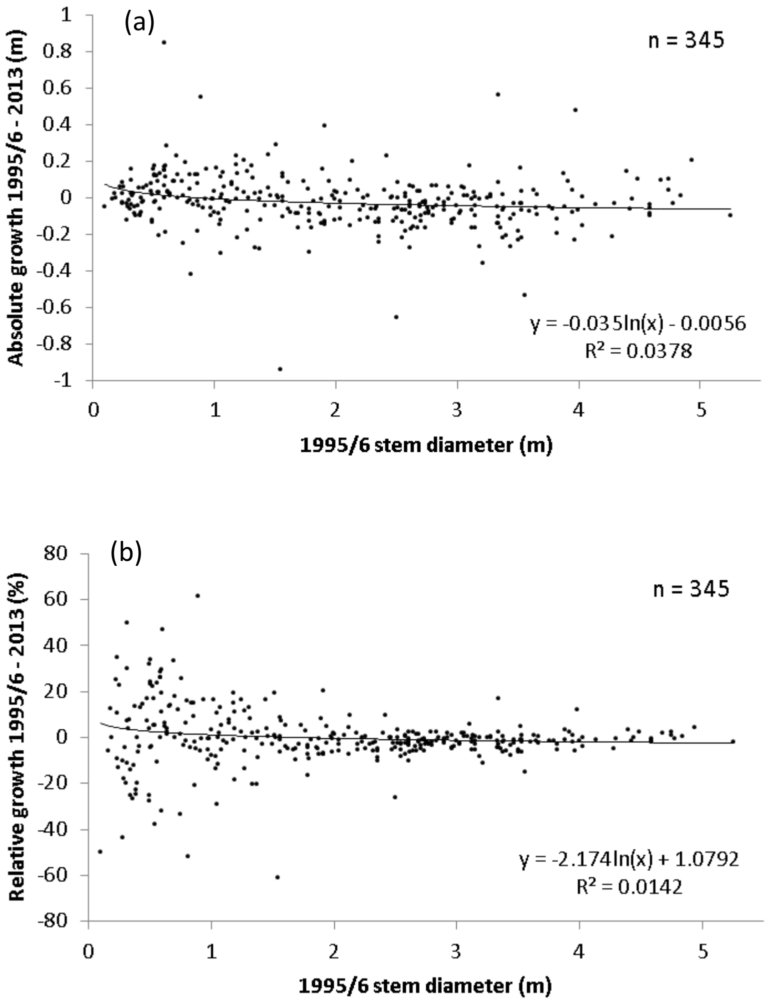

Figure 3. Absolute (a) and relative (b) stem-diameter growth of sampled baobabs surviving between 1995/6 and 2013. Diameter measured at 1.3m above ground height.

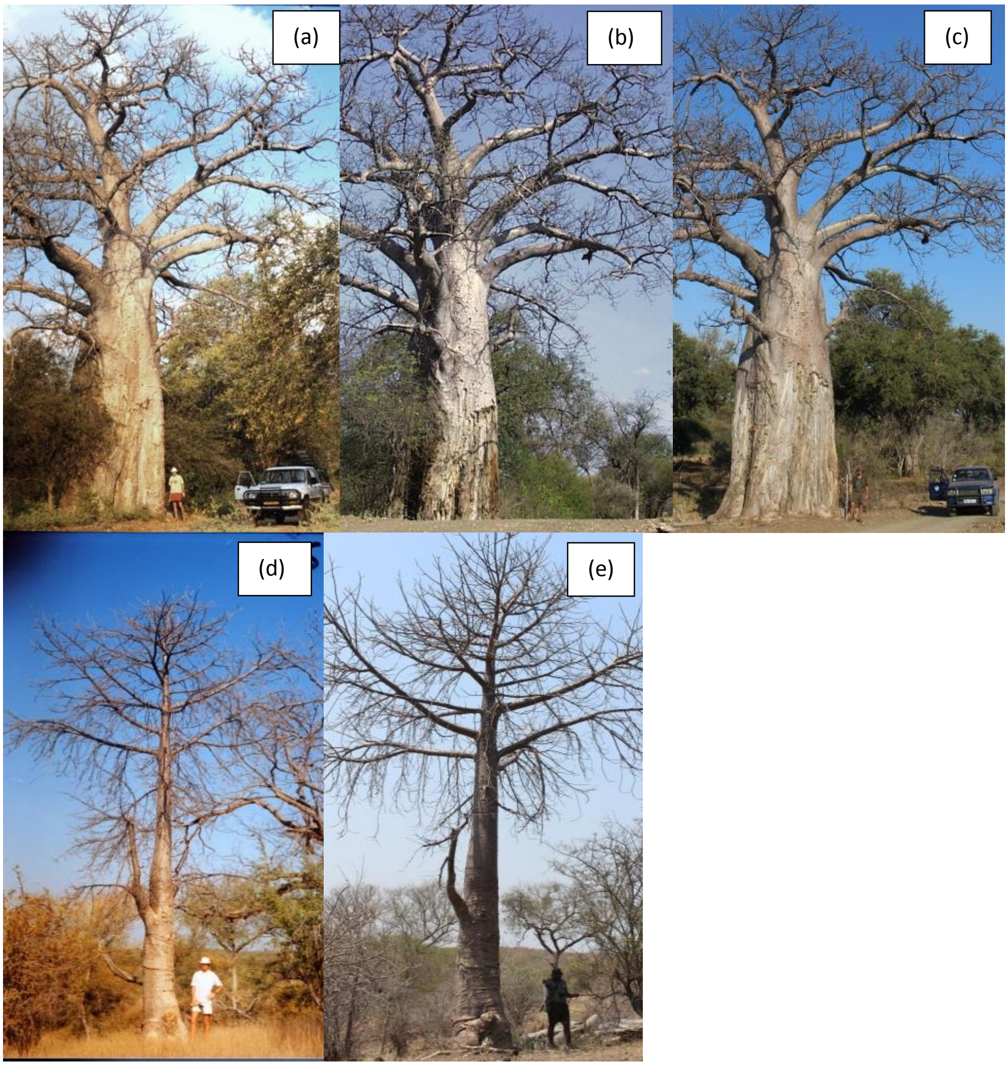

Figure 4. Very little or no growth is observed in trees with stem-diameters >1m: (a) 1995, (b) 2001 and (c) 2013. Alternatively, positive growth is noticeable in trees <1m in stem-diameter: d) 1995 and (e) 2013. Photographs (a) and (d), by Dr Ian Whyte; (b) by Michele Hofmeyr; (c) by Simon Smit.

SCD differed significantly between surviving baobabs and those baobabs that died over the study period ($D = 0.32287$, $P < 0.0001$). SCD of surviving baobabs showed that the frequency of individuals declined with increasing stem-diameter resulting in an inverse J-shaped population structure (Figure 5).

For those baobabs that died between 1995/6 and 2013, the SCD showed the highest proportion of mortality in the smaller size classes (22 of 186 (12%) and 19 of 169 (11%) trees dying in the <0.5m and 0.5-1m size classes, respectively).

Further, there were relative increases in the mortality of trees falling in the 3.5-4m, 4-4.5m and 5-5.5m size-classes (4 of 44 (9%), 6 of 29 (21%), and 2 of 7 (29%), respectively) as compared to the similar classes of surviving trees.

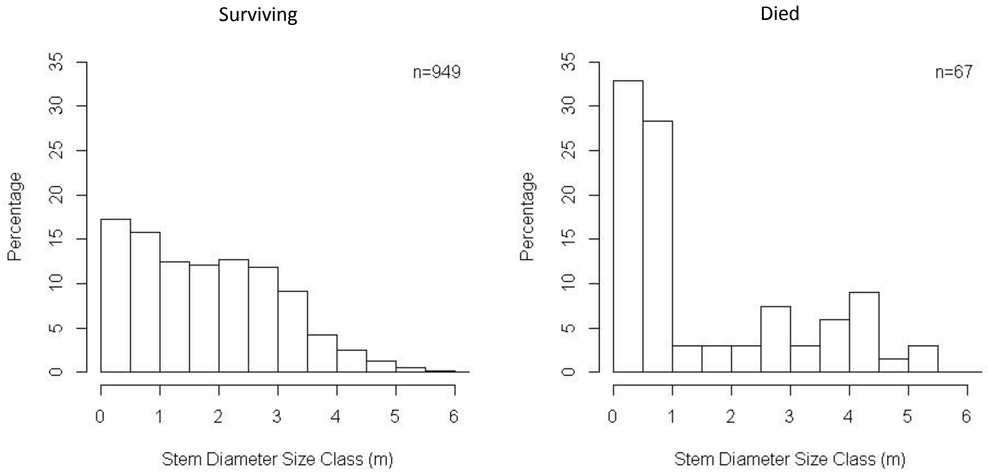

Figure 5. Comparison of the size class distribution (SCD) of surviving baobabs compared to those that died, over the period 1995/6 to 2013.

Changes in SCD over time

The overall pattern showed a consistent negatively skewed distribution with a high proportion of baobabs in the smaller size classes, and with the proportion of trees generally declining with increasing stem-diameter (Figure 6). No significant differences in size-class distribution were found between 1995/6, 2001 or 2013 (1995/6 and 2001: D=0.0792, P=0.0628; 1995/6 and 2013: D=0.0695, P=0.150; 2001 and 2013: D=0.0358, P=0.659). The increased sample sizes of 2001 and 2013 made little difference to the population structure; SCD did not differ significantly between years.

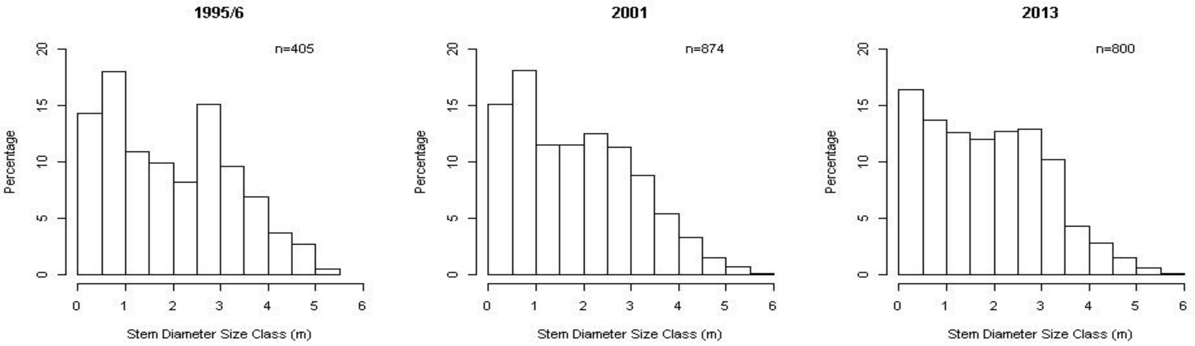

Figure 6. Comparison of the SCDs of baobabs sampled in 1995/6, 2001 and 2013 in northern Kruger National park (KNP).

Changes in SCD relative to Maximum Fire Return Period

Two significantly different SCDs for baobabs were found in relation to maximum fire return interval (Table 3). Baobabs growing in areas unburned for periods of 30 years or more showed roughly inverse J-shaped distributions with high proportions of smaller baobabs (43% of individuals having diameter <1m) and a low proportions (3%) of baobabs in the largest 2 size classes (Figure 7). However, baobabs occurring in areas with more frequent burns lacked this high proportion of smaller baobabs (Figure 7). In particular, baobabs growing in those areas experiencing a maximum fire return interval of <15 years showed a uni-modal distribution, with relatively low proportions of both small and large trees, but with a relatively high proportion, 17% and 19%, of trees falling in the intermediate 1.5-2m and 2-2.5m stem-diameter classes, respectively.

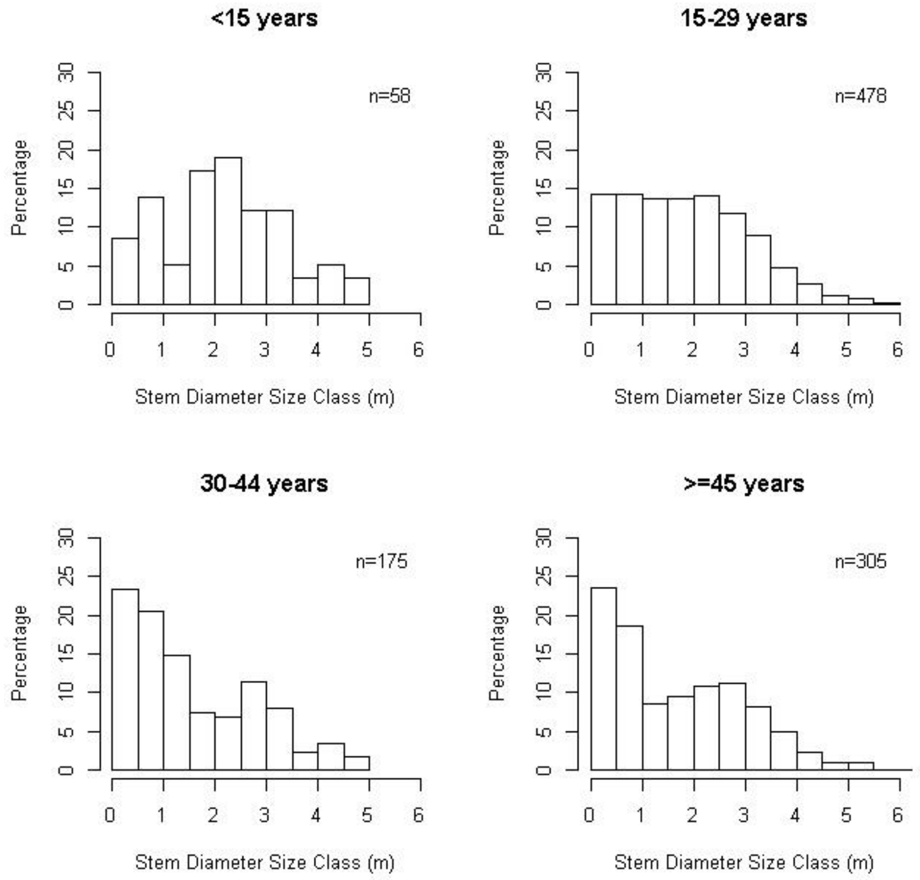

Figure 7. Comparison of the SCD of sampled baobabs across areas differing in maximum fire return period between 1941-2006 (Smit *et al*, 2012).

Table 3. The D- and p-values for two-sample Kolmogorov-Smirnov tests to determine if size classes occur in similar proportions between areas with differing maximum fire return period. Bold indicates significantly different population size structures.

	<15 years	15-29 years	30-44 years
15-29 years	D = 0.16556, P = 0.1174		
30-44 years	**D = 0.32414, P = 0.0002**	**D = 0.18496, P = 0.0003**	
≥45 years	**D = 0.24873, P = 0.0048**	**D = 0.14833, P = 0.0006**	D = 0.086089, P = 0.382

In 2013 a hillside in Punda Maria section (Lat: -22.591; Long: 31.108) showed signs of a past hot fire. The forest of Lebombo ironwood (*Androstachys johnsonii*) that dominated the slope suffered major topkill but was coppicing (Figure 8). According to the SANParks (2013) fire records, a medium to very high intensity, unintentional fire burnt this area in October 2001. In September 2001, immediately prior to the fire, thirteen baobabs were located on this hillslope. By 2013 the two smallest trees had died (Figure 8b; Stem-diameters 0.46 and 0.56m and heights 5 and 6m respectively). The surviving trees ranged from 0.64 to 3.79m in stem-diameter and 9 to 16m tall. The two smallest baobabs displayed severe and very severe elephant damage in 2001 and notes were made that parts of their canopies and strips of bark had been removed. This damage likely confounded the impacts of the subsequent fire. Other trees in the area displayed only slight and moderate elephant damage in 2001, and again in 2013.

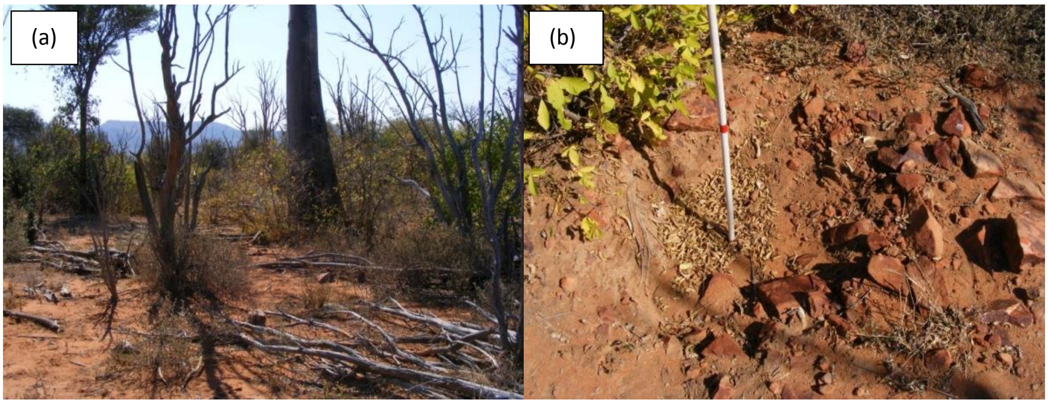

Figure 8. A Lebombo ironwood (*Androstachys johnsonii*) forest (a) pictured in 2013 suffering severe topkill after a hot fire in 2001. A surviving 0.97m stem-diameter, 10m tall baobab is shown in the middle of the picture; and (b) a hollow in the ground where a 0.46m stem-diameter, 5m tall baobab had stood before the fire. Reminants of baobab bark is still present in the root-channels and rocks displaced by the stem can be seen surrounding the hollow.

Changes in SCD relative to Elephant Utilization

The majority of baobabs displayed moderate (52% of sampled trees) and slight (36%) damage in 2013. All baobabs greater than 2m in stem-diameter had some level of elephant damage by 2013 and all baobabs greater than 3.5m in stem-diameter displayed more than slight damage. Baobabs with no or slight damage showed negatively skewed distributions which were significantly different to those of the other levels of damage (Table 4). Baobabs with moderate levels of elephant damage had a bell-shaped SCD, with 54% of individuals being between 2-3.5m in stem-diameter (Figure 9). Severely damaged trees showed a bimodal SCD with 21% of individuals occurring in the 0-0.5m stem-diameter size-class and 32% of individuals occurring in the 2.5-3.5m stem-diameter size classes. Very severe damage was seen in nearly all stem-diameter classes, but the low sample sizes prohibit meaningful interpretation thereof (Figure 9).

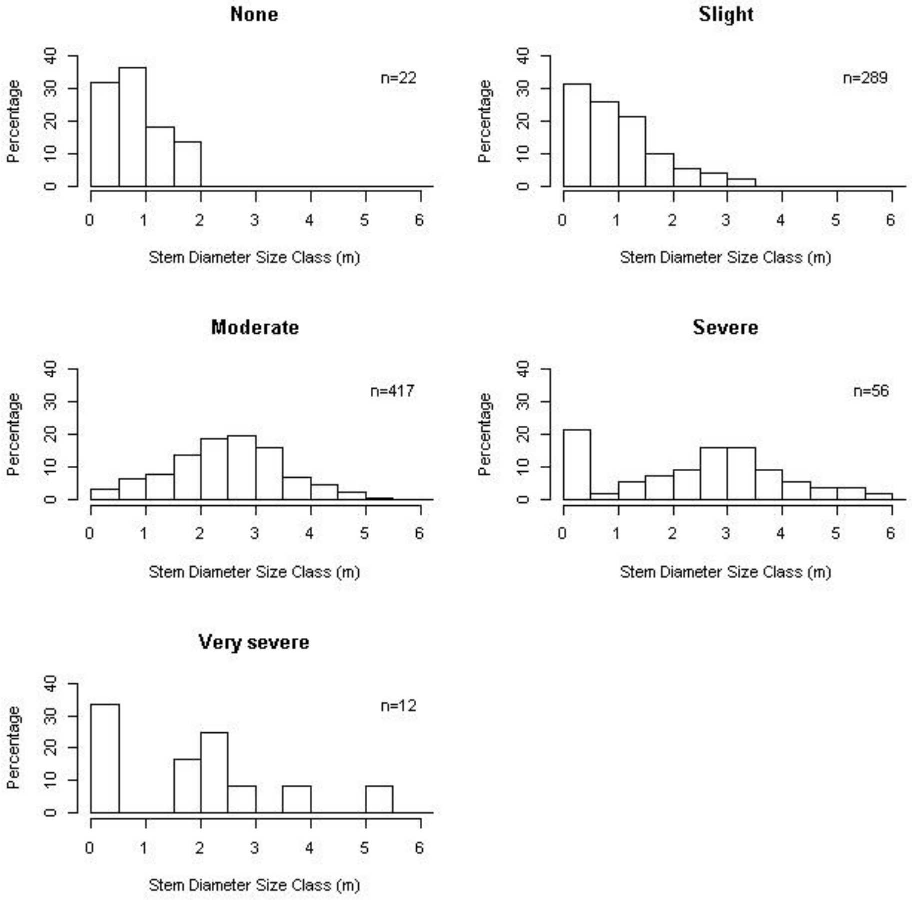

Figure 9. Comparison of the SCDs of baobabs showing different levels of elephant utilization in 2013.

Table 4. The D- and p-values calculated for two-sample Kolmogorov-Smirnov tests to determine if size classes occur in similar proportions at different levels of elephant damage in 2013. Bold indicates significantly different pair-wise population size structures.

	None	Slight	Moderate	Severe
Slight	D = 0.17883, P = 0.5303			
Moderate	**D = 0.72204, P < 0.0001**	**D = 0.63648, P < 0.0001**		
Severe	**D = 0.64286, P < 0.0001**	**D = 0.53905, P < 0.0001**	**D = 0.19617, P = 0.0448**	

Changes in SCD relative to Rainfall and Temperature

No significant differences were found in the SCD of baobab populations growing in the areas defined by the different rainfall isohyets (Table 5). The trend across all rainfall isohyets showed many smaller and intermediate trees declining in proportion with increasing stem size. However, visual comparison shows that the proportion of baobabs <1m in diameter declines with increasing rainfall (33% in areas receiving 375mm MAP to 29% in areas receiving >525mm MAP), resulting in a negatively skewed bell-shaped distribution of baobabs populations occurring in areas receiving >525mm of rainfall (Figure 10).

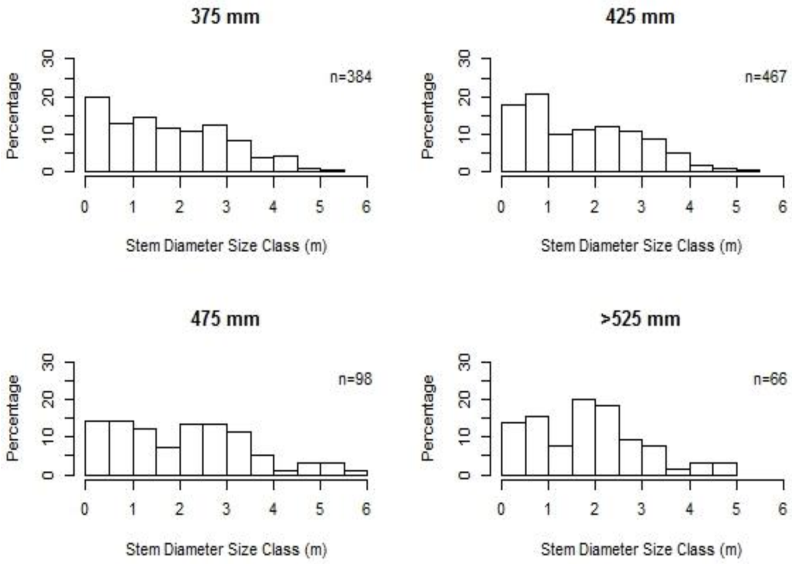

Figure 10. Comparison of the SCDs of baobabs growing in the areas defined by the different rainfall isohyets in northern KNP.

Table 5. The D- and p-values calculated for two-sample Kolmogorov-Smirnov tests to determine if size classes occur in similar proportions between areas defined by different rainfall isohyets. Population size structures did not differ significantly.

	375 mm (n=384)	425 mm	475 mm
425 mm (n=467)	D = 0.0764, P = 0.1747		
475 mm (n=98)	D = 0.127, P = 0.1648	D = 0.1309, P = 0.1278	
525 mm (n=66)	D = 0.1216, P = 0.3836	D = 0.1433, P = 0.1921	D = 0.1664, P = 0.2315

The SCD of baobabs located within the area defined by the 23°C isotherm was significantly different to that of baobabs within the area defined by the 22°C isotherm (D = 0.12103, P = 0.0025) showing a significantly higher proportion of small baobabs (39% as opposed to 29% of baobabs with stem-diameters <1m). The number of baobabs within the area defined by the 21°C isotherm, encompassing the higher altitudes of the species distribution range in KNP, was low (n = 25), but showed a further decline in proportion of smaller baobabs with decreased temperature (Figure 11). Baobabs growing within the area defined by the 21°C isotherm showed a uni-modal bell-shaped distribution, with 52% of individuals being between 1.5m – 2.5m in stem-diameter, rather than the negatively skewed distributions of the warmer regions.

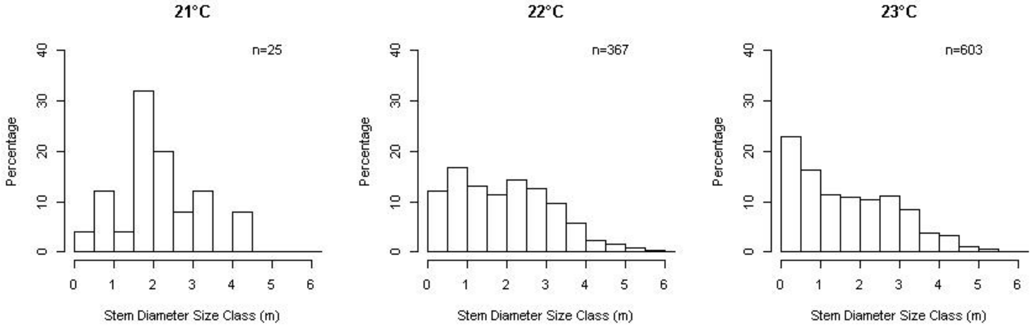

Figure 11. Comparison of the SCD of baobab populations situated within the areas defined by the 21, 22, and 23°C isotherms in KNP.

Changes in SCD across Vegetation Units

The SCD of baobabs growing in subtropical alluvial vegetation differed significantly from all other vegetation units except lowveld riverine forest, with both showing typical inverse J-shaped distributions (Figure 12; Tables 6 & 7). The SCD of baobabs within lowveld riverine forest was not significantly different from that of cathedral mopane bushveld which whilst also inverse J-shaped had a reduced proportion of <0.5m stem-diameter baobabs (Table 7). Baobabs growing within the Limpopo ridge bushveld had the least variable SCD and whilst negatively skewed the SCD plateaus in the 0-2.5m stem-diameter size classes. This was not significantly different to the negatively skewed bell-shaped distribution of baobabs in the ironwood dry forest. Baobabs within Makuleke sandy bushveld showed the most typical bell-shaped distribution (Figure 12; Tables 6 & 7). The SCD of baobabs growing in Makuleke sandy bushveld did not differ significantly from that of ironwood dry forest.

Table 6. Description of the vegetation units within the study area, together with physical and climatic parameters, and the SCDs of baobabs occurring within them.

Vegetation unit[1]	Equivalent landscape[2]	Vegetation structure[1]	Topography[2]	Soils[2]	Fire[3]	Elephant abundance	Climate[4]	Water availability[4]	Baobab density[6]	SCD shape
Lowveld Riverine Forest	Limpopo/Luvubu floodplain	Tall, multi-levelled, gallery forest fringing larger rivers	Flat	Deep, alluvial sediments along the Limpopo and Luvuvhu rivers	Very infrequent >30year maximum fire return interval	Elephant bulls are listed in the dominant fauna in 1983[2], but numbers in family groups have since increased substantially[4] and are common place[5]	Mean temp: 23°C, MAP: 375mm	Close proximity to permanent water and impacted by frequent flooding	0.32 baobabs /ha	Inverse J-shaped
Subtropical Alluvial Vegetation		Low riparian thicket								Inverse J-shaped
Cathedral Mopane Bushveld	*Colophospermum mopane* forest	Moderately closed savanna dominated by *Colophospermum mopane* trees	Flat	Deep soils	Moderate to low maximum fire returns (<20 years)	Ideal habitat for elephant breeding herds[2]	Mean temp: 22°C, MAP: 425mm	Far from major rivers	0.11 baobabs /ha	Inverse J-shaped but low proportion of <0.5m stem-diameter trees
Limpopo Ridge Bushveld	*Adansonia digitata* /*Colophospermum mopane* Rugged Veld	Moderately open savanna with a poorly developed ground layer	Rugged ridges and hills above the Limpopo valley	Shallow soils	Moderate maximum fire return interval (15-29 years)	Elephants are infrequent[2] and predominantly bulls[5]	Mean temp: 22-23°C, MAP: 375-425mm	Not easily accessible to permanent water	0.11 baobabs /ha	Negatively skewed but lacking high proportions of smaller trees
Makuleke Sandy Bushveld	Punda Maria sandveld on Waterberg & Cave sandstone	Tree or tall shrub savanna	Irregular plains and hills	Deep sandy soils	Moderate to low maximum fire returns (<20 years)	Low to moderate numbers of elephant[2]	Mean temp: 21-23°C, MAP: 375-575mm	Ranging in distance from the Luvuvhu river	0.05 baobabs /ha	Bell-shaped
Ironwood Dry Forest	Punda Maria sandveld on Waterberg sandstone	Dominated by dense forests of *Androstachys johnsonii*	Rugged moderate to steep rocky slopes in Punda Maria	Shallow soils.	Moderate maximum fire return interval (15-29 years)	Elephants are infrequent[2] and predominantly bulls[5]	Mean temp: 21-22°C, MAP: 425-575mm	Not easily accessible to permanent water	0.05 baobabs /ha	Bell-shaped but with a peak in 0.5-1m stem-diameter trees

[1]Mucina & Rutherford (2006), [2]Gertenbach (1983), [3]Smit *et al.* (2012), [4]SANParks (2013),[5]Personal observation, [6]Kelly (2000)

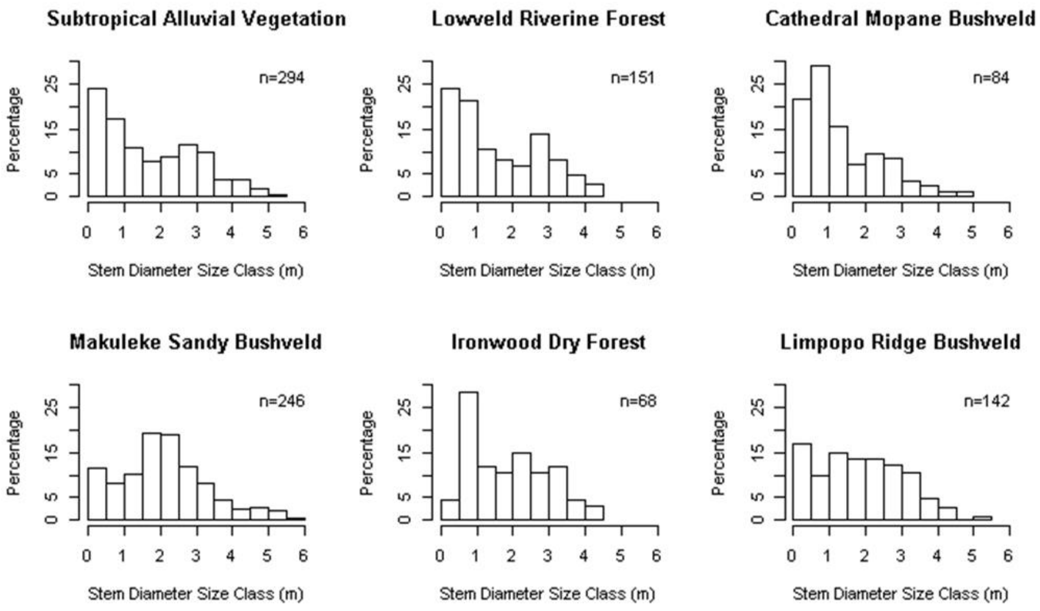

Figure 12. Comparison of the SCDs of baobab populations occurring in different Mucina & Rutherford (2006) vegetation units in northern KNP.

Table 7. The D- and p-values for two-sample Kolmogorov-Smirnov tests to determine if baobab size classes occurred in similar proportions between Mucina & Rutherford (2006) vegetation units. Bold indicates significantly different pair-wise population size structures.

	Cathedral Mopane Bushveld	Ironwood Dry Forest	Limpopo Ridge Bushveld	Lowveld Riverine Forest	Makuleke Sandy Bushveld
Ironwood Dry Forest	**D = 0.2293, P = 0.0406**				
Limpopo Ridge Bushveld	**D = 0.2833, P = 0.0005**	D = 0.1254, P = 0.4724			
Lowveld Riverine Forest	D = 0.1298, P = 0.329	**D = 0.2257, P = 0.0179**	**D = 0.1905, P = 0.0102**		
Makuleke Sandy Bushveld	**D = 0.3769, P < 0.0001**	D = 0.1634, P = 0.1203	**D = 0.1579, P = 0.0231**	**D = 0.2765, P < 0.0001**	
Subtropical Alluvial Vegetation	**D = 0.1756, P = 0.0370**	**D = 0.2116, P = 0.0151**	**D = 0.1537, P = 0.0223**	D = 0.0824, P = 0.5103	**D = 0.2311, P < 0.0001**

2.6 Discussion

Recruitment, Growth and Mortality

As in studies elsewhere in Africa (Caughley 1976; Barnes 1980; Wilson 1988; Assogbadjo *et al.* 2005; Edkins *et al.* 2007), no recruitment of baobab seedlings was observed in KNP. This, however, is not necessarily cause for concern as baobabs, with long lifespans and very low adult mortality rates, do not need high levels of recruitment to maintain population sizes (Venter & Witkowski 2010).

Saplings recorded in 1995/6 and 2001 showed little or no growth over the ~18 and 12 year study periods, respectively by 2013. It would appear that constant browsing and trampling and possibly unfavourable climatic conditions have stunted these trees. In their population model, Venter & Witkowski (2013b) suggested that saplings take up to 2 years to recruit into the next stage class as a juvenile tree. Under unfavourable conditions this could take much longer. Limited or no growth can occur in all size stages of baobabs allowing them to eke out their resources until periods of favourable conditions return. The absence of growth has been noted in several large baobabs, where growth rings show long periods of stasis (Patrut *et al.* 2015). The resources stored in larger baobabs would likely ensure their survival for longer than smaller baobabs. Previous studies have suggested that cohorts of baobabs might germinate and develop during periods of low predation and favourable climatic conditions (Kelly 2000; Whyte 2001; Hofmeyr *et al.* 2004). These same favourable conditions would allow for stunted baobabs to escape their bonsai conditions and grow as a cohort into larger trees.

With stunted saplings not necessarily indicative of recent recruitment, and no previous season recruitment recorded, it appears that current recruitment of the species is poor in the northern KNP. However as baobabs are very long-lived, very few seedlings need to survive, both spatially and temporally, in order for the population to be maintained. Within planted seed and seedling trials, Venter and Witkowski (2013a) found that recruitment is micro-site limited and that infrequent rainfall resulted in the desiccation and mortality of almost all seedlings within several days of germination. Only a small number of ideal micro-sites within a largely hostile environment would be needed in order to sustain the necessary low recruitment.

Two possible explanations exist for the relatively high variability in growth measurements recorded over time for individual baobabs in this study. Baobabs shrink and swell between wet and dry years as they withdraw or accumulate water within their tissues (Wickens & Lowe 2008). Secondly, slight inconsistencies in measurement could result in some of the observed variability. The stems of baobabs are seldom conical and smooth, and lumps, buttresses and scars can result in large differences in circumference, and hence diameter, within a few centimetres of height. Where soil has been deposited or eroded (Figure 13), a termite mound has grown or slumped alongside a baobab or where slight inconsistency in the determination of the highest point on the ground has occurred, substantial variation in stem-diameter results.

A slight trend of positive growth was observed in the <1m stem-diameter baobabs and very little growth in larger baobabs. The comparison of photographs between years clearly shows these trends. This trend of more rapid growth in smaller trees and little or no growth in larger trees is consistent with other studies on growth rates of baobabs in Africa (Condit *et al*. 1998; Wickens and Lowe 2008).

Mortality was predominantly in the smaller size classes. However there is concern regarding the high proportion of the large and very large trees that died. 21% and 29% of the 4-4.5m and 5-5.5m stem-diameter baobabs sampled died over the study period. Sample sizes were however small for these larger trees.

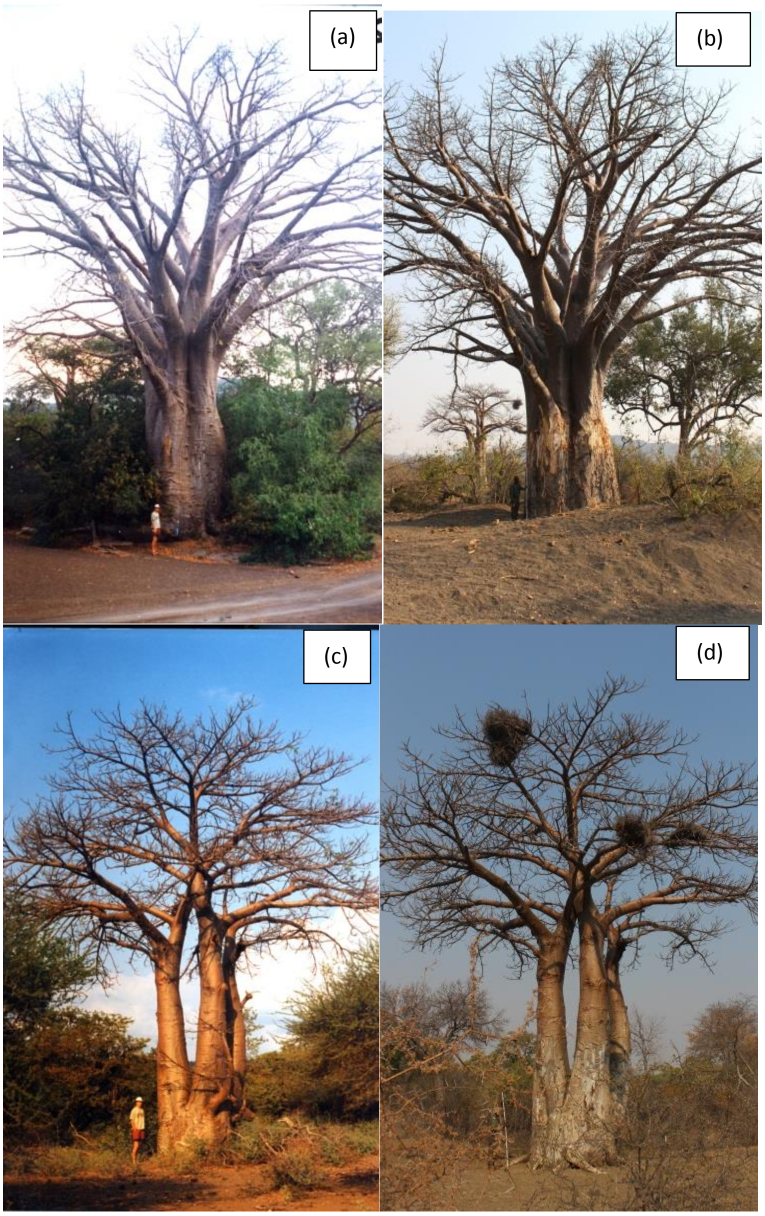

Figure 13. The deposition (a & b) and erosion (c & d) of soil, all pictures photographed in 1995 and again in 2013 respectively, impacts on the height at which stem diameter is measured. Photographs (a & c) by Dr Ian Whyte

Comparisons of SCD over time

With no recruitment of seedlings evident and little recruitment between size classes, mortality of individuals alone was not enough to significantly change the baobab population structure between 1995/6, 2001 and 2013. This might change should more very large (>4.5m stem-diameter) trees die, as these size classes make up less than 2% of the population. Recruitment into these size classes is likely to take many decades should conditions allow for growth. The increase in proportion of <0.5m stem-diameter trees seen in 2013 is due to the intensive searches within 50m of each previously sampled tree and is not an indication of recruitment over the past 12 years. The general pattern in population size-structure is an inverse J-shape, with a higher proportion of smaller baobabs and lower proportions of larger baobabs.

A study done in Vhembe in 2006 (Venter & Witkowski 2010), adjacent to the western boundary of the Pafuri section, showed an overall population structure very similar to that in northern KNP, particularly that of the 1995/6 and 2001 samples which had a low proportion of baobabs in the <0.5m stem-diameter size-class. This low proportion of the <0.5m stem-diameter baobabs in Vhembe was explained by extensive livestock browsing and trampling (Venter & Witkowski 2013a). Elsewhere in Africa many populations have shown bell-shaped population structures often attributed to the impact of elephant browsing on and destroying smaller trees (Wickens & Lowe 2008).

Changes in SCD relative to Maximum Fire Return Period

Differences were found between the SCD of baobabs in areas with a maximum fire return interval less than 30 years compared to areas with longer maximum fire return intervals. In areas where the maximum fire return interval was greater than 30 years, the population had an inverse J-shaped SCD. These areas of longer maximum fire return period tend to occur in the northern parts of Pafuri section where low annual rainfall and increased herbivory close to major rivers results in low and patchy fuel-loads and where high-order streams and undulating topography acts as natural fire breaks (Smit *et al.* 2012). Low fire intensity and the patchy nature of burns would allow for a higher proportion of small, fire-sensitive baobabs to survive. Wickens & Lowe (2008) are of the opinion that much of the observed absence in natural regeneration of baobabs in Africa is due to seedlings and saplings succumbing to the combined effects of both fire and browsing. In a demographic study on the Australian baobab (*Adansonia gibbosa*), locally called boabs, Bowman (1997) found high densities of <0.1m stem-diameter boabs near rivers, with decreasing proportions with increased distance from the rivers. Bowman (1997) notes that fires typically extinguish when approaching rivers due to high moisture levels in fuels closer to rivers. He suggests that the local distribution of the boab tree is controlled by fire; sites exposed to fire were missing the smaller size classes whilst sites topographically protected from fire had higher densities of small boabs.

Changes in SCD relative to elephant utilization

All baobabs larger than 2m in stem-diameter had some level of elephant damage and all baobabs greater than 3.5m in stem-diameter had more than slight damage. This suggests that moderate damage is accumulative and that frequent elephant returns do not allow for baobabs to heal between visits. The SCDs of severely damaged baobabs showed a bimodal distribution with a peak in the proportion of <0.5m stem-diameter baobabs and a second peak in 2.5-3m stem-diameter individuals. The peak in <0.5m stem-diameter trees is not present in the moderately damaged trees and suggests that smaller trees either escape elephant utilization, or suffer severe or fatal damage. Any level of elephant utilization on small baobabs is likely to result in severely damaged and disproportionally more severely damaged smaller trees compared to larger tree. Increased levels of elephant damage are expected to decrease the ability of baobabs to persist under unfavourable conditions.

Changes in SCD relative to Rainfall and Temperature

Rainfall showed no significant effect on the population structure of baobabs in northern KNP yet annual rainfall, together with temperature seasonality, were considered as important predictors of baobab distribution in Africa (Cuni Sanchez *et al.* 2011). However, in a model including only eastern and southern Africa, rainfall did not feature as a major predictor and mean temperature of the four coldest months and temperature seasonality were considered more important (Cuni Sanchez *et al.* 2011). Drought, together with elephant damage, is considered a major cause of mortality of baobabs in South Africa (Nel 1988; Kelly 2000; Whyte 2001; Edkins *et al.* 2007; Venter & Witkowski 2010). Long-term averaged annual rainfall would not pick up the effects of drought and hence would not show its effects on the SCD of baobabs.

Mean annual temperature did have an effect on the SCD of baobabs in northern KNP where trees occurring in the warmer regions (23°C mean annual temperature) had an inverse J-shaped distribution compared to the bell-shaped curve of baobabs growing in the cooler regions. As mentioned previously, measures of temperature (mean temperature of the four coldest months and temperature seasonality) played a major role in predicting the distribution of baobabs in Africa (Cuni Sanchez *et al.* 2011). Increases in mean annual temperature expected in future climates (DEA 2013) would increase the area of northern KNP experiencing a mean annual temperature ≥ 23°C, presumably increasing the optimal range for baobabs in KNP. This correlates with the predictions of Cuni Sanchez *et al.* (2011) which list northern KNP as currently suitable habitat for baobabs that will remain suitable in the future.

Changes in SCD across Vegetation Units

Gertenbach's (1983) Limpopo/Luvubu floodplains landscape incorporates the subtropical alluvial vegetation and lowveld riverine forest vegetation units of Mucina & Rutherford (2006). The characteristics of these two units are very similar (Table 6), with the major difference being in vegetation structure. Whilst subtropical alluvial vegetation consists of low riparian thicket, true lowveld riverine forest is tall, multi-leveled, gallery forest (Mucina & Rutherford 2006). This forest is mostly a narrow band, along rivers and pans, in which baobabs seldom occurred. The baobabs listed as occuring in this vegetaion unit are instead growing mostly in the forest fringes. Not surprisingly, the baobab populations in these two vegetation units show similar inverse J-shaped SCDs.

The baobab population structure in cathedral mopane bushveld is similar to that of baobabs growing in the fringes of lowveld riverine forest, but differ in lower lower proportion of <1m stem-diameter trees. Both these vegetation units occur on flat topography and deep soils, and are dominated by tall trees. However they differ in that cathedral mopane bushveld has shorter maximum fire return intervals and lower mean annual temperatures (Table 6), possibly resulting in the lower proportion of small baobabs.

Ironwood dry forests are mostly restricted to koppies within the Makuleke sandy bushveld. Both these vegetation units support baobab population structures with bell-shaped distributions however, populations within ironwood dry forests showed a peak in 0.5-1m stem-diameter baobabs, negatively skewing the distribution. Similarly, populations of baobabs within the Limpopo ridge bushveld also showed a negatively skewed distribution, however the distribution appears to plateaus in the 0-2.5m stem-diameter size classes with a dip in the 0.5-1m stem-diameter baobabs. All three of these vegetation units have moderate or moderate to short maximum fire return intervals (Table 6).

Venter & Witkowski (2010) compared baobab population structures on rocky outcrops, plains and two modified habitats, *viz.* fields and villages, in Vhembe. A total of 465 baobabs were sampled in transects amounting to 4.5km^2 (Venter & Witkowski 2010). Two vegetation units in Vhembe overlaped with that of northern KNP, namely Limpopo ridge bushveld and Makuleke sandy bushveld. The landscape description of rocky outcrops closely matches that of Limpopo ridge bushveld of Mucina & Rutherford (2006) whilst the plains best match that of Makuleke sandy bushveld. However, the population structures of baobabs within these habitats are not congruent with that of baobabs in similar vegetation units in KNP. The baobabs within rocky outcrops show bell-shaped SCDs similar to that of baobabs in Makuleke sandy bushveld in northern KNP whilst baobabs growing on plains show inverse J-shaped SCDs similar to that of the subtropical alluvial vegetation in northern KNP. It is thought that high baboon predation of unripe fruit in the rocky outcrops resulted in increased seed mortality and the low proportions of smaller baobabs in that habitat (Venter & Witkowski 2010). The low herbaceous biomass together with grazing by cattle, goats and donkeys in the plains results in very infrequent veld-fires. Elephants too, are infrequent visitors (Venter & Witkowski 2010). This exclusion of fire and elephants could afford better protection to small baobabs on the plains. Similar protection from fire is afforded to baobabs growing along the flood plains of the Luvuvhu and Limpopo rivers in KNP.

Edkins *et al.* (2007) compared sample populations of baobabs in northern KNP and neighbouring Limpopo National Park (LNP), Mozambique. Totals of 308 baobabs in KNP and 306 baobabs in LNP were sampled using nearest neighbour and transect methods. The KNP sampled baobabs, located predominantly within Makuleke sandy bushveld and some within subtropical alluvial vegetation, were described as having a mono-modal population size-structure with the highest proportion of baobabs in the 0.64 to 0.95m stem-diameter (2 to 3m circumference) size-class. This distribution is similar to that reported for the Makuleke sandy bushveld from the current study. Further, Edkins *et al.* (2007) recorded an inverse J-shaped size-class distribution for the baobabs population south of the Limpopo River in LNP, where elephant densities were lower than in KNP. Edkins *et al.* (2007) suggest that this healthy distribution is the direct result of the lower elephant densities. However, it is not mentioned if this region has other conditions more favourable to baobabs resulting in a similar population structure to those baobabs found in the Limpopo and Luvuvhu floodplains of KNP.

Kelly (2000) walked transects of variable sizes, depending on visibility, in order to record the demographics of baobabs north and south of the Luvuvhu River in KNP, effectively sampling across areas with lower (north) and higher (south) elephant densities. Both baobab populations showed negatively skewed distributions, but with the population south of the river showing reduced proportions of the smallest size-class with a peak recorded in the proportion of 0.32-0.64m stem-diameter (1-2m circumference) baobabs. The differences between the SCDs of baobabs growing in these two regions were however not significant. Elephants, however, are not the only drivers impacting on baobabs. North of the Luvuvhu is dominated by the flood plain habitats of subtropical alluvial vegetation and lowveld riverine forest, whilst south of the Luvuvhu is dominated by the more rugged and drier vegetation of the Limpopo ridge bushveld and Makuleke sandy bushveld. We suggest that both climate and maximum fire return intervals, which differ between north and south of the Luvuvhu River, have significantly impacted on the SCD of baobabs in these regions.

Baobab densities varied by two orders of magnitude across the vegetation units of northern KNP (Kelly 2000). Kelly (2000) calculated the highest baobab densities of 32.2 baobabs/km^2 in the subtropical alluvial vegetation (and lowveld riverine forest fringes), down to 5.3 baobabs/km^2 in Makuleke sandy bushveld and ironwood dry forest, with the lowest recorded densities in the Mopane basalt shrubland at 0.3 baobabs/km^2 (Kelly 2000), although this is not included in the present study. All densities for KNP were substantially lower than the 103 baobab/km^2 recorded in Vhembe (Venter & Witkowski 2010) and the even higher densities further north, up to 200 baobabs/km^2 in central Mali and localised densities of over 1000 baobabs/km^2 in both the Kibwezi district in Kenya and the southern Lake Malawi region in Malawi (listed in Cuni Sanchez 2010). Located at the southern limit of its distribution, KNP is unlikely to have supported these high baobab densities under current climatic conditions. The relatively higher density of baobabs within the Limpopo/Luvuvhu floodplains compared to other regions of KNP, together with the inverse J-shaped distributions of baobabs in these vegetation units, suggests that this is a healthy core population. The lower densities in populations with SCDs differing from the typical inverse J-shape were growing in the less favourable vegetation units elsewhere.

We conclude that although recruitment was not observed during the course of this study, this may be of little concern as the long lifespan and low adult mortality rate of baobabs negates the necessity for high levels of recruitment. Saplings appeared to be stunted by unfavourable conditions, however growth was observed in several individuals. Very little or no growth in stem diameter was observed for baobabs >1m stem-diameter. Mortality was predominantly in the smaller size classes. However the high proportion of the large and very large trees that have died is a point of concern. The overall population SCD did not change over the ~18 study period. Longer (>30 years) maximum fire return intervals and higher mean annual temperatures (23°C) supported a negatively skewed baobab population structure whilst shorter (<30 years) maximum fire return intervals and lower mean annual temperatures (21-22°C) supported a bell-shaped population structure. Elephant damage affected smaller sized trees disproportionally more than large trees, where trees <0.5m in stem-diameter, generally, either escaped elephant utilization, or suffered severe or worse damage. The increasing levels of elephant damage over time (see Chapter 3) are expected to decrease the ability of baobabs to persist under unfavourably conditions. The inverse J-shaped SCDs of baobabs in the vegetation units associated with the Limpopo/Luvuvhu floodplains suggests that this is a healthy core population which is significant different from the bell-shaped SCDs for baobabs growing in less favourable vegetation units elsewhere. Long maximum fire return intervals, warmer climates and historically low densities of elephant in the Limpopo/Luvuvhu region are likely to support the healthy baobab population found there.

It is recommended that regular monitoing of the baobabs sampled in this project continue to assess changes in demography which could be exacerbated by increasing elephant densities, changing fire regimes and changing climate. Further, the sample size should be increased to include more baobabs in the cathedral mopane bushveld and within those areas defined by the 21°C isotherm, and between the 475 and 525mm isohyets to provide a more complete overview.

2.7 Acknowledgements

We thank Dr Ian Whyte, who initiated the measurement of baobabs in KNP in1995, and Michele Hofmeyr, who repeated and added to the sampling in 2001.

Both gave their data freely, without which this project would not have been possible. We thank South African National Parks scientific services Sharon Thompson, Sandra MacFadyen, Jacques Venter, and Chenay Simms, section rangers Sandra Visagie and Thomas Mbokota, field rangers Corporal Solomon, Carlos, Amos, Vusi, Jackson, Simon, Rirhandzu, and Pieter and game guards Isaac, Thomas, and Jacob for providing logistical support, geographical data, access, and protection in KNP. EcoTraining is thanked for accommodation in Pafuri. We further thank Janet Taylor, Dr Ricky Taylor and Simon Smit for assistance in the field, Melissa Whitecross for advice with R-code, and Dr Izak Smit, Dr Ricky Taylor, Dr Tony Swemmer, Dr Daryl Codron and Tracey Johnson for advice and discussions relating to the study. This project was supported by the Botanical Education Trust, the University of the Witwatersrand, Johannesburg, the South African Environmental Observation Network (SAEON), and the South African National Research Foundation (NRF) Innovation fund (SFH12082710827). Opinions expressed and conclusions arrived at, are those of the authors and are not necessarily to be attributed to the NRF or SAEON.

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CHAPTER THREE

An elephant-sized meal: Increasing stem damage to baobabs (1995-2013) in the Kruger National Park, South Africa

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Target journal: *Forest Ecology and Management*

3.1 Abstract

An increasing elephant population in the Kruger National Park (KNP) has given rise to concern regarding their impacts on the structure and composition of the savanna and on large tree species in particular. The northern region of the park supports an established population of baobabs, a tree favoured by elephants. Comparisons of elephant damage to stems and bark were made from 424, 899 and 884 baobab individuals, sampled repeatedly in 1995/6, 2001 and 2013, respectively, with the majority sampled 2 or 3 times. This study aimed to determine whether elephant damage to baobabs increased with the concurrent increase in elephant density; and how the severity of damage and tree fate were distributed between tree sizes and across landscapes of varying accessibility to elephants. Increases in damage between years correlated with increases in elephant density, specially of mature male elephants. Smaller baobabs – those <1m in stem diameter at breast height (1.3m), generally escaped elephant utilization altogether, or suffered very severe damage by elephants. Annualised mortality increased three-fold between the periods 1995/6-2001 (0.25%) and 2001-2013 (0.79%), with trees that had previously sustained severe and very severe damage contributing a significantly higher proportion of those dying than trees which sustained lesser damage. Smaller trees had a higher proportion of mortality than larger trees, with 61% of the observed mortality being ascribed to trees <1m in diameter. The cumulative effect of increased elephant damage, together with below average rainfall in general during the period 2002 to 2013, is likely to have resulted in the increased mortality observed.

3.2 Keywords

Adansonia digitata, bark stripping, bull elephants, destructive utilisation, *Loxodonta africana,* photographic comparisons

3.3 Introduction

African elephants (*Loxodonta africana* Blumenbach) are important drivers of savanna ecosystems (Ben-Shahar 1993; van Langevelde *et al.* 2003; Whyte 2003; Shannon *et al.* 2011). Their utilization of the landscape is intensive and often destructive, and can alter floral composition and structure (Ben-Shahar 1993; Whyte 2003; Helm & Witkowski 2012). Elephants have a mixed diet of grass and woody plants and strip branches, pollard stems, remove bark and uproot trees and herbaceous species. Rapid population growth rates of elephant populations and restricted reserve sizes have resulted in high elephant densities within many of Africa's conservation areas (Caughley 1976; Whyte 2003).

Elephant utilization of the landscape is not uniform. Elephants appear to avoid obstacles such as steep slopes and areas with higher relative rock cover, which impede access (Gertenbach 1983; Edkins *et al.* 2007). In addition elephants spend a large portion of their time near water sources and habitat-use generally increases with proximity to water (Harris 2008). Behaviour of elephants also differs between age classes and sexes, with mature males (hereafter referred to as bull elephants) being notably more destructive than individuals in a mixed family group comprising females and juvenile males (Croze 1974; Guy 1976; Stokke & Du Toit 1999; Midgley *et al.* 2005). Bull elephants contribute more to the destruction of large trees than do family groups, spending more time per tree as well as selecting trees with larger stem diameters and regularly toppling them to the ground (Stokke & Du Toit 1999). The felling of trees and stripping of bark is often too excessive to be solely for feeding, and is likely related to social or sexual behaviours (Midgley *et al.* 2005).

The African baobab, *Adansonia digitata* L. (Malvaceae), is a tree favoured by elephants (Robertson-Bullock 1960; Caughley 1976; Barnes 1980; Weyer-Haeuser 1985; Swanepoel 1993; Whyte 2001b; Wickens & Lowe 2008) which eat the leaves, stems (including the bark), and fruit, and rest in its shade. Elephant utilization of baobabs is often destructive and has been flagged as the major cause of declining baobab populations throughout Africa (Barnes 1980; Swanepoel & Swanepoel 1984; Barnes *et al.* 1994; Edkins *et al.* 2007; Ndoro *et al.* 2014).

An established population of baobabs occurs in the northern sections of the Kruger National Park (KNP), South Africa where the southern-most limit of the baobab's natural distribution reaches approximately 24.5°S. Similar to occurrences in other conservation areas in Africa (Caughley 1976), KNP has been experiencing rapidly increasing elephant densities. By the end of the 19th century, all elephants in the area that was later to become KNP, were removed by hunting (Whyte *et al.* 2003). The first elephants began to return in the early 1900's. Under management this population grew to over 6000 individuals by 1970, with a culling programme implemented in the late 1970's to maintain the population at about 7000 individuals. Culling ceased in 1995 and the population reached 10000 in 2000 and exceeded 16000 in 2012 (SANParks 2013). Two regions in KNP, including the northern parts of Pafuri (the most northern management section of the park), have been designated as botanical reserves and, where possible, translocations of elephant from these regions have been conducted in an unsuccessful attempt to maintain lower elephant densities (Whyte 2001).

There has been growing, but scientifically uninformed, concern over the negative impacts of elephants on baobabs within KNP. Whyte (2001) and Hofmeyr *et al.* (2004) considered extended periods of drought to be the primary agent of mortality in mature baobab trees. During the drought of the late 1980's and early 1990's more than 1000 large baobabs died in KNP (Whyte 2001). Although they recorded widespread elephant impacts, few trees were extensively damaged. Whyte (2001) suggests that an increased density of elephants may have a negative effect on the baobab population by increasing individual vulnerability to drought. However, Kelly (2000) found no evidence from his 1999 study that elephants played a significant role in the mortality of adult baobabs in northern KNP. Five years later in 2004, Edkins *et al*. (2007) compared a subset of the northern KNP baobab population with a subpopulation in Limpopo National Park (LNP) in neighbouring Mozambique, with substantially lower relative elephant densities.

Edkins *et al.* (2007) found increased mortality of smaller individuals in KNP, which they attributed to heavy elephant utilization. They also suggested that 'refugia' in the form of steep slopes and rock cover were important for the survival of baobabs in the presence of high elephant densities.

Whyte (2001) recognised that long-term monitoring was required in order to quantify changes occurring within the KNP baobab population, with particular reference to the impact of an increasing elephant population. Sampling conducted by Whyte (2001) in 1995/6 together with sampling conducted by Hofmeyr in 2001 (unpublished data) and the 2013 sampling done in this study provide an ~18 year data set for monitoring such changes. This study, which complements the demographic/population structure assessment of the KNP baobab population (Chapter 2), aims to determine: (1) if elephant damage to baobabs has increased with the increase in elephant density over time, (2) how the severity of damage is distributed across baobab size classes and landscapes of variable accessibility to elephants (slopes, rock cover and distance to water), and (3) how the fates of baobabs are distributed between trees displaying varying severities of elephant damage, size classes, and ease of accessibility to elephants.

3.4 Methods

3.4.1 Study area

KNP is South Africa's largest protected area and it is situated in the north east of the country on the Mozambique border (Figure 2). KNP is divided into 22 managerial sections. This study was conducted in the 3 most northerly sections, *viz*. Pafuri, Punda Maria, and Vlakteplaas, bordered by the Limpopo River in the north, the Luvuvhu River in the west, and the Lebombo Mountains in the east.

Landscapes vary from the *Colophospermum mopane* tree savanna north-east of Punda Maria, to the *Terminalia sericea* savanna sandveld communities to the east and west and the alluvial plains of the Limpopo and Luvuvhu rivers dominated by

Faidherbia albida tree savanna (SANParks, 2013). Elephants do well on the mixed diet afforded by these savanna habitats and their population in the 3 most northern sections of KNP has increased from an estimated 0.381 elephants/km^2 in 1995 to 0.664 elephants/km^2 in 2012 (SANParks, 2013; Figure 1), a 74% increase. Whilst the general trend in total elephant densities showed consistent increases over the study period, bull elephant densities estimated at 0.0719 elephant bulls/km^2 in 1995 peaked at 0.11 elephant bulls/km^2 for the period 2001 -2005 before falling to 0.0848 elephant bulls/km^2 in 2012 (SANParks, 2013; Figure 1).

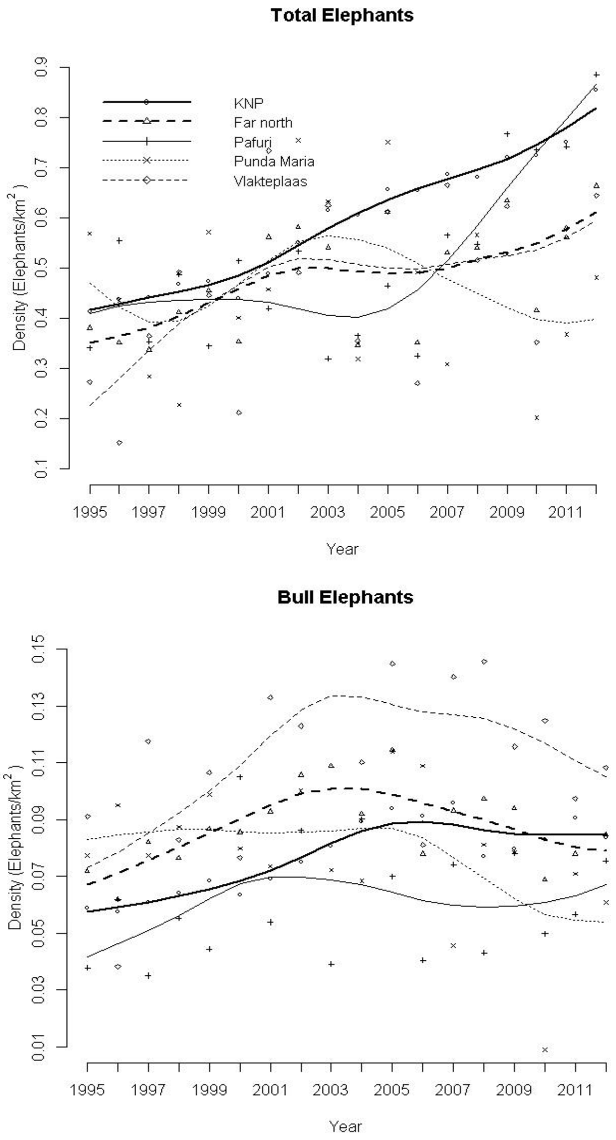

Figure 14. Changes in total and bull elephant densities for the entire KNP, the 3 northern-most sections combined (Far north), and for the Punda Maria, Pafuri, and Vlakteplaas sections, from 1995 to 2012 (SANParks 2013) with fitted cubic smoothing splines (d.f. = 5), respectively.

3.4.2 Study species

The African baobab, with adult height and stem girth measurements exceeding 20m, is a charismatic and iconic large tree of the African savanna (Wickens 1982; Kelly 2000; Venter & Witkowski 2010).

Baobabs play a keystone role in ecosystem functioning, providing habitat, food and nesting habitat for many animals (Kelly 2000). Baboons, elephants, and a variety of antelope utilize various parts of the tree for forage. Moths and fruit bats utilize the nectar and pollen (Wickens 1982) and large trees provide important nesting sites for many species of birds, including several rare and locally threatened species such as grey-headed parrots, southern ground-hornbills, white-headed vultures and two species of spinetail (Kelly 2000, Whyte 2001a; 2001b, Edkins *et al*. 2008, Venter & Witkowski 2011). The African baobab is also highly valued by humans for the many well documented services it provides including important sources of food, fodder, building material, water, medicine, shelter, and spiritual and cultural services (Wickens 1982; Sidibe *et al*. 2002; Wickens & Lowe 2008; Cuni Sanchez *et al*. 2011;Venter & Witkowski 2013a).

Due to its importance as a keystone species, its cultural and spiritual value and the potential threat of over-utilization, baobabs are formally protected under South African legislation in the National Forests Act of 1998 and in the revised Act of 2012. Furthermore, the listing of the baobab as a species of special concern, a functionally important and locally threatened species by SANParks (McGeoch *et al.* 2010), highlights the significance of this species and provides motivation for on-going monitoring and, where necessary, conservation action.

3.4.3 Sampling

This study extends on earlier surveys conducted by SANParks staff; in 1995/6 by Dr Ian Whyte (2001) and in 2001 by Michele Hofmeyr (unpublished). In 1995/6, 424 baobab trees in northern KNP were located in Pafuri and morphometrics and damages were recorded. Nearly all of these trees were located in 2001. An additional 468 trees, located predominantly in the Punda Maria section were added to this sample. Baobabs were sampled close to access roads, as a result large areas of wilderness, where baobabs likely occur, were not sampled.

In 2013, the majority of sampled trees were located and resampled, a number were not sampled due to access constraints imposed by security concerns relating to poaching. In addition all baobab individuals within 50m of previously measured trees were recorded, involving careful searching whilst walking in concentric circles around each tree for 20 minutes adding a further 126 trees of all sizes. In total 1036 trees were sampled at least once during the ~two decade period, of which, 278 (27%) were sampled once, 345 trees (33%) were sampled twice, and 413 (40%) were sampled three times (Figure 2).

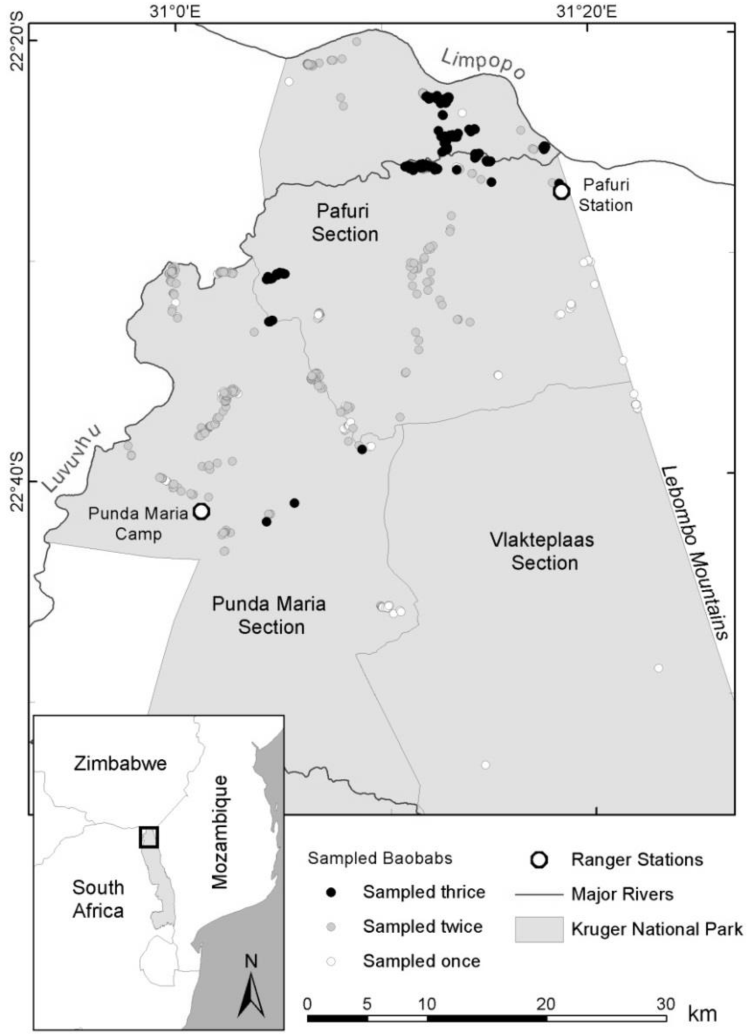

Figure 15. The location of all baobabs sampled in the three northern-most sections of the Kruger National Park, South Africa, between 1995 and 2013. Individuals sampled once, twice and thrice are shown. Many tree localities overlap at this

scale, so not all are visible. Baobabs were sampled close to access roads, as a result large areas of wilderness, where baobabs likely occur, were not sampled.

Both the initial sampling and the 2013 resampling followed several years of below average rainfall, while the 2001 field campaign followed several years of above average rainfall (Figure 3).

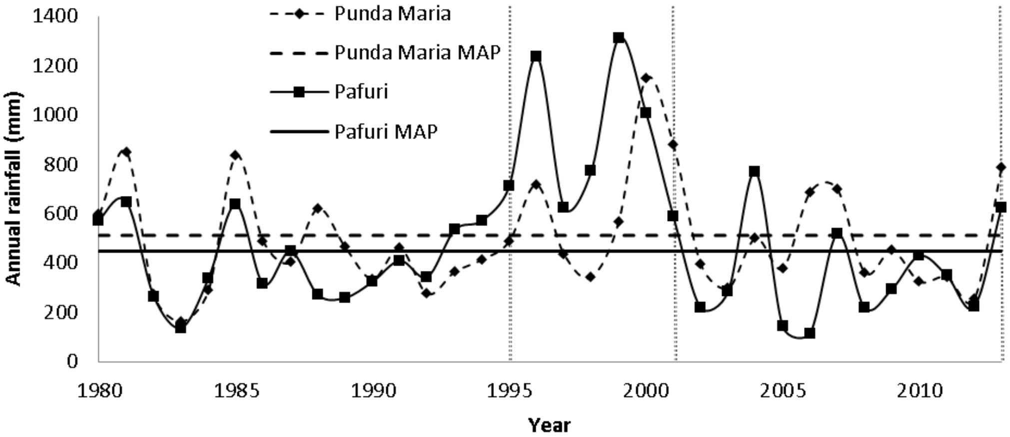

Figure 16. Variation in annual rainfall at Punda Maria rest camp and the Pafuri ranger station during and including the 15 years prior to this study (SANParks, 2013). Long-term means for the period 1980-2013 are included. Vertical dotted lines indicate years of each sampling event (1995/6, 2001 & 2013).

During each sampling event the circumference of each tree was measured (in meters, to two decimal places) at 1.3m above the most elevated ground at the base of the tree and perpendicular to the vertical axis of the stem using a taut, non-stretchable tape measure that did not follow the contours of the tree. Circumference measurements were converted to diameters for better visualisation, as recommended by Wickens and Lowe (2008). Photographs taken of each tree sampled in 1995/6 were replicated and the focal length, direction and distance to the tree from the point of photography were recorded. A 1.5m graduated height pole was held next to each tree for scale. These repeat photographs allow for the simultaneous direct visual comparison of bark damage between 1995/6 and 2013 by the same observer reducing inherent and unintentional observer bias. At each tree the percentage of the ground within 5m of the stem covered in rocks >10cm tall was estimated and the angle of the slope was measured using a hand-held digital inclinometer. Distance to permanent water was recorded off aerial imagery.

In the field, an estimate of elephant damage was recorded for each tree sampled. Overall elephant damage was recorded as i) none, ii) slight (some utilization, but not ring-barked), iii) moderate (utilization shallow and tree ring-barked), iv) severe (tree ring-barked and utilization affecting the shape of the stem), and v) very severe (utilization dramatically affecting the shape of the stem) following Whyte (2001, Figure 4). The age of utilization for the dominant damage class was recorded as i) very old (a new layer of bark completely covering the damaged parts, and the damage indicated only by scars), ii) old (colour greyish-white and new bark beginning to form), iii) recent (wounds dried and faded yellow) and iv) fresh (wounds deep orange-yellow in colour) after Kelly (2000) and Whyte (2001) (Figure 4). Personal observations suggest that wounds lose their rich colour after 1 - 3 weeks. Comparisons with notes made on the recovery of other savanna tree species (Bruce Page, unpublished) and personal observations suggest that it may take up to 3 months for the wound to turn grey/white and half a decade or more for a wound to heal over. Romero *et al.* (2001) suggests that once harvested for its bark, a baobab may take between 2 and 10 years to recover sufficiently to be reharvested. Scars persist for decades, as seen outside of national parks where trees have not been affected by elephants for many years.

For the purposes of this study, fate is used to describe the resulting change in level of elephant damage over the study period. Each resampled tree was allocated to a fate category (recovered, unchanged, deteriorated, or died) based on the net change in damage since the previous sampling.

After death, the above ground tissue of a baobab disintegrates completely within 1 - 2 years (S. Woodborne pers. comm., 2015). However, the hollows resulting from trees that were recorded as dead in 1995/6 still showed distinctive baobab bark in 2013 where it had been preserved in root channels. Therefore a previously sampled tree was confirmed dead in the 2013 survey if i) the rotting remains of the tree were visible, ii) an appropriately-sized hollow with remnants of baobab bark was present, or iii) the location of the coordinates matched the view in the 1995/6 photograph, but lacked the baobab (Figure 4). Individuals were recorded as missing if no tree was visible at the given coordinates and if the vista could not be matched to the 1995/6 photograph. In 2001, two of the trees surveyed in 1995/6 were classified as missing and in 2013, 10 of the trees recorded in 2001 were missing. The two trees from 1995/6 remained missing in 2013. Only three of the 12 missing trees were less than 5m tall and less than 30cm in diameter, suggesting that they were mostly substantial trees. The data were robust, showing similar trends whether these missing trees were excluded, included as dead, or partly included, depending on their size. As extensive searches for these missing trees were conducted in 2013, it was reasonably assumed that they were dead.

Desktop comparisons were made between photographs taken in 1995/6 and repeated in 2013. Adobe Photoshop® CS2 was used to overlay each pair of photographs exactly. A grid indicating 1m height intervals was superimposed and calibrated with the height pole (Figure 4). For each vertical meter, up to 5m, the percentage of the stem showing elephant damage was estimated, from which an overall damage percentage per tree was calculated. The minimum and maximum heights of damage were also recorded, and the range calculated. A score of 1 - 4 was allocated based on the age of the dominant damage class as described previously. The presence or absence of very old and fresh damage, where it was not the predominant damage class, was also noted. As initial sampling was done predominantly in Pafuri these photographic comparisons represent only this section of the park.

Figure 17. Varying degrees of elephant damage to baobabs in northern KNP: None (A), Slight (B), Moderate (C), Severe (D), and Very severe damage (E). Dead baobabs were confirmed by the absence of the baobab from the landscape (when compared with previous photos) (F) - in this case the foreground baobab seen in photo (A), the presence of rotting remains (G), or a hollow in the ground (H). Examples of variously-aged elephant damage can be seen in (I) including very old (i), old (ii), recent (iii) and fresh damage (iv). Repeat images from 1995/6 (C) and 2013 (D) show changes in the level of elephant damage, here increasing from moderate to severe. Horizontal lines indicate 1m height intervals. Photographs (A, B, & C) by Dr Ian Whyte.

3.4.4 Statistical analysis

Changes in elephant damage

The elephant damage data collected in 1995/6, 2001 and 2013 differed significantly from a normal distribution. Log, arcsine, square-root and power transformations were unsuccessful in normalising these differences and, as such, non-parametric Spearman's rank correlations were run to test how elephant damage score relates to time, and total- and bull- elephant densities. Elephant densities were calculated from aerial census data provided by South African National Parks (SANParks 2013).

The differences between the 1995/6 and 2013 baobab stem damage scores deviated significantly from a normal distribution for all variables. Transformations were unsuccessful in normalising these differences and, as such, non-parametric tests were consequently used to analyse the data. Wilcoxon signed rank tests were run to determine if the maximum and minimum heights, height range, depth and age of the dominant damage class, and percentage damage to baobab stems by elephants varied significantly between the sampling efforts of 1995/6 and 2013.

Distribution of elephant damage

Two-sample Kolmogorov–Smirnov tests were run to determine if the distribution of elephant damage score (none, slight, moderate, severe or very severe) differed significantly between baobabs of differing diameters, rock cover, distance to water and slope, for all years (1995/6, 2001 and 2013).

Baobab fate and mortality

Two-sample Kolmogorov–Smirnov tests were run to determine if the distribution of baobab fate (recovered, unchanged, deteriorated, or died) differed significantly between baobabs of differing diameters, initial damage, rock cover, distance to water and slope, for all periods (1995/6 to 2001, 2001 to 2013 and 1995/6 to 2013).

All statistics were performed in R (R Core Team, 2013).

3.5 Results

Changes in elephant damage

Significant positive relationships exist between year (Figure 5a), elephant density (Figure 5b), and bull elephant density (Figure 5c) and damage score to baobabs ($S = 1141100000$, $P < 0.0001$, $r_s = 0.254$; $S = 1142700000$, $P < 0.0001$, $r_s = 0.253$; and $S = 1148900000$, $P < 0.0001$, $r_s = 0.249$ respectively). Mean elephant damage score was higher for baobabs in Punda Maria section than Pafuri for all years sampled (Figure 5a). The mean damage score was substantially higher in Vlakteplaas than both Punda Maria and Pafuri in 2001.

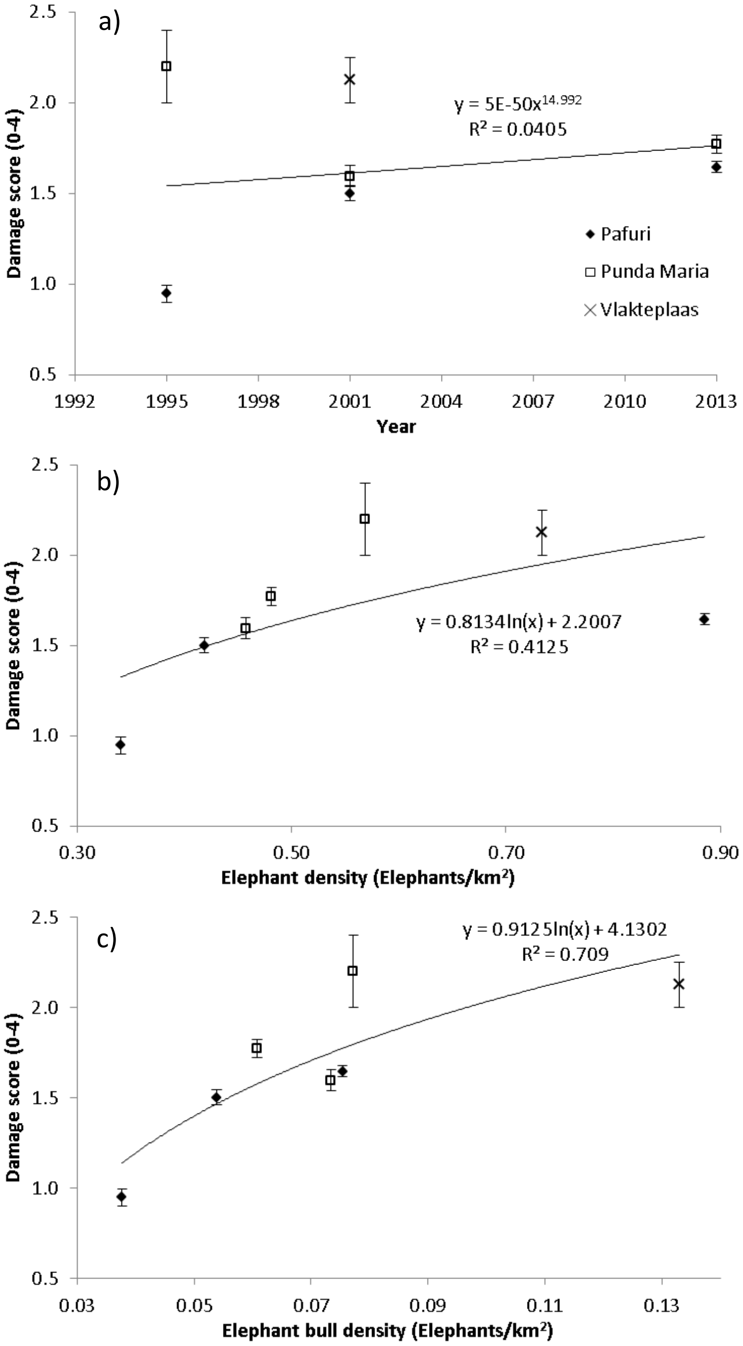

Figure 18. Elephant damage score (mean ± S.E.) to baobab trees in Punda Maria, Pafuri, and Vlakteplaas sections of KNP (a) over time, (b) in relation to total and (c) bull elephant densities. Damage ranged between none (0) and very severe (4). Lines indicate the fitted trends.

There were significant increases from 1995/6 to 2013 for all damage cover metrics recorded (Table 2). The median value for vertical range of damage increased from 3.45m in 1995/6 to 3.70m in 2013. The median value for the percentage of the stem damaged, below 5m, increased 5-fold from 4% in 1995/6 to 20% in 2013. Elephants preferentially utilised the first 3m of baobab stems (Figure 6; Table 2), with a mean utilization of 21% in 1995/6 and 36% in 2013, compared to less than 5% and 12% average damage above this height, respectively.

The maximum heights of damage recorded were 5.2m in 1995/6 and 5.3m in 2013, while the minimum height of damage was ground level (0m) for both years. In 1995, 50% of the trees showed very old, healed, damage; this increased to 66% of trees in 2013. In 1995/6 just under 4% of trees showed signs of fresh damage, this near quadrupled to 15% of trees in 2013.

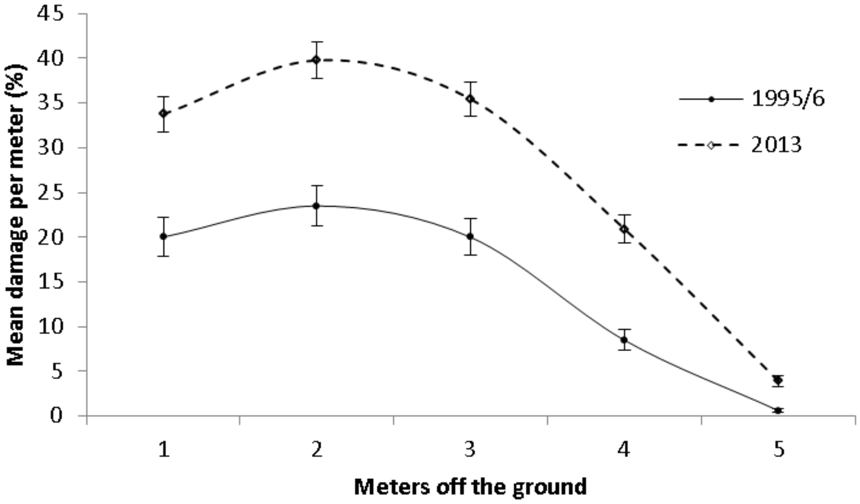

Figure 19. A comparison of the percentage of the stem damaged per meter of vertical stem height between 1995/6 and 2013 with fitted smoothed lines. Bars indicate standard error.

Table 2. Differences in stem damage between 1995/6 and 2013 assessed from the matched photographs. The means (M), standard deviations (SD) and medians (Mdn) are indicated for each year. Wilcoxon signed rank tests (d.f. =258 throughout) were used to compare between years, with significant differences (P<0.05) indicated in bold.

	1995			2013			W	P
	M	SD	Mdn	M	SD	Mdn		
Maximum height of damage (m)	3.31	1.05	3.50	3.61	0.96	3.80	9	**<0.0001**
Minimum height of damage (m)	0.17	0.39	0.00	0.19	0.40	0.00	863	**<0.0001**
Vertical range of damage (m)	3.14	1.22	3.45	3.43	1.18	3.70	52	**<0.0001**
Age of damage score (1-4)	1.20	1.08	2	1.84	0.74	2	547	**<0.0001**
Overall damage below 5m (%)	14.54	20.52	3.80	27.18	24.65	20.00	3461	**<0.0001**
Damage in the 1st meter (%)	20.02	31.22	0.00	33.75	34.61	20.00	2366	**<0.0001**
Damage in the 2nd meter (%)	23.49	32.66	8.00	39.77	35.68	30.00	3256	**<0.0001**
Damage in the 3rd meter (%)	19.99	29.33	2.00	35.43	33.53	20.00	2720	**<0.0001**
Damage in the 4th meter (%)	8.49	16.79	0.00	20.91	26.16	10.00	1582	**<0.0001**
Damage in the 5th meter (%)	0.63	2.52	0.00	3.94	10.38	0.00	190	**<0.0001**

Distribution of elephant damage

The distribution of damage to all trees sampled differed significantly between years. An increased proportion of severe and very severely damaged trees, and a decreased proportion of trees with no damage were observed in the later years. The highest proportion of very severe damage was consistently recorded in 2001 (Figure 7; Appendix 1).

The distribution of elephant damage to trees growing on steep slopes greater than 20° differed significantly from other slopes for all years sampled (Figure 7; Appendix 1). Slopes steeper than 20° had the highest proportion of trees without damage with 60%, 50% and 45.8% of the population showing no signs of damage in 1995, 2001 and 2013, respectively. These slopes also supported the least severely damaged individuals (0%, 3.6% and 4.2% of the population in 1995, 2001 and 2013, respectively) and no trees with very severe damage. Whilst the distribution of damage severity did not differ significantly between the other less steep slope classes, the highest proportion of severely damaged trees observed in this study (20.1%) was found on gentle slopes (1 - 10°) in 2001. The lowest proportion of trees without damage was consistently seen on flat (0° gradient) areas, reaching a minimum of 6.3% in 2001. Trees growing on steep slopes steeper than 20° represent the smallest proportion of the sample, accounting for just 4% of trees sampled each year (Figure 7). The majority of sampled trees (69% in 1995/6 and 68% in both 2001 and 2013) were growing on gentle 1 - 10° slopes.

The distribution of elephant damage on trees with a stem diameter of 1m or less was significantly different to that on larger trees. Trees <1m in stem diameter had the highest proportion of undamaged individuals (71.4%, 39% and 33.5% in 1995, 2001 and 2013, respectively) but also the highest proportion of very severely damaged trees (0.8%, 5% and 2.4% in 1995, 2001 and 2013, respectively; Figure 7; Appendix 1). Trees with stem diameters of greater than 2.0m were seldom undamaged, or very severely damaged.

Trees growing in areas with no rock cover within 5m from the stem had a significantly higher proportion of very severe damage in 2001 and 2013 (0% in 1995/6, 5.4% in 2001 and 1.6% in 2013) compared with trees growing amongst rocks (0% in 1995/6, < 1.7% in 2001 and <1.1% in 2013), and hence rocks confer some protection. More than 33% of trees in areas with more than 60% rock cover had no damage compared to <29% of trees surrounded by fewer rocks (Figure 7; Appendix 1).

Trees further than 1500m from a perennial river seldom showed very severe elephant damage, with no trees showing very severe damage in 1995/6 and 2013, and only 2 of 392 trees being very severely damaged in 2001. The highest proportion of very severely damaged trees (up to 4% of trees in 2001) were situated 1001-1500m from rivers.

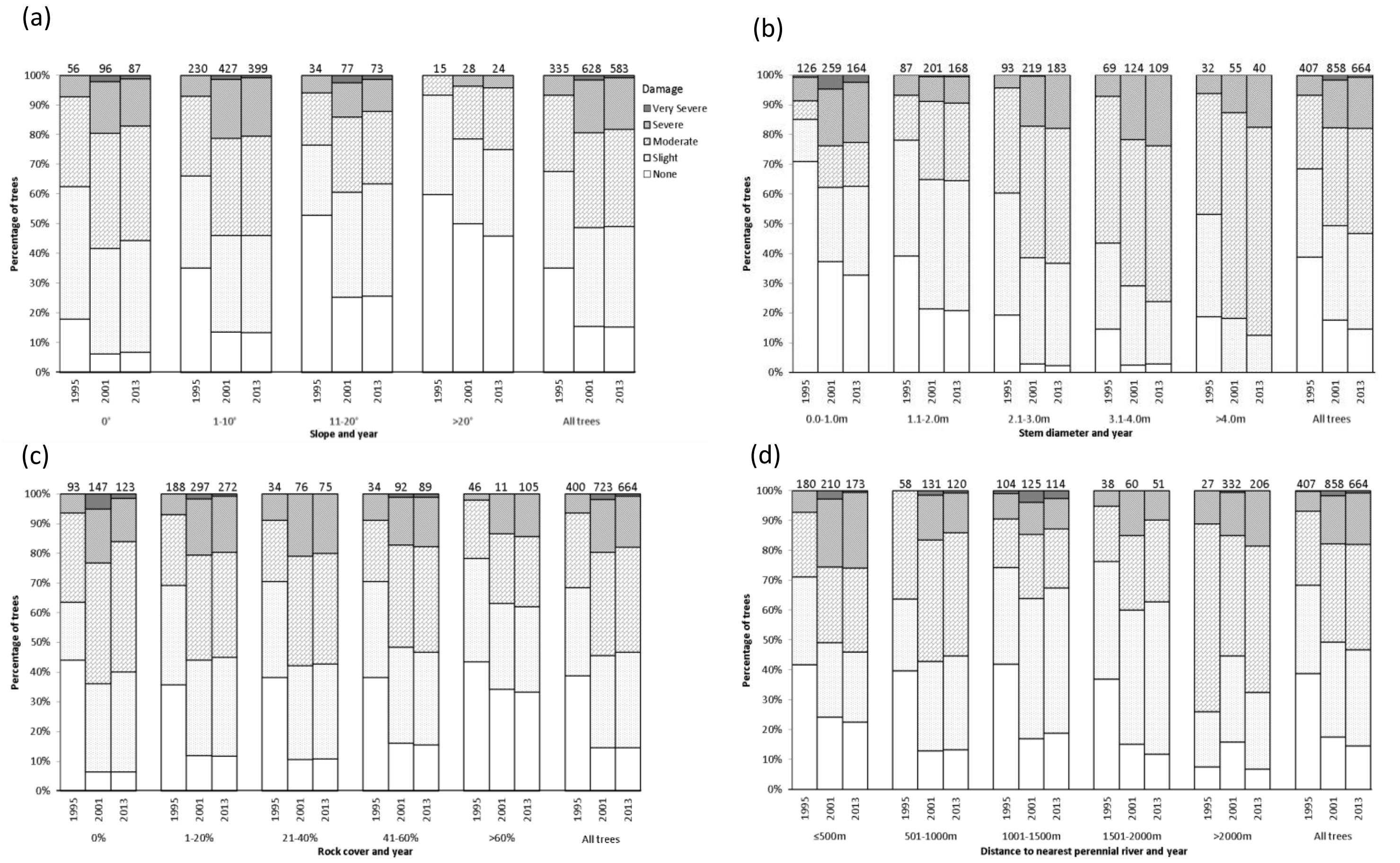

Figure 20. The distribution of elephant damage to baobabs in 1995/6, 2001 and 2013 across classes of (a) gradient / slope inclination, (b) stem diameter at 1.3m, (c) proportion of rock cover within 5m of the stem, and (d) distance to the nearest perennial river. The numbers above each bar indicate the sample size.

Baobab fate and mortality

There were significant differences between the fates of all trees sampled over 1995/6 to 2001 compared with both the 2001-2013 and 1995/6-2013 intervals (Figure 8; Appendix 4), with the biggest difference ascribed to a high proportion of trees dying after 2001. The annualised mortality was 0.25% for the period 1995/6 to 2001 but tripled to 0.79% between 2001 and 2013.

By the end of the study period (1995-2013) 50% of severe and very severely damaged trees recovered, showing lesser levels of damage. However, less than 7% of trees suffering moderate or slight initial damage recovered. The majority of the recovery occurred after 2001, when 66.4% of severe and very severely damaged trees in 2001 recovered by at least one damage level by 2013. However, these severe and very severely damaged trees showed the highest proportion of mortality (32.1% over the entire study; 10.7% in 1995 to 2001; and 17.1% in 2001 to 2013; sample sizes differ between the different periods hence percentages cannot be summed to achieve the overall percentage mortality; Figure 8). Trees with lesser levels of damage experienced <14% mortality over the entire study (<2% in 1995 to 2001 and <10% in 2001 to 2013). The majority (82.6%) of trees with no initial elephant impact suffered some damage over the study period, with the highest increase (80.4% of previously undamaged trees being damaged in some way) occurring between 2001 and 2013. Further, 64.7% of trees undamaged in 1995 received some damage by 2001. Overall the level of damage to trees with moderate or slight damage was the most stable between years, with 75% and 26.1% respectively remaining unchanged (53% and 50% unchanged between 1995 and 2001; and 70.4% and 43.5% unchanged in 2001 to 2013). These were also the most likely trees to survive, with survival at 96% and 88.3%, respectively (99% and 98.3 % in 1995 to 2001; 92.2% and 93.5% in 2001 to 2013; Figure 8; Appendix 3).

No significant differences were observed between the fates of trees on different slopes within years; however a significant difference was noted between years. On steep slopes >20°, 73.3% of trees remained unchanged in their level of damage for the period 1995/6-2001, compared with 39.3% for 2001-2013. This suggests an increase in elephant utilization on steeper slopes over the last 12 years of the study. For these steeper slopes over the same periods the proportion of trees that deteriorated in level of damage increased from 20% to 35.7%, and those that died increased from 0% to 14.3%.

The distribution of individual tree fates was not significantly different between trees <1m and those >4m stem-diameter (Appendix 4). Trees less than 1m in diameter suffered 25.8% mortality over the study period, the bulk occurring between 2001-2013 (20.8%). Similarly, large mortalities were seen in trees >4m in diameter, with 21.9% mortality over the study period (17.3% from 2001 to 2013). Trees >1m and <4m received <7% mortality over the study period (<6% mortality from 2001 to 2013).

Baobab fate differed little over distance to the nearest perennial river, except for those trees further than 2000m away, which differed significantly from other distances for the period 2001 to 2013. Individuals >2000m from rivers had significantly lower proportions of trees that have deteriorated to an increased level of damage or died (19.0% and 4.2% respectively) than trees situated closer to rivers (>31.6% and >8.3%; Figure 8; Appendix 3).

No significant differences were observed between the distribution of fates of trees growing in areas of differing rock cover. However, it is notable that 19.9% of trees afforded no rock protection died between 2001 and 2013, more than double the mortality recorded in trees in more rocky areas.

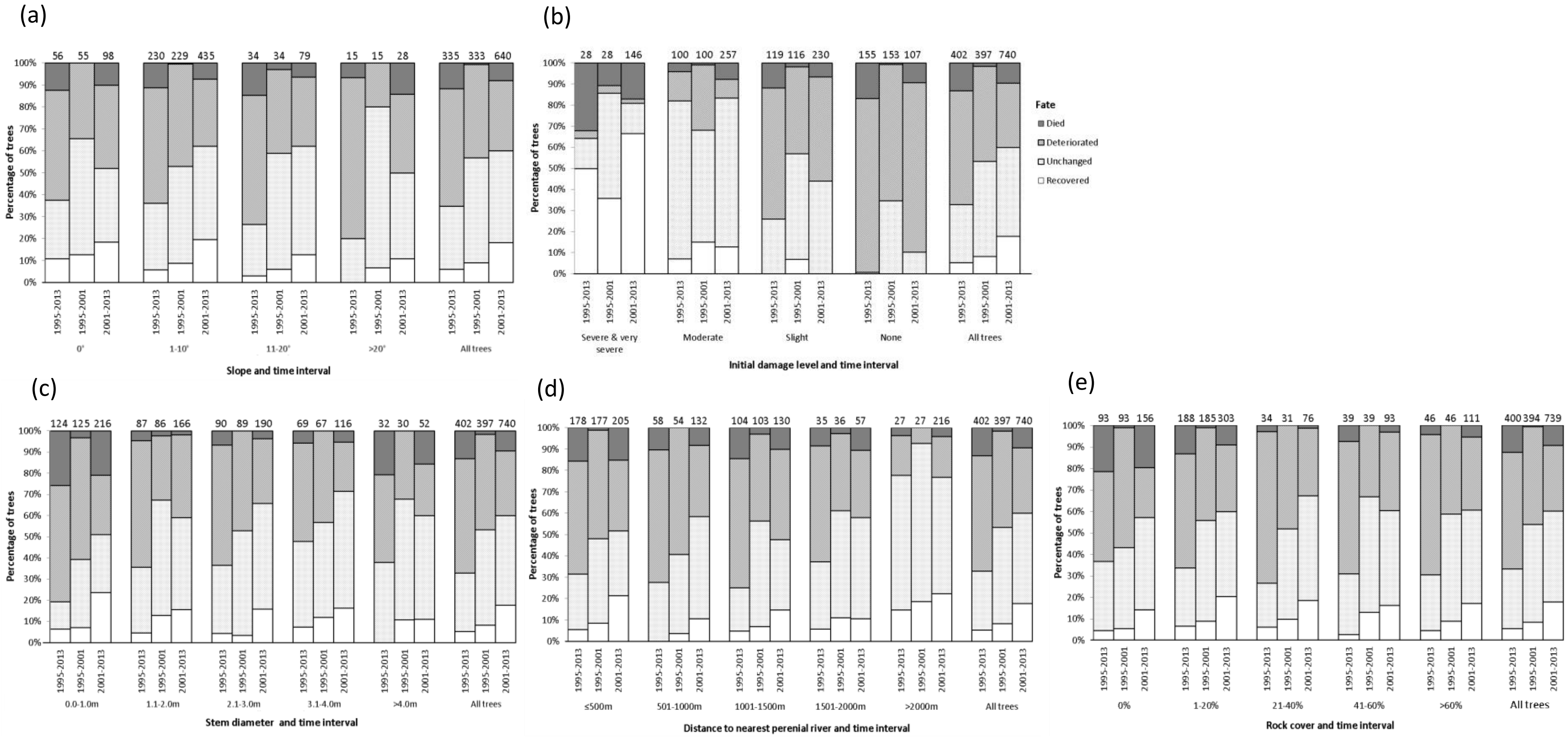

Figure 21. The distribution of the fates of baobabs over the intervals 1995/6 to 2013, 1995/6 to 2001 and 2001 to 2013 across: (a) gradient / slope inclination, (b) initial damage levels, (c) stem diameter at 1.3m, (d) distance to the nearest perennial river, and (e) proportion of rock cover within 5m of the stem. The numbers above each bar indicate the sample size.

3.6 Discussion

Changes in elephant damage

Increases in both total elephant density and in elephant bull density alone correlated with an increase in baobab bark damage over the period 1995/6 to 2013. Of these, bull density had the stronger correlation. Further, consistently higher mean damage scores recorded from Punda Maria, as compared to Pafuri, reflect the relatively stable, but higher, bull elephant densities in the former section until 2010. This is despite erratic total elephant densities for both sections over the study period. Barnes (1980) recorded heavy elephant utilization of baobabs in 1975 in Ruaha National Park, Tanzania; this impact decreased in the years prior to 1989 (Barnes *et al.* 1994) which was attributed to the selective removal of bull elephant by poaching. Further, Barnes (1980) suggested that the social behaviour of bull elephants allows them to spend more time foraging on a baobab without the influence of a moving herd.

Not only are more trees being damaged in recent years as bull densities have increased, but elephants are also reaching higher, removing greater proportions of bark, and returning more frequently to the same individual as shown by increases in the vertical range of damage, the proportion of bark removed within each meter height interval, and the fresher ages of damage.

Elephants use their tusks to pierce baobab bark (pers. obs.). They then strip the bark both upwards and downwards from this initial injury. In this manner an elephant is able to debark (‘peel’) large areas of the baobab stem. The preferred forage height of below 3m suggests a convenient height for elephants to manoeuvre their tusks. This preferential utilization of the first 3m of the baobab stem compares with Stokke and du Toit (2000), who showed elephants prefer to browse below 2m.

The presence of fresh bark damage increased approximately four-fold between 1995/6 and 2013 in Pafuri section from 4% to 15%. This was seldom the predominant level of damage, indicted by superficial nicks and cuts, and can likely be attributed to elephants passing by a tree or resting in the shade, rather than by bull elephants destructively foraging. Very little (0.2 % and 0% for 1995/6 and 2013 respectively) of the moderate, severe and very severe damage was recorded as fresh. Fresh damage, which lasts up to 3 weeks before fading, therefore indicates an increased frequency of visits by elephants in recent years. In the mid-1990's the area north of the Luvuvhu River had a low elephant density (0.34 elephants/km^2) that was maintained by culling (Whyte 2001b). In the 2000's this area was managed as a botanical reserve (Whyte 2001b), but without culling the elephant population rapidly grew and the total elephant density in Pafuri more than doubled between 2004 (0.37 elephants/km^2) and 2012 (0.89 elephants/km^2). The increased total elephant density, rather than increased bull density, could explain the increase in the frequency of elephant visits to baobabs in the Pafuri section.

Distribution of elephant damage

Baobabs have become progressively more damaged over the study period, with 67% shifting into a higher damage class between 1995/6 and 2013.. The smallest stem diameter size class of <1m had relatively higher proportions of both very severe and no damage compared to larger trees. It is likely that it takes less time and effort for an elephant to very severely damage a smaller tree to the point that the shape of the stem is impacted upon than it would a larger tree. Similarly, the likelihood of remaining undetected by foraging elephants increases with decreasing size, allowing smaller individuals to escape damage. This combination of being easier to damage also explains the relative lack of small trees displaying moderate damage. Edkins *et al.* (2007) found fewer small, <0.64m stem diameter (2m circumference), baobabs in KNP than in Limpopo National Park, Mozambique, which was attributed to heavy elephant browsing given the higher densities in the former park. The suggestion here is that these smaller trees were less resilient to damage, and hence are more likely to die following the severe levels of damage noted in the current study.

Steep slopes of >20° consistently supported trees with lower levels of elephant damage than more gentle slopes. A similar trend was found with rock cover, where lower levels of elephant damage were recorded on trees surrounded by >60% rock cover. This supports the findings of Edkins *et al*. (2007) who reported that steep slopes and rocky ground in northern KNP act as ‘refugia’ for baobabs from elephants. Signs of elephant were however noted on steep slopes and among high rock cover (pers. obs.), and some elephant damage was evident on trees occurring in these areas. This suggests that these barriers may impede, but seldom prohibit, elephant movement. Damage to baobabs in these ‘refugia’ increased in both severity and intensity over the period of study, reflecting reduced refuge as a result of increasing elephant densities.

Trees further than 1500m from perennial rivers consistently showed less extreme (very severe and severe) damage from elephants, than trees growing closer to rivers; suggesting elephants spend more time utilizing baobabs closer to rivers. These findings concur with those of Harris *et al*. (2008), where presence of water was considered the best predictor of elephant distribution. Here, the increased elephant distribution/density near rivers translates to increased cumulative and more severe levels of damage to locally-occurring baobabs. However, this would not explain the consistently higher levels of very severe damage seen in baobabs located between 1001-1500m compared with baobabs growing closer to the water.

Overall the highest proportion of very severely damaged trees was recorded in 2001. This is congruent with bull elephant densities which increased between 1995 and 2001, peaked at 0.11 elephant bulls/km^2 for the period 2001 to 2005, and thereafter decreased to 0.0848 elephant bulls/km^2 by 2012.

Baobab fate and mortality

Annualised mortality increased three-fold from 0.25% for the period 1995/6-2001 to 0.79% during 2001-2013. As mentioned previously, 2001 was the year in which the highest proportion of very severe damage to trees was recorded, as well as higher mortality for severely and very severely, rather than less damaged individuals. Annualised mortality for both periods are well below the 3% mortality recorded in Ruaha National Park, Tanzania in 1975 (Barnes 1980) and the 2.9% annualised mortality reported from Mana Pools National Park, Zimbabwe between 1984 to 2005 (Swanepoel & Swanepoel 1984; Ndoro *et al.* 2014). These very high mortalities both correlated with high elephant densities (4 elephant/km^2 in Ruaha in 1975 and 1.6 and 2.7 elephant/km^2 in Mana Pools in 1984 and 2005, respectively) and the associated damage. Barns (1980) suggested that bull elephants were most likely responsible for the destruction of mature baobabs.

Overall baobabs <1m and >4m in stem diameter suffered higher mortality than trees in the middle size classes. The mortality in the <1m stem-diameter size class relates to the proportions of severe and very severe damage they received for all three years sampled (Appendix 1); however, it does not explain the high proportion of mortality in the >4m stem-diameter size class where similar or lower proportions of severe and very severe damage to those of baobabs in the intermediate size-classes were seen for all three years (Appendix 1). The cause of death for these large trees is unknown; we suggest the probable combined effect of multiple threats which weakened and eventually killed these individuals. For both 1995-2001 and 2001-2013 mortality was highest in severe or very severely damaged trees and within areas of low and intermediate rock cover. The observed mortality relating to intermediate slopes and intermediate distance from rivers in 1995-2001 was not present in 2001-2013. Mortality in the largest size-class was not observed in the period 1995-2001.

It is expected that above an unknown threshold level of elephant damage a baobab will eventually die, and that this threshold is likely to be dependent on tree size, existing damage and physiological stress, amongst other factors. In KNP elephant density has increased over time, as has the frequency and severity of the imparted damage. Results indicate that a higher proportion of the trees that died over the study period fell into the severe and very severe damage categories. Small baobabs seem more susceptible to elephant damage, and so suffered higher levels of mortality. Trees that had previously sustained moderate or only slight damage were most likely to survive, and generally displayed unchanged levels of damage over 18 years. Elephants have been shown to have significant impacts on several savanna tree species (Kerley *et al.* 2008). Within KNP, the annual mortality rate of marula trees (*Sclerocarya birrea* subsp. *caffra*) has been recorded as high as 4.6% (Helm & Witkowski 2012) with up to 25% of mature individuals dying between 2001 and 2010. Elephant damage was regarded as one of the major causes of marula mortality and, together with fire, explained the high levels of mortality in the park (Helm *et al.* 2009). Recruitment of marula seedlings was very limited (Helm *et al.* 2009).

Not all mortality in baobabs can be attributed to elephant damage. Other drivers also play significant roles in shaping the population structure of baobabs in KNP (Chapter 2), with interactions between temperature, fire and elephants all contributing towards total and size-dependent baobab mortality. Whyte (2001b) had previously suggested that damage could negatively affect the KNP baobab population by increasing their vulnerability to droughts. Whilst the period 1995/6-2001 had above average rainfall (653mm in Punda Maria and 893mm in Pafuri), the period leading up to 2013 experienced below average rainfall (455mm in Punda Maria and 348mm in Pafuri). It is likely that a combination of drought stress and elephant damage resulted in the increased annualised mortality after 2001. Smaller trees and individuals with extensive bark damage are likely to be less resilient to periods of drought. In addition several drought-related factors could modify elephant behaviour to the detriment of baobabs. Elephants are likely to be concentrated around permanent water sources during droughts (Harris *et al.*

2008), impacting heavily on baobabs in these areas. Alternatively, away from easily accessible water elephants might actively seek out baobabs for the water stored in their stem tissue. In addition, reduced vegetation cover during periods of drought is likely to expose baobabs of all sizes, making them more visible to elephants and so less likely to escape utilization.

Kelly (2000) noted that baobabs in KNP appear to have grown in cohorts of similar-sized trees, and proposed that these cohorts established during periods of decreased herbivore pressure. It is possible that a cohort of similarly-aged trees experiencing similar combined stresses could die within several years of each other, causing a spike in mortality within a single size-class such as was seen in the increased mortality of large (>4m stem diameter) baobabs leading up to 2013.

In conclusion elephant damage has increased for all measures recorded. The level of damage correlated most strongly with the population density of bull elephants. Baobabs <1m in stem-diameter generally either escaped browsing, or suffered very severe utilization by elephants. Annualised mortality increased three-fold between the periods 1995/6-2001 (0.25%) and 2001-2013 (0.79%), with trees that had previously sustained severe and very severe damage contributing a significantly higher proportion to mortality than trees which sustained lesser or no damage. Smaller trees had a higher proportion of mortality than larger trees, with 61% of the observed mortality afflicting trees <1m in diameter. However, high proportions of mortality in the >4m stem diameter size classes was not explained by elephant damage, and is likely to be the result of cumulative impacts of a multitude of divers.

Monitoring of baobabs in KNP should continue at intervals relevant to increases in elephant density and changes in climate. Predicted warming and increases in extreme rainfall events and rainfall variability in southern Africa (Engelbrecht *et al* 2013; DEA 2013) are likely to further impact on baobabs. With the baobab’s capacity to outlive unfavourable conditions reduced by fire and elephant impacts, future droughts and extreme weather could continue to increase the mortality of established baobabs in KNP. With very low recruitment rates, long-lived baobabs are reliant on the survival of these established trees in order for the population to persist. Currently this ~18 year dataset represents a mere ~1% of a baobab’s possible lifespan (Patrut *et al.* 2013). Whilst already displaying important trends, continued monitoring will add significantly to our understanding of this species. This project has benefited from the exemplary data records and data-sharing philosophies of SANParks and its staff, as advocated by Scholes (2015). The additional 2013 data will be housed with SANParks and other organisations involved as it is important that the monitoring of the KNP baobabs should continue under changing conditions.

3.7 Acknowledgements

We thank Dr Ian Whyte, who initiated the measurement of baobabs in KNP in1995, and Michele Hofmeyr, who repeated and added to the sampling in 2001. Both gave their data freely, without which this project would not have been possible. We thank South African National Parks scientific services Sharon Thompson, Sandra MacFadyen, Jacques Venter, and Chenay Simms, section rangers Sandra Visagie and Thomas Mbokota, field rangers Corporal Solomon, Carlos, Amos, Vusi, Jackson, Simon, Rirhandzu, and Pieter and game guards Isaac, Thomas, and Jacob for providing logistical support, geographical data, access, and protection in KNP. EcoTraining is thanked for accommodation in Pafuri. We further thank Janet Taylor, Dr Ricky Taylor and Simon Smit for assistance in the field, Melissa Whitecross for advice with R-code, and Dr Izak Smit, Dr Ricky Taylor, Dr Tony Swemmer, Dr Daryl Codron and Tracey Johnson for advice and discussions relating to the study. This project was supported by the Botanical Education Trust, the University of the Witwatersrand, Johannesburg, the South African Environmental Observation Network (SAEON), and the South African National Research Foundation (NRF) Innovation fund (SFH12082710827). Opinions expressed and conclusions arrived at, are those of the authors and are not necessarily to be attributed to the NRF or SAEON.

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3.9 Appendices

Appendix 1. The percentage of baobabs in each damage class (none, slight, moderate, severe or very severe) across (a) stem diameters, (b) proportions of rock cover within 5m of the stem, (c) distance to the nearest perennial river and (d) gradient / slope inclination for each sampling effort: 1995, 2001 and 2013.

a)

	1995						2001						2013					
Diameter	n	None	Slight	Moderate	Severe	Very Severe	n	None	Slight	Moderate	Severe	Very Severe	n	None	Slight	Moderate	Severe	Very Severe
0.0 - 1.0m	126	71.4	14.3	6.3	7.9	0.8	259	39.0	26.3	14.7	20.1	5.0	164	33.5	30.5	15.2	20.7	2.4
1.1 - 2.0m	87	39.1	39.1	14.9	6.9	0.0	201	21.4	43.8	26.4	8.5	0.5	168	20.8	44.0	26.2	8.9	0.6
2.1 - 3.0m	93	19.4	40.9	35.5	4.3	0.0	219	2.7	36.1	44.3	16.9	0.5	183	2.2	34.4	45.4	18.0	0.0
3.1 - 4.0m	69	14.5	29.0	49.3	7.2	0.0	124	2.4	26.6	49.2	21.8	0.0	109	2.8	21.1	52.3	23.9	0.0
>4.0m	32	18.8	34.4	40.6	6.3	0.0	55	0.0	18.2	69.1	12.7	0.0	40	0.0	12.5	70.0	17.5	0.0
Total	407	38.8	29.7	24.8	6.6	0.2	858	17.8	32.4	33.4	16.3	1.7	664	14.6	32.4	35.7	17.3	0.8

b)

	1995						2001						2013					
Rock cover	n	None	Slight	Moderate	Severe	Very Severe	n	None	Slight	Moderate	Severe	Very Severe	n	None	Slight	Moderate	Severe	Very Severe
0%	93	44.1	19.4	30.1	6.5	0.0	147	6.8	31.3	42.9	19.0	5.4	123	6.5	34.1	44.7	14.6	1.6
1-20%	188	35.6	33.5	23.9	6.9	0.0	297	12.1	32.7	36.0	19.2	1.7	272	11.8	33.5	35.7	19.1	0.7
21-40%	34	38.2	32.4	20.6	8.8	0.0	76	10.5	31.6	36.8	21.1	0.0	75	10.7	32.0	37.3	20.0	0.0
41-60%	39	35.9	28.2	28.2	7.7	0.0	92	16.3	32.6	34.8	16.3	1.1	89	15.7	31.5	36.0	16.9	1.1
>60%	46	43.5	34.8	19.6	2.2	0.0	111	34.2	28.8	23.4	13.5	0.0	105	33.3	28.6	23.8	14.3	0.0
Total	400	38.8	29.8	25.0	6.5	0.0	723	14.8	31.7	35.4	18.1	1.9	664	14.6	32.4	35.7	17.3	0.8

c)

	1995						2001						2013					
Distance from river	n	None	Slight	Moderate	Severe	Very Severe	n	None	Slight	Moderate	Severe	Very Severe	n	None	Slight	Moderate	Severe	Very Severe
≤500m	180	41.7	29.4	21.7	7.2	0.0	210	24.8	25.7	26.2	23.3	2.9	173	22.5	23.7	28.3	25.4	0.6
501-1000m	58	39.7	24.1	36.2	0.0	0.0	131	13.0	30.5	41.2	15.3	1.5	120	13.3	31.7	41.7	13.3	0.8
1001-1500m	104	42.3	32.7	16.3	8.7	1.0	125	17.6	48.8	22.4	11.2	4.0	114	19.3	50.0	20.2	10.5	2.6
1501-2000m	38	36.8	39.5	18.4	5.3	0.0	60	15.0	45.0	25.0	15.0	0.0	51	11.8	51.0	27.5	9.8	0.0
>2000m	27	7.4	18.5	63.0	11.1	0.0	332	16.0	28.9	40.7	14.5	0.6	206	6.8	25.7	49.0	18.4	0.0
Total	407	38.8	29.7	24.8	6.6	0.2	858	17.8	32.4	33.4	16.3	1.7	664	14.6	32.4	35.7	17.3	0.8

d)

	1995						2001						2013					
Slope	n	None	Slight	Moderate	Severe	Very Severe	n	None	Slight	Moderate	Severe	Very Severe	n	None	Slight	Moderate	Severe	Very Severe
0°	56	17.9	44.6	30.4	7.1	0.0	96	6.3	36.5	39.6	17.7	2.1	87	6.9	37.9	39.1	16.1	1.1
1-10°	230	35.2	30.9	27.0	7.0	0.0	427	13.8	33.0	33.0	20.1	1.4	399	13.5	32.8	33.8	19.8	0.8
11-20°	34	52.9	23.5	17.6	5.9	0.0	77	26.0	36.4	26.0	11.7	2.6	73	26.0	38.4	24.7	11.0	1.4
>20°	15	60.0	33.3	6.7	0.0	0.0	28	50.0	28.6	17.9	3.6	0.0	24	45.8	29.2	20.8	4.2	0.0
All trees	335	35.2	32.5	25.7	6.6	0.0	628	15.8	33.8	32.5	18.0	1.6	583	15.4	34.1	32.9	17.5	0.9

Appendix 2. Comparison of the distribution of damage class (none, slight, moderate, severe or very severe) across (a) stem diameters, (b) distance to the nearest perennial river, (c) proportions of rock cover within 5m of the stem and (d) gradient / slope inclination for each sampling effort: 1995, 2001 and 2013. Two-sample Kolmogorov–Smirnov tests were used to test for significant differences (P<0.05) in distribution between years and between variables. Significant differences indicated in bold.

a)

	Diameter	0-1m	1-2m	2-3m	3-4m	>4m
				1995		
	0.0 - 1.0m		**D = 0.31786, P < 0.0001**	**D = 0.51511, P < 0.0001**	**D = 0.56373, P < 0.0001**	**D = 0.52116, P < 0.0001**
	1.1 - 2.0m			D = 0.19726, P = 0.06051	**D = 0.34683, P = 0.0002**	D = 0.25036, P = 0.1065
	2.1 - 3.0m				D = 0.16737, P = 0.2171	D = 0.070901, P = 0.9998
1995	3.1 - 4.0m					D = 0.096467, P = 0.9871
				2001		
	0.0 - 1.0m	**D = 0.3387, P < 0.0001**				
	1.1 - 2.0m		**D = 0.17793, P = 0.0425**			
	2.1 - 3.0m			**D = 0.21579, P = 0.0045**		
	3.1 - 4.0m				D = 0.15154, P = 0.259	
1995	>4.0m					**D = 0.34943, P = 0.0143**
	0.0 - 1.0m		**D = 0.15709, P = 0.0065**	**D = 0.34269, P < 0.0001**	**D = 0.34596, P < 0.0001**	**D = 0.43723, P < 0.0001**
	1.1 - 2.0m			**D = 0.26215, P < 0.0001**	**D = 0.36051, P < 0.0001**	**D = 0.4667, P < 0.0001**
	2.1 - 3.0m				D = 0.098364, P = 0.4235	D = 0.20455, P = 0.0504
2001	3.1 - 4.0m					D = 0.10618, P = 0.7823
				2013		
	0.0 - 1.0m	**D = 0.64287, P < 0.0001**				
	1.1 - 2.0m		**D = 0.35545, P < 0.0001**			
	2.1 - 3.0m			**D = 0.4796, P < 0.0001**		
	3.1 - 4.0m				**D = 0.36161, P < 0.0001**	
1995	>4.0m					**D = 0.53125, P < 0.0001**
	0.0 - 1.0m	**D = 0.30417, P < 0.0001**				
	1.1 - 2.0m		**D = 0.17752, P = 0.0037**			
	2.1 - 3.0m			**D = 0.26381, P < 0.0001**		
	3.1 - 4.0m				**D = 0.21483, P = 0.0065**	
2001	>4.0m					D = 0.18182, P = 0.4022
	0.0 - 1.0m		**D = 0.26183, P < 0.0001**	**D = 0.64938, P < 0.0001**	**D = 0.69876, P < 0.0001**	**D = 0.77193, P < 0.0001**
	1.1 - 2.0m			**D = 0.38755, P < 0.0001**	**D = 0.43693, P < 0.0001**	**D = 0.5101, P < 0.0001**
	2.1 - 3.0m				D = 0.049378, P = 0.9921	D = 0.12255, P = 0.6604
2013	3.1 - 4.0m					D = 0.079221, P = 0.9883

b)

	Distance to river	<500m	500-1000m	1000-1500m	1500-2000m	>2000m
1995						
1995	≤500m		D = 0.069149, P = 0.979	D = 0.026089, P = 1	D = 0.06231, P = 0.9993	**D = 0.46414, P < 0.0001**
	501-1000m			D = 0.095238, P = 0.8713	D = 0.12442, P = 0.833	**D = 0.40203, P = 0.0046**
	1001-1500m				D = 0.047619, P = 1	**D = 0.4836, P < 0.0001**
	1501-2000m					**D = 0.52646, P = 0.0002**
2001						
1995	≤500m	**D = 0.23266, P < 0.0001**				
	501-1000m		**D = 0.30766, P = 0.0007**			
	1001-1500m			**D = 0.24982, P = 0.0014**		
	1501-2000m				**D = 0.27857, P = 0.0432**	
	>2000m					D = 0.18419, P = 0.3646
2001	≤500m		D = 0.11292, P = 0.2446	D = 0.14772, P = 0.0579	D = 0.10926, P = 0.6294	D = 0.10284, P = 0.1239
	501-1000m			**D = 0.20989, P = 0.0061**	D = 0.17143, P = 0.1759	D = 0.029919, P = 1
	1001-1500m				D = 0.038462, P = 1	D = 0.19501, P = 0.0016
	1501-2000m					D = 0.15655, P = 0.1649
2013						
1995	≤500m	**D = 0.40393, P < 0.0001**				
	501-1000m		**D = 0.41436, P < 0.0001**			
	1001-1500m			**D = 0.41229, P < 0.0001**		
	1501-2000m				**D = 0.37772, P = 0.0018**	
	>2000m					D = 0.095442, P = 0.9802
2001	≤500m	**D = 0.20318, P = 0.0003**				
	501-1000m		**D = 0.17505, P = 0.0297**			
	1001-1500m			D = 0.16247, P = 0.0518		
	1501-2000m				D = 0.099153, P = 0.9318	
	>2000m					**D = 0.12782, P = 0.0221**
2013	≤500m		D = 0.14085, P = 0.0681	D = 0.1259, P = 0.1255	D = 0.13106, P = 0.4055	D = 0.039665, P = 0.9947
	501-1000m			**D = 0.26675, P < 0.0001**	**D = 0.2719, P = 0.0042**	D = 0.10118, P = 0.3261
	1001-1500m				D = 0.044091, P = 1	**D = 0.16557, P = 0.0139**
	1501-2000m					D = 0.17072, P = 0.1282

c)

	Rock cover	0%	1-20%	21-40%	41-60%	>60%
				1995		
1995	0%		D = 0.084477, P = 0.7663	D = 0.071474, P = 0.9996	D = 0.081886, P = 0.9928	D = 0.15283, P = 0.4594
	1-20%			D = 0.02597, P = 1	D = 0.050464, P = 1	D = 0.095745, P = 0.8809
	21-40%				D = 0.064857, P = 1	D = 0.081352, P = 0.9995
	41-60%					D = 0.14621, P = 0.7523
				2001		
1995	0%	**D = 0.37676, P < 0.0001**				
	1-20%		**D = 0.25255, P < 0.0001**			
	21-40%			**D = 0.28483, P = 0.0442**		
	41-60%				D = 0.19768, P = 0.2332	
	>60%					D = 0.1566, P = 0.3929
2001	0%		D = 0.07997, P = 0.5255	D = 0.062078, P = 0.9893	D = 0.1249, P = 0.3234	**D = 0.27824, P < 0.0001**
	1-20%			D = 0.017891, P = 1	D = 0.044927, P = 0.9988	**D = 0.22353, P = 0.0006**
	21-40%				D = 0.062818, P = 0.9965	**D = 0.23708, P = 0.0126**
	41-60%					D = 0.18105, P = 0.0725
				2013		
1995	0%	**D = 0.43419, P < 0.0001**				
	1-20%		**D = 0.3402, P < 0.0001**			
	21-40%			**D = 0.38235, P = 0.0011**		
	41-60%				**D = 0.34917, P = 0.0021**	
	>60%					**D = 0.33142, P = 0.0011**
2001	0%	D = 0.13077, P = 0.1462				
	1-20%		**D = 0.13996, P = 0.005**			
	21-40%			D = 0.10526, P = 0.713		
	41-60%				D = 0.15149, P = 0.2142	
	>60%					**D = 0.22696, P = 0.0042**
2013	0%		D = 0.032039, P = 0.9999	D = 0.014286, P = 1	D = 0.047059, P = 0.9993	**D = 0.22256, P = 0.002**
	1-20%			D = 0.046325, P = 0.996	D = 0.079098, P = 0.7234	**D = 0.20353, P = 0.001**
	21-40%				D = 0.032773, P = 1	**D = 0.2359, P = 0.0031**
	41-60%					**D = 0.20649, P = 0.0153**

d)

	Slope	0%	1-10%	11-20%	>20%
			1995		
1995	0°		D = 0.1736, P = 0.1324	**D = 0.35084, P = 0.0109**	**D = 0.44643, P = 0.014**
	1-10°			D = 0.17724, P = 0.3099	D = 0.27663, P = 0.2024
	11-20°				D = 0.17279, P = 0.9014
			2001		
1995	0°	D = 0.20663, P = 0.0954			
	1-10°		**D = 0.21654, P < 0.0001**		
	11-20°			D = 0.27625, P = 0.0531	
	>20°				D = 0.15179, P = 0.9731
2001	0°		D = 0.074408, P = 0.7677	D = 0.19194, P = 0.0797	**D = 0.43878, P = 0.0005**
	1-10°			D = 0.14782, P = 0.1076	**D = 0.36437, P = 0.0019**
	11-20°				D = 0.24684, P = 0.161
			2013		
1995	0°	**D = 0.35397, P = 0.0002**			
	1-10°		**D = 0.33699, P < 0.0001**		
	11-20°			**D = 0.49715, P < 0.0001**	
	>20°				D = 0.33088, P = 0.1845
2001	0°	D = 0.14734, P = 0.2168			
	1-10°		**D = 0.12703, P = 0.0015**		
	11-20°			**D = 0.22091, P = 0.0309**	
	>20°				D = 0.20588, P = 0.5332
2013	0°		D = 0.11509, P = 0.2002	**D = 0.32037, P < 0.0001**	**D = 0.46427, P < 0.0001**
	1-10°			**D = 0.20528, P = 0.0029**	**D = 0.34918, P = 0.0009**
	11-20°				D = 0.26186, P = 0.0658

Appendix 3. The percentage of baobabs in each fate class (recovered, unchanged, deteriorated or died) across (a) level of initial damage, (b) stem diameters, (c) distance to the nearest perennial river, (d) gradient / slope inclination and (e) proportions of rock cover within 5m of the stem for each for the periods 1995/6 to 2001, 2001 to 2013 and 1995/6 to 2013.

a)

	1995-2001					2001-2013					1995-2013				
Initial damage	n	Recovered	Unchanged	Deteriorated	Died	n	Recovered	Unchanged	Deteriorated	Died	n	Recovered	Unchanged	Deteriorated	Died
Severe & very severe	28	35.7	50.0	3.6	10.7	146	66.4	14.4	2.1	17.1	28	50.0	14.3	3.6	32.1
Moderate	100	15.0	53.0	31.0	1.0	257	12.8	70.4	8.9	7.8	100	7.0	75.0	14.0	4.0
Slight	116	6.9	50.0	41.4	1.7	230	0.4	43.5	49.6	6.5	119	0.0	26.1	62.2	11.8
None	153	-	34.6	64.7	0.7	107	-	10.3	80.4	9.3	155	-	0.6	82.6	16.8
Total	397	8.3	45.1	45.1	1.5	740	17.7	42.3	30.5	9.5	402	5.2	27.6	54.0	13.2

b)

	1995-2001					2001-2013					1995-2013				
Diameter	n	Recovered	Unchanged	Deteriorated	Died	n	Recovered	Unchanged	Deteriorated	Died	n	Recovered	Unchanged	Deteriorated	Died
0.0 - 1.0m	125	7.2	32.0	57.6	3.2	216	23.6	27.3	28.2	20.8	124	6.5	12.9	54.8	25.8
1.1 - 2.0m	86	12.8	54.7	30.2	2.3	166	15.7	43.4	39.2	1.8	87	4.6	31.0	59.8	4.6
2.1 - 3.0m	89	3.4	49.4	47.2	0.0	190	15.8	50.0	30.5	3.7	90	4.4	32.2	56.7	6.7
3.1 - 4.0m	67	11.9	44.8	43.3	0.0	116	16.4	55.2	23.3	5.2	69	7.2	40.6	46.4	5.8
>4.0m	30	10.0	56.7	33.3	0.0	52	9.6	44.2	28.8	17.3	32	0.0	34.4	43.8	21.9
Total	397	8.3	45.1	45.1	1.5	740	17.7	42.3	30.5	9.5	402	5.2	27.6	54.0	13.2

c)

	1995-2001					2001-2013					1995-2013				
Distance to river	n	Recovered	Unchanged	Deteriorated	Died	n	Recovered	Unchanged	Deteriorated	Died	n	Recovered	Unchanged	Deteriorated	Died
≤500m	177	8.5	39.5	50.8	1.1	205	21.5	30.2	33.2	15.1	178	5.6	25.8	52.8	15.7
501-1000m	54	3.7	37.0	59.3	0.0	132	10.6	47.7	33.3	8.3	58	0.0	27.6	62.1	10.3
1001-1500m	103	6.8	49.5	40.8	2.9	130	14.6	33.1	42.3	10.0	104	4.8	20.2	60.6	14.4
1501-2000m	36	11.1	50.0	36.1	2.8	57	10.5	47.4	31.6	10.5	35	5.7	31.4	54.3	8.6
>2000m	27	18.5	74.1	7.4	0.0	216	22.2	54.6	19.0	4.2	27	14.8	63.0	18.5	3.7
Total	397	8.3	45.1	45.1	1.5	740	17.7	42.3	30.5	9.5	402	5.2	27.6	54.0	13.2

d)

	1995-2001					2001-2013					1995-2013				
Slope	n	Recovered	Unchanged	Deteriorated	Died	n	Recovered	Unchanged	Deteriorated	Died	n	Recovered	Unchanged	Deteriorated	Died
0°	55	12.7	52.7	34.5	0.0	98	18.4	33.7	37.8	10.2	56	10.7	26.8	50.0	12.5
1-10°	229	8.7	44.1	46.7	0.4	435	19.5	42.5	30.6	7.4	230	5.7	30.4	52.6	11.3
11-20°	34	5.9	52.9	38.2	2.9	79	12.7	49.4	31.6	6.3	34	2.9	23.5	58.8	14.7
>20°	15	6.7	73.3	20.0	0.0	28	10.7	39.3	35.7	14.3	15	0.0	20.0	73.3	6.7
Total	333	9.0	47.7	42.6	0.6	640	18.1	41.9	32.0	8.0	335	6.0	28.7	53.7	11.6

e)

	1995-2001					2001-2013					1995-2013				
All rocks	n	Recovered	Unchanged	Deteriorated	Died	n	Recovered	Unchanged	Deteriorated	Died	n	Recovered	Unchanged	Deteriorated	Died
0%	93	5.4	37.6	55.9	1.1	156	14.1	42.9	23.1	19.9	93	4.3	32.3	41.9	21.5
1-20%	185	8.6	47.0	43.2	1.1	303	20.1	39.6	31.0	9.2	188	6.4	27.1	53.2	13.3
21-40%	31	9.7	41.9	48.4	0.0	76	18.4	48.7	31.6	1.3	34	5.9	20.6	70.6	2.9
41-60%	39	12.8	53.8	33.3	0.0	93	16.1	44.1	36.6	3.2	39	2.6	28.2	61.5	7.7
>60%	46	8.7	50.0	41.3	0.0	111	17.1	43.2	34.2	5.4	46	4.3	26.1	65.2	4.3
Total	394	8.4	45.4	45.4	0.8	739	17.7	42.4	30.6	9.3	400	5.3	27.8	54.3	12.8

Appendix 4. Comparison of the distribution of baobab fates (recovered, remained unchanged, deteriorated or died) across (a) level of initial damage, (b) stem diameters, (c) distance to the nearest perennial river, (d) proportions of rock cover within 5m of the stem and (e) gradient / slope inclination for each of the periods 1995/6 to 2001, 2001 to 2013 and 1995/6 to 2013. Two-sample Kolmogorov–Smirnov tests were used to test for significant differences (P<0.05) in distribution between periods and between variables. Significant differences indicated in bold.

a)

	Initial damage	Severe	Moderate	Slight	None
				1995-2013	
1995-2013	Severe		**D = 0.43, P = 0.0006**	**D = 0.5, P < 0.0001**	**D = 0.63641, P < 0.0001**
	Moderate			**D = 0.5595, P < 0.0001**	**D = 0.81355, P < 0.0001**
	Slight				**D = 0.25405, P = 0.0003**
				1995-2001	
1995-2013	Severe	D = 0.21429, P = 0.5412			
	Moderate		D = 0.13, P = 0.3667		
	Slight			**D = 0.30846, P < 0.0001**	
	None				**D = 0.33995, P < 0.0001**
1995-2001	Severe		D = 0.20714, P = 0.3049	**D = 0.28818, P = 0.0472**	**D = 0.51074, P < 0.0001**
	Moderate			D = 0.12103, P = 0.411	**D = 0.34359, P < 0.0001**
	Slight				**D = 0.22256, P = 0.0029**
				2001-2013	
1995-2013	Severe	D = 0.16536, P = 0.5417			
	Moderate		D = 0.058405, P = 0.9667		
	Slight			**D = 0.17863, P = 0.0134**	
	None				D = 0.096352, P = 0.5993
1995-2001	Severe	**D = 0.30724, P = 0.0237**			
	Moderate		D = 0.14268, P = 0.1066		
	Slight			D = 0.12984, P = 0.1485	
	None				**D = 0.2436, P = 0.0011**
2001-2013	Severe		**D = 0.53598, P < 0.0001**	**D = 0.66004, P < 0.0001**	**D = 0.70542, P < 0.0001**
	Moderate			**D = 0.39355, P < 0.0001**	**D = 0.72988, P < 0.0001**
	Slight				**D = 0.33633, P < 0.0001**

b)

	Diameter	0-1m	1-2m	2-3m	3-4m	>4m
		1995-2013				
1995-2013	0.0 - 1.0m		**D = 0.21209, P = 0.0201**	**D = 0.1914, P = 0.0438**	**D = 0.28471, P = 0.0015**	D = 0.1502, P = 0.6145
	1.1 - 2.0m			D = 0.02069, P = 1	D = 0.12194, P = 0.6164	D = 0.17277, P = 0.4873
	2.1 - 3.0m				D = 0.11159, P = 0.7155	D = 0.15208, P = 0.6458
	3.1 - 4.0m					D = 0.16078, P = 0.6242
		1995-2001				
1995-2013	0.0 - 1.0m	**D = 0.22606, P = 0.0035**				
	1.1 - 2.0m		**D = 0.3181, P = 0.0003**			
	2.1 - 3.0m			D = 0.16142, P = 0.194		
	3.1 - 4.0m				D = 0.088903, P = 0.951	
	>4.0m					D = 0.32292,P = 0.0792
1995-2001	0.0 - 1.0m		**D = 0.28242, P = 0.0006**	D = 0.13609, P = 0.2907	D = 0.17516, P = 0.1375	D = 0.27467, P = 0.052
	1.1 - 2.0m			D = 0.14633, P = 0.3062	D = 0.10725, P = 0.7792	D = 0.023256, P = 1
	2.1 - 3.0m				D = 0.085695, P = 0.9416	D = 0.13858, P = 0.782
	3.1 - 4.0m					D = 0.099502, P = 0.9865
		2001-2013				
1995-2013	0.0 - 1.0m	**D = 0.31571, P < 0.0001**				
	1.1 - 2.0m		**D = 0.23404, P = 0.0038**			
	2.1 - 3.0m			**D = 0.29123, P < 0.0001**		
	3.1 - 4.0m				**D = 0.23726, P = 0.0153**	
	>4.0m					D = 0.19471, P = 0.4404
1995-2001	0.0 - 1.0m	**D = 0.17633, P = 0.0145**				
	1.1 - 2.0m		D = 0.084057, P = 0.8183			
	2.1 - 3.0m			D = 0.1298, P = 0.2589		
	3.1 - 4.0m				D = 0.14835, P = 0.3073	
	>4.0m					D = 0.17308, P = 0.6189
2001-2013	0.0 - 1.0m		**D = 0.19026, P = 0.0022**	**D = 0.17149, P = 0.0052**	**D = 0.20626, P = 0.0033**	D = 0.13996, P = 0.3844
	1.1 - 2.0m			D = 0.067533, P = 0.8139	D = 0.12516, P = 0.2351	D = 0.155, P = 0.2974
	2.1 - 3.0m				D = 0.057623, P = 0.9705	D = 0.13623, P = 0.4348
	3.1 - 4.0m					D = 0.17706, P = 0.2103

c)

	Distance to river	<500m	500-1000m	1000-1500m	1500-2000m	>2000m
				1995-2013		
1995-2013	≤500m		D = 0.05618, P = 0.9991	D = 0.064607, P = 0.9469	D = 0.071589, P = 0.9983	**D = 0.46317, P < 0.0001**
	501-1000m			D = 0.048077, P = 1	D = 0.095567, P = 0.9885	**D = 0.50192, P = 0.0002**
	1001-1500m				D = 0.12143, P = 0.8348	**D = 0.52778, P < 0.0001**
	1501-2000m					D = 0.40635, P = 0.013
				1995-2001		
1995-2013	≤500m	**D = 0.16562, P = 0.0154**				
	501-1000m		D = 0.13155, P = 0.7185			
	1001-1500m			**D = 0.31311, P < 0.0001**		
	1501-2000m				D = 0.23968, P = 0.2597	
	>2000m					D = 0.14815, P = 0.9284
1995-2001	≤500m		D = 0.072819, P = 0.9807	D = 0.082881, P = 0.7624	D = 0.13089, P = 0.6847	**D = 0.4457, P = 0.0002**
	501-1000m			D = 0.1557, P = 0.3569	D = 0.2037, P = 0.3315	**D = 0.51852, P = 0.0001**
	1001-1500m				D = 0.048004, P = 1	**D = 0.36282, P = 0.0072**
	1501-2000m					D = 0.31481, P = 0.0939
				2001-2013		
1995-2013	≤500m	**D = 0.20247, P = 0.0008**				
	501-1000m		**D = 0.30747, P = 0.001**			
	1001-1500m			**D = 0.22692, P = 0.0052**		
	1501-2000m				D = 0.20752, P = 0.3078	
	>2000m					D = 0.074074, P = 0.9994
1995-2001	≤500m	**D = 0.13992, P = 0.0485**				
	501-1000m		D = 0.17593, P = 0.1864			
	1001-1500m			D = 0.086184, P = 0.7868		
	1501-2000m				D = 0.077485, P = 0.9994	
	>2000m					D = 0.15741, P = 0.5917
2001-2013	≤500m		D = 0.10857, P = 0.3002	D = 0.06848, P = 0.8497	D = 0.10937, P = 0.6602	**D = 0.25145, P < 0.0001**
	501-1000m			D = 0.10641, P = 0.4485	D = 0.02193, P = 1	**D = 0.18519, P = 0.0073**
	1001-1500m				D = 0.10202, P = 0.8039	**D = 0.2916, P < 0.0001**
	1501-2000m					D = 0.18957, P = 0.0782

d)

	Rock cover	0%	1-20%	21-40%	41-60%	>60%
		1995-2013				
	0%		D = 0.082075, P = 0.796	D = 0.18564, P = 0.3575	D = 0.13813, P = 0.6709	D = 0.17158, P = 0.3252
	1-20%			D = 0.10357, P = 0.9169	D = 0.056056, P = 1	D = 0.0895, P = 0.9286
	21-40%				D = 0.047511, P = 1	D = 0.039642, P = 1
1995-2013	41-60%					D = 0.033445, P = 1
		1995-2001				
	0%	**D = 0.2043, P = 0.0412**				
	1-20%		**D = 0.22165, P = 0.0002**			
	21-40%			D = 0.25142, P = 0.2569		
	41-60%				**D = 0.35897, P = 0.0131**	
1995-2013	>60%					D = 0.28261, P = 0.0508
	0%		D = 0.12665, P = 0.274	D = 0.086022, P = 0.9954	D = 0.23656, P = 0.0924	D = 0.15685, P = 0.4352
	1-20%			D = 0.040628, P = 1	D = 0.10991, P = 0.8313	D = 0.0302, P = 1
	21-40%				D = 0.15054, P = 0.8287	D = 0.070827, P = 1
1995-2001	41-60%					D = 0.07971, P = 0.9993
		2001-2013				
	0%	**D = 0.20492, P = 0.015**				
	1-20%		**D = 0.26225, P < 0.0001**			
	21-40%			**D = 0.40635, P = 0.0009**		
	41-60%				**D = 0.29446, P = 0.0171**	
1995-2013	>60%					**D = 0.29926, P = 0.0059**
	0%	**D = 0.18797, P = 0.0326**				
	1-20%		D = 0.11483, P = 0.0967			
	21-40%			D = 0.15492, P = 0.666		
	41-60%				D = 0.064516, P = 0.9998	
1995-2001	>60%					D = 0.084215, P = 0.9752
	0%		D = 0.10631, P = 0.1949	D = 0.18556, P = 0.0592	D = 0.16646, P = 0.0792	D = 0.14466, P = 0.1324
	1-20%			D = 0.079251, P = 0.8399	D = 0.060151, P = 0.959	D = 0.038355, P = 0.9998
	21-40%				D = 0.068902, P = 0.9887	D = 0.067449, P = 0.9864
2001-2013	41-60%					D = 0.021796, P = 1

e)

	Slope	0%	1-10%	11-20%	>20%
				1995-2013	
1995-2013	0°		D = 0.050621, P = 0.9998	D = 0.11029, P = 0.9591	D = 0.175, P = 0.8617
	1-10°			D = 0.096164, P = 0.947	D = 0.16087, P = 0.8594
	11-20°				D = 0.080392, P = 1
				1995-2001	
1995-2013	0°	**D = 0.27955, P = 0.0262**			
	1-10°		**D = 0.16751, P = 0.0032**		
	11-20°			D = 0.32353, P = 0.0569	
	>20°				**D = 0.6, P = 0.009**
1995-2001	0°		D = 0.12616, P = 0.4804	D = 0.068449, P = 1	D = 0.14545, P = 0.9644
	1-10°			D = 0.059851, P = 0.9999	D = 0.27162, P = 0.2501
	11-20°				D = 0.21176, P = 0.739
				2001-2013	
1995-2013	0°	D = 0.14541, P = 0.4383			
	1-10°		**D = 0.25982, P < 0.0001**		
	11-20°			**D = 0.35555, P = 0.0049**	
	>20°				D = 0.3, P = 0.343
1995-2001	0°	D = 0.13414, P = 0.5504			
	1-10°		D = 0.10807, P = 0.0602		
	11-20°			D = 0.067759, P = 0.9999	
	>20°				D = 0.3, P = 0.343
2001-2013	0°		D = 0.10028, P = 0.3971	D = 0.099845, P = 0.7758	D = 0.076531, P = 0.9996
	1-10°			D = 0.06882, P = 0.9095	D = 0.12069, P = 0.8381
	11-20°				D = 0.12025, P = 0.926

CHAPTER FOUR

Synthesis

Recruitment of seedlings/saplings since the previous monitoring (from 2001-2013) was not observed for the baobabs of Kruger National Park despite intense searches within 50m of sampled trees, accumulating in a total area of 4 km^2. This is not unusual as several studies throughout Africa have shown very low recruitment rates for baobabs (Caughley 1976; Barnes 1980; Wilson 1988; Assogbadjo *et al.* 2005; Edkins *et al.* 2007). However, Venter & Witkowski (2010) suggest that the lack of seedlings alone is of little concern as the long lifespan and low adult mortality rate of baobabs negate the necessity for high levels of recruitment. Saplings appeared to be stunted by unfavourable conditions or heavy disturbance, however growth was observed in some of the >0.15m but <1m stem-diameter baobabs. Very little growth, however, was observed in larger baobabs >1m stem-diameter. This trend of visible growth in smaller baobabs and little or no growth in larger trees is consistent with other studies on growth rates of baobabs in Africa (Condit *et al*. 1998; Wickens and Lowe 2008).

Annualised mortality increased three-fold from 0.25% to 0.79% between the periods 1995/6-2001 and 2001-2013. As with other studies (Barnes 1980; Swanepoel 1993) mortality was predominantly in the smaller size classes. These <1m stem-diameter trees are considered less resilient than larger trees and succumb to the likely combined threat from fire, browsing and drought. Of more concern is the high proportion (>21%) of the large and very large trees – collectively those exceeding 4m stem-diameter, which died between 1995/6 and 2013. The cause of death for these large trees is unknown and it is suggested that the combined effects of multiple threats might have weakened and eventually killed these baobabs.

Mortality, in the absence of seedling/sapling recruitment and only limited recruitment between size classes, did not significantly impact on baobab population structure between 1995/6, 2001 and 2013. This might change should more very large (>4m stem-diameter) trees die, as these size classes make up less than 2% of the population. Recruitment into these size classes is likely to take many decades should conditions allow for growth. The increase in the relative proportion of <0.5m stem-diameter in 2013 is due to the intensive searches conducted within 50m of each previously sampled tree, and is not an indication of recruitment over the past 12 years.

The general trend in population size-structure is that of an inverse J-shape, with a high proportion of smaller baobabs and lower proportions of larger baobabs. An inverse J-shaped population distribution is generally indicative of a healthy recruiting population over longer time periods than the total 18 years of this overall study.

4.1 Baobab growth and survival

Baobabs at different stages in their life history have differing requirements for growth and face different threats. These different life stages, following Wickens and Louw (2008), together with their requirements, are outlined below.

Seeds and seedlings

The small, hard, kidney-shaped baobab seeds are found together with the powdery fruit within the pod. Seeds rely on humans, baboons and elephants for their dispersal (Wickens & Lowe 2008). Scarification by chewing or partial digestion by stomach acid is thought to assist germination (Esenowo 1991). However, undamaged seeds have been shown to persist for up to 15 years under laboratory conditions with a 95% germination success (Wickens & Lowe 2008), and at least 2 years in the soil under fluctuating conditions with a 97% germination success (Venter & Witkowski 2013a). The attainment of specific moisture and temperature requirements are likely to stimulate germination and seedling emergence. Baobabs in their first year after germination grow by using the reserves from their cotyledons, producing a soft green stem with alternate, simple leaves. Seedling survival is very low and appears to be micro-site limited in the communal lands of Venda rather than seed limited (Venter & Witkowski 2010), with seedlings especially sensitive to desiccation during this first growing season. It is likely to be the same in conserved area in the region including in KNP where no seedlings were recorded despite intense searches over an area of 4 km^2 during the course of this study.

Saplings

Saplings, defined as older than 1 year but under 2m tall and less than 0.15m in basal stem-diameter, start to develop the typical grey, sturdy stem of more mature baobabs. Typically, saplings are derived through survival from the seedling stage although they can result from basal pollarding of a larger tree which, whilst having greater stores available in rootstock, faces similar threats. Saplings where found in very low numbers during this study however they showed little or no growth. Several of the saplings observed in KNP had been pollarded at or close to the base and had resprouted multiple stems from the base. We suggest that unfavourable conditions combined with herbivory maintained them in a bonsai-like state.

Large trees

Beyond the sapling life stage, baobab growth stages are described on shape as sizes can vary dramatically due to differences in site and genetic variation (Breitenbach 1985 cited in Wickens & Lowe 2008). Breitenbach (1985) described baobabs as having 3 main stages of growth after sapling: a cone-shaped phase, a bottle-shaped phase and the ultimate phase with a grotesque stem and flat spreading branches. Although Wickens & Lowe (2008) agreed with these growth stages, they suggested that two ultimate phases occur; one for trees growing from the more upright bottle-shape and another for stouter, multi-stemmed trees (Figure 1).

Growth is fastest during the smaller stages of a baobab (Dhillion & Gustad 2004). Our study showed that in KNP only baobabs < 1m in stem-diameter showed significant growth over the study period. Small trees grow rapidly upwards to attain height whilst remaining spindly. The bases then start to swell to form the cone shape and branches generally reach upwards. Venter & Witkowski (2011) defined baobabs with stem-diameters <1m as sub-adults and found that whilst some flowering and fruiting does occur, it is insignificant compared to that of larger trees. Damage can result in stumpy/deformed shapes not conforming to the typical cone-shape.

Growing beyond the cone-shape, stems fill out and become cylindrical or bottle-shaped. Buttressing forms below the main branches to support horizontal growth. Flowering and fruiting generally becomes more prolific in trees >1m in stem diameter (Venter & Witkowski 2011).

The ultimate growth phase for both single- and multi-stemmed trees loses the cylindrical appearance of the stem as buttresses reach the ground. Branches begin to droop and if multi-stemmed, the stems begin to collapse apart (Patrut *et al.* 2015). Within KNP this baobabs generally has stem diameters >4m in diameter and make up less than 2% of the population.

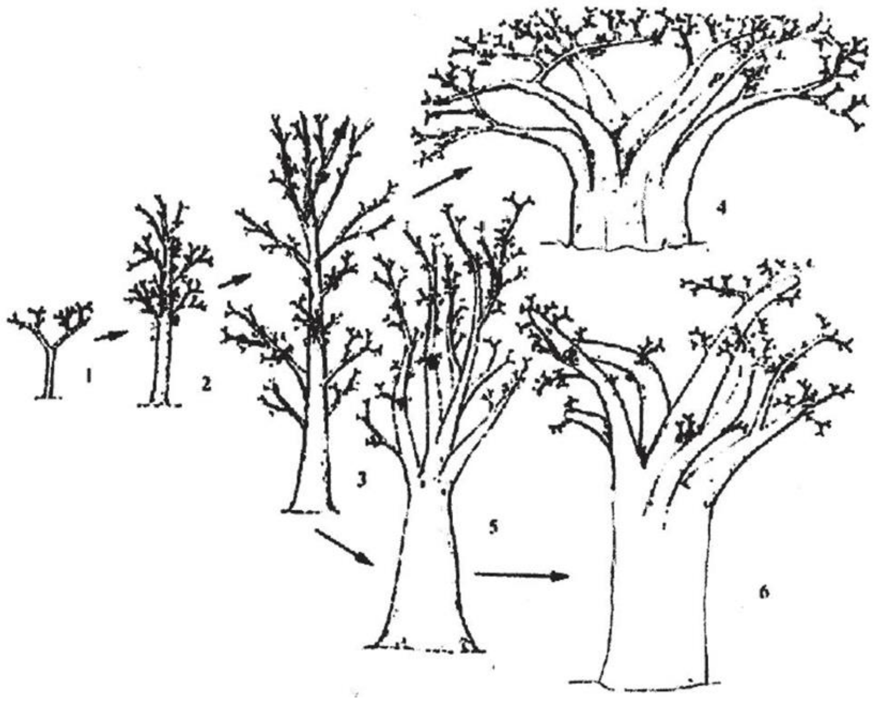

Figure 22. The growth of baobabs trees through the different stages from sapling (1) growing into the cone shape with upward reaching branches (2 & 3), the stouter, multi-stemmed ultimate stage (4) and the upright bottle-shape (5) with the alternative ultimate upright stage with branches flat and spreading (6). Growth stages not to scale. (From Wickens & Lowe 2008)

4.2 Threats

Elephant damage

The baobab is a tree favoured by elephants and this utilization is often destructive (Robertson-Bullock 1960; Caughley 1976; Barnes 1980; Weyer-Haeuser 1985; Swanepoel 1993; Edkins *et al.* 2005). Baobab demographic studies within areas highly impacted by elephants often show bell-shaped distributions suggesting that elephants have the greatest impact on small baobabs (Barnes 1980; Weyer-Haeuser 1985; Swanepoel 1993). Barns (1980) suggested that bull elephants were most likely responsible for the destruction of mature baobabs. This study shows that within KNP increases in frequency and severity of elephant damage correlated most strongly with the increases of bull elephant density. Baobabs that suffered the highest severity of elephant damage were those in the smallest, <1m stem-diameter, size class, growing within 1500m of rivers, on flat topography and which were unprotected by rocks (Figure 2). Not surprisingly, these small individuals also suffered the highest level of mortality as a result of suffering severe and very severe damage.

Fire

Wickens & Lowe (2008) suggest that fire could be one of the reasons for the observed absence of natural regeneration of baobabs in Africa. The results of this study confirmed that smaller baobabs are sensitive to fire and that population structures are shaped, in part, by fire. The maximum fire return interval is the longest period of time that a baobab has to grow in the absence of fire.
Within KNP differences were found between the SCD of baobabs in areas where the maximum fire return intervals less than 30 years compared to areas with longer maximum fire return intervals. Baobabs growing in those areas with less frequent fire had an inverse J-shaped SCD. Baobabs most likely to escape the effects of fire are those growing where low annual rainfall and increased herbivory close to major rivers result in low and patchy fuel-loads, and where high-order streams and undulating topography act as natural fire breaks (Figure 2; Smit *et al*. 2012).

Desiccation and drought

Seedling survival is micro-site limited as opposed to seed limited and seedlings need to remain moist throughout their first growing season in order to survive (Venter & Witkowski 2013a). Increased mortality rates of all sizes of trees have been associated with drought stress and it is thought that drought conditions increase the vulnerability of baobabs to other threats (Whyte 2001; Hofmeyr *et al.* 2004). Baobab girths shrink and swell depending on water availability (Wickens & Lowe 2008); the shrinking of stems is likely to reduce the rigidity and strength of buttresses and branches possibly resulting in the loss of branches and leading towards the collapse of multi-stemmed trees. Mean annual rainfall had no significant effect on the population structure of baobabs in KNP; however the effect of drought are obscured by the long-term averages.400-800mm of annual rainfall is considered optimal for establishment and growth of baobabs (Wickens & Lowe 2008; Cuni Sanchez *et al.* 2010).

Temperature

Cuni Sanchez *et al.* (2010; 2011) modelled the distribution of baobabs in Africa. Temperature seasonality and the mean temperature for the coldest 4 months were considered important predictors of distribution. Cuni Sanchez (2010) suggested that baobabs require mean temperature of the warmest 4 months to be within the 21-31°C range whilst the mean temperature of the coldest 4 months should be within the 14-22 ° C range. In KNP, baobabs growing within the area defined by the 23°C mean annual temperature isotherm showed a healthy inverse J-shaped distribution as opposed to the uni-modal bell-shaped curves of baobabs growing in cooler regions.

4.3 Additional threats

The following threats to baobabs were not incorporated within the key focus of this study however personal observations and discussions from other studies are summarized below.

Green fruit predation

Baboons are known to consume baobab fruit (Pochron 2001) and Venter and Witkowski (2011) suggest that baboon consumption of or damage to of immature fruit is a major contributor to seed destruction and is thus a threat to recruitment of baobabs in Venda. This is not always the case and Wickens & Lowe (2008) note that baboon consumption of mature baobab fruit not only assists in the dispersal of the seed, often on steep slopes, but also aids in germination, with the baboons stomach acids softening the hard outer layer of the seed. Seeds collected from baboon scat in the KNP have been shown to successfully germinate under nursery conditions (M.V. Hofmeyr pers. comm. 2012).

Small and moderate selective browsers

Most browsers will eat the leaves and twigs of baobabs when they are within reach (Wickens & Lowe 2008). Therefore intensive selective browsing is likely to have the greatest effect on the seedling and sapling baobabs with larger individuals escaping being browsed. In their study within the communal grazing lands of Venda, South Africa, Venter & Witkowski (2013a) found that any seedlings that managed to establish, within suitably moist micro-sites, were subsequently eaten by livestock. KNP has many small and moderate browsers that are likely to consume recruiting baobabs having a similar effect to that of livestock in communal grazing areas. Browsers in KNP would have contributed to mortality of seedlings and sapling resulting in the lack of observed recruitment. Many of the baobabs sampled in this study, particularly those <1m in stem diameter, were growing in amongst thorn trees which afforded them some protection from selective browsers.

Fungi

Fungi have been associated with baobab mortality in southern Africa (Roux 2002). Initial symptoms of fungal infection include the loss of branches, sunken areas in the stem and the release of sap (Wickens & Lowe 2008). One fungus isolated on diseased baobabs in South Africa was the opportunistic, stress-related pathogen, *Lasiodiplodia theobromae* (Roux 2002). In addition, sooty mould fungus, *Antennulariella sp*. was found on baobabs in Zimbabwe (Wickens & Lowe 2008). The effects of these fungi appear to be exacerbated by drought stress which can result in the death of infected trees. One tree sampled in the current study was noted as having black mould growing on it in 1995; this tree was still alive in 2013 although some traces of infection were still present.

Floods

On flat terrain and foot slopes fringing the floodplains of the Luvuvhu and Limpopo rivers, trees of several species were found pushed over or leaning downstream; obvious effects of recent flooding in the area in 2013. Whilst baobabs growing on these gentle slopes are easily accessible to elephants, and so heavily impacted by utilization, these individuals face additional impacts from flooding and the saturation of soil.

Anthropogenic impacts

Currently there are minimal anthropogenic impacts on the baobabs of KNP. Human communities have not been living in the park since the removal of the Makuleke community in the 1920s and 1930s (Carruthers 1995) There are however still signs of previous bark harvesting, visible as large rectangular sheets of recovering bark, and wooden and metal spikes have been hammered into the stems to access bee hives and lookout points.

Outside of KNP anthropogenic impacts continue in the form of fruit and bark harvesting and indirectly through high stocking densities of livestock eating smaller trees. Densities of baobabs near homesteads can be increased through the planting of seeds from pods harvested for their powdery fruit.

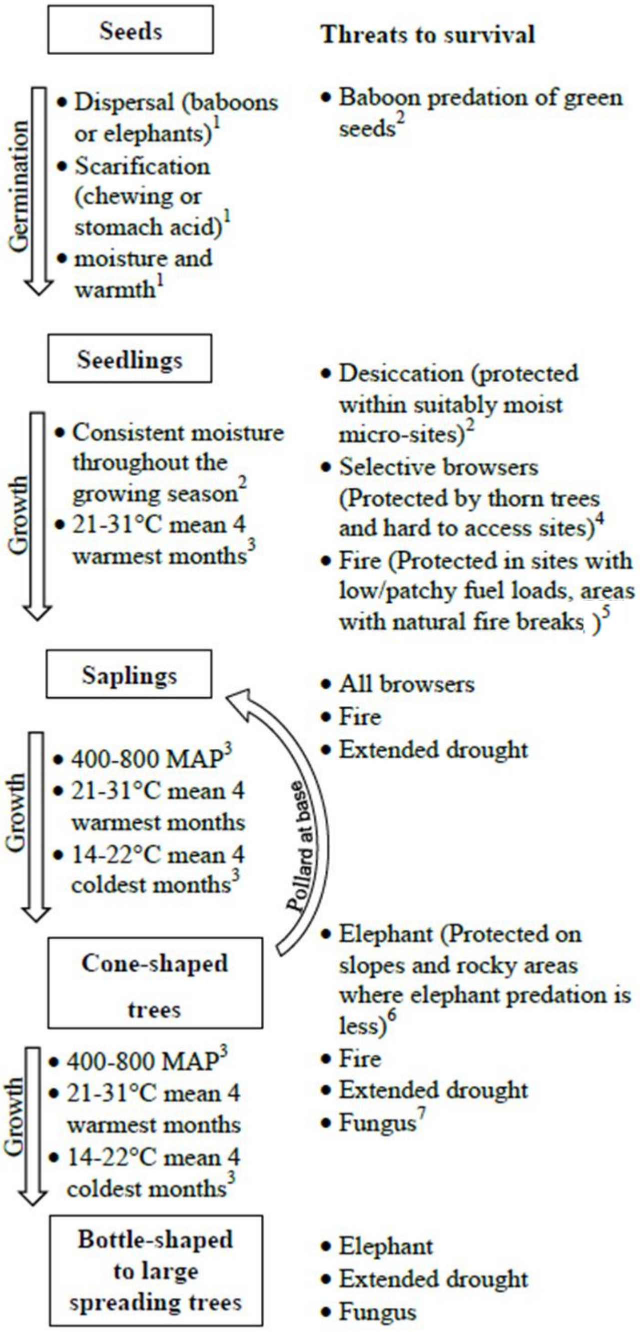

Figure 2. Diagram of the requirements of, and threats to, baobabs through their different life stages ([1]Wickens & Lowe 2008; [2]Venter & Witkowski 2010; [3]Cuni Sanchez *et al.* 2010; [4]Pers. obs. 2013; [5]Smit *et al.* 2012; [6]Edkins *et al.* 2005; [7]Roux 2002).

4.4 The future of baobabs in KNP

This study revealed temporal changes to the KNP baobab population, with a three-fold increase in annualized mortality between 1995/6-2001 and 2001-2013. This however did not significantly change the inverse J-shaped SCD over the study period. The high proportion of mortality in large, >4m stem diameter baobabs is concerning as these baobabs are uncommon in KNP and often represent baobabs in their ultimate life stage. Recruitment into these size-classes is very slow and further mortality is likely to reflect in changes in the population SCD.

Elephant damage to baobabs has increased, in both severity and frequency, over the study period with the increase in elephant density. This damage is best correlated with the growth in bull elephant density. It is expected that without management intervention the elephant population is expected to continue growing. With the increase in elephants it is expected that the resulting baobab damage is likely to continue increasing. The high proportion of severe and very severely damaged baobab trees that died during this study would suggest that mortality is likely to continue increasing with further increases in severity of damage.

The relatively higher density of baobabs within the Limpopo/Luvuvhu floodplains compared to other regions of KNP together with the inverse J-shaped distributions of baobabs in these vegetation units suggests that this is a healthy core population with other lower density populations with SCDs differing from the typical inverse J-shape growing under less favourable conditions and in less favourable vegetation units elsewhere.

Spatial differences across northern KNP were observed between maximum fire return intervals and mean annual temperatures. Longer (>30 years) maximum fire return intervals and higher mean annual temperatures (23°C) supported a negatively skewed baobab population structure whilst shorter maximum fire return intervals and lower mean annual temperatures (21-22°C) supported a bell-shaped population structure.

The low fuel loads in northern KNP is unlikely to increase and together with the topography acting as natural firebreaks, it is unlikely that fires will increase in frequency in this region. However the climatic conditions are expected to change. Predicted warming and increases in extreme rainfall events and rainfall variability in southern Africa (Engelbrecht *et al* 2013; DEA 2013) is likely to further impact on baobabs. An increase in temperature is likely to increase the area of the park within the more favourable 23°C mean annual temperature. However droughts associated with predicted increased rainfall variability and increased flooding associated with the predicted increase in extreme rainfall events will both stress the baobab population, and increase their vulnerability to other impacts such as fire, elephant damage and fungal infection, thus reducing the species capacity to outlive unfavourable conditions locally.

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