THE DEMOGRAPHY OF BALANITES MAUGHAMII:
AN ELEPHANT-DISPERSED TREE

By

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Abstract

Balanites maughamii is an ecologically and culturally valuable tree species, heavily impacted by elephants, which strip bark selectively off the largest trees, increasing their susceptibility to fire damage. Elephants also break intermediate sized trees extensively, keeping them trapped in non-reproductive stages. The trees can however survive breaking, stripping and toppling by elephants, as well as topkill by fires, because they resprout vigorously in response to damage. They also produce root suckers independently of disturbance. Vegetative reproduction buffers the populations from the infrequent recruitment of seedlings, and facilitates the maintenance of populations over the short term.

Balanites maughamii trees are reliant on African elephants (*Loxodonta africana*) for seed dispersal and to provide a germination cue through mastication. In the absence of elephants, the population experiences a recruitment bottleneck, but root suckers functionally replace seedlings and fill the "recruitment gap", so over the short term, the population is resilient.

In all populations, whether elephants are present or not, another hurdle affects recruitment, and it is seed limitation due to seed predation pre- and post- dispersal. Cafeteria experiments revealed that bushveld gerbils (*Tatera leucogaster*) were removing many seeds but do not scatter- or larder-hoard. They are simply seed predators.

Keywords: *Balanites maughamii*, demographic bottlenecks, elephant dispersal, resprouting, scatter-hoarding.

CONTENTS

INTRODUCTION

Processes such as recruitment, size class transitions, and mortality influence the size and structure of a population (Midgley *et al.,* 2010), and in so doing, shape its demographic profile. Recruitment in savanna trees depends on seed production, dispersal and germination occurring successfully, despite disturbance and predation, which create "hurdles" that must be overcome. Midgley and Bond (2001) identified a number of potential demographic hurdles that influence African *Acacias* in savanna ecosystems, and some of these hurdles were: 1) seed set limitation due to pollinator failure in outcrossing individuals, 2) seed limitation due to seed predation pre- and post- dispersal, 3) seed dispersal limitation in zoochorous species, 4) germination limitation due to lack of appropriate germination cues, 5) establishment limitation due to disturbance or climatic variables and 6) transition limitation from seedlings to saplings to adults, due to disturbance by fire and elephants. These recruitment bottlenecks were identified for *Acacias*, but they may apply to other savanna species too, because the ecosystem processes and disturbance regimes are the same. And then, even if recruitment is successful, trees must persist to ensure the continued regeneration of the population. Savanna trees rely on thick bark for protection, or have rapid growth rates allowing apical buds to escape being scorched by frequent, low intensity fires. Many species also rely on the ability to resprout after disturbance (Nefabas & Gambiza, 2007).

Balanites maughamii is an ecologically and culturally valuable tree species (Sands, 2001; Sprague, 1939), but little is known about its demography and how it responds to disturbance. This study aims to: 1) create a demographic profile for a *B. maughamii* population, and assess whether the species is able to persist in the face of disturbance, based on its bark thickness, growth rate and capacity to resprout, and 2) study closely the recruitment dynamics of *B.*

maughamii trees. This will involve identifying the mode(s) of seed dispersal that *B. maughamii* trees depend on, and following the fate of seeds at each stage of dispersal.

The fruit of *Balanites* are large and heavy, with a pungent smell when ripe, and it has been found that *B. wilsoniana*, a forest species, is reliant on African elephants (*Loxodonta africana*) for dispersal. Seeds that pass through elephants have increased germination rates and, in the absence of elephants, recruitment is limited (Chapman & Chapman, 1995; Chapman *et al.,* 1992; Cochrane, 2003; Lieberman *et al.,* 1987). It is unclear how elephant ingestion facilitates germination, but Midgley *et al.* (2012) believe mastication is important. The fruit of *B. maughamii* are slightly smaller than *B. wilsoniana*, but also have a strong smell when ripe, and in the Kruger National Park (KNP), in South Africa, elephants have been observed eating the fruit of *B. maughamii* (*pers. obs.*), It is therefore possible that *B. maughamii* trees also have a mutualistic relationship with elephants as their primary seed-dispersal agents.

In order to assess the role that elephants play in *B. maughamii* seed dispersal and recruitment, the demographic profiles of populations in the presence and in the absence of elephants will be compared. To test the hypothesis of Midgley *et al.* (2012), that through mastication, elephants alone can apply a force great enough to crack the seed coat without destroying the seed inside, elephants will be observed eating *B. maughamii* fruit. Germination trials will also be carried out on ingested and passed seeds, and the strength of seed coats will be measured. The role of rodents as potential secondary dispersal agents will be investigated as well. Finally, the extent to which these populations rely on dispersal mutualisms for seedling recruitment and continued population regeneration over short and long time scales will be considered.

Methods

Study species

Balanites maughamii is a deciduous or semi-deciduous tree 20-25 meters tall, found from Southern Tanzania to KwaZulu Natal with the centre of its distribution in Mozambique (Sands, 2001). *B. maughamii* subsp. *maughamii* is also common in the Kruger National Park (Coates-Palgrave, 1977). Trees observed in the Lebombo Mountains were found to yield fruit after four years of growth, and produced an average of 1,200 lbs (±545 kg) of nuts annually. It flowers every second or third year, from July to October, and the fruit appear around January, ripening and falling from the tree between May and July (http;//www.ecotravel.co.za). *B. maughamii* fruit have a thin, firm exocarp, a fibrous, oily mesocarp, and a hard, woody endocarp about six millimetres thick. The fruit are about eight centimetres long and 3.7 centimetres wide. The seeds are 2.5 centimetres long and become loose in mature fruit (Sands, 2001). Prior to germination, the seed coat splits apically into five flanges (Appendix: Image 1). The foliage is browsed by elephants and giraffes and the fruit eaten by many game animals and monkeys (Sands, 2001).

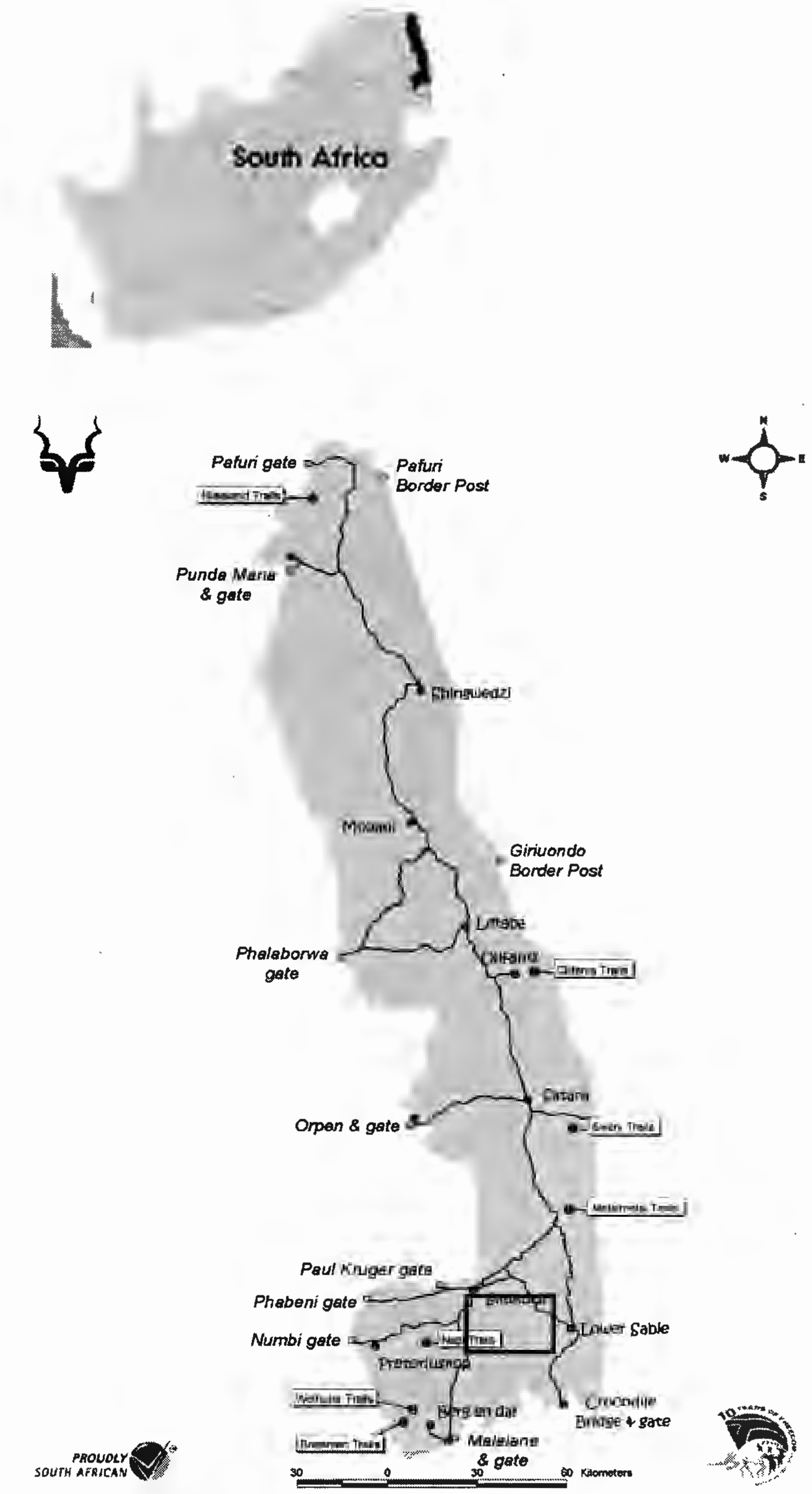
Cultural and economic value

B. maughamii trees have valuable hard timber (Sprague, 1939), which is used in Swaziland for wagon-wood (Sands, 2001), and the roots and bark are used in magic and medicine. The bark and roots are boiled to produce an emetic, and in Zululand, to keep away evil spirits, a froth is made by beating the roots and bark in water, with other ingredients. The froth is licked three times and then poured over a hut roof so that it drips over the entrance and protects the interior. Sands (2001) reported that Zulu people enjoy bathing in water in which the bark of *Balanites maughamii* has been soaked. *B. maughamii* seeds yield colourless, edible oil, used in manufacturing and as a lubricant. In parts of the Northern Province of

South Africa it is also used as a hide and skin dressing. Sprague (1939) claims the oil is "similar to the finest olive oil and burns with a bright flame". In some areas the seeds are burnt as torches, hence the South African vernacular name, "Torchwood". This was tested, and is indeed true (*pers. obs.*).

A saponin-glucoside, found particularly in the fruit, is very toxic to freshwater invertebrates, including hosts to stages of bilharzia (schistosomiasis) and water fleas, the alternate hosts of the guinea worm. *B. maughamii* trees contribute to the control of these diseases by occurring naturally (or being planted) near locally-used water sources. In southern Malawi the fruits are also used to make leg rattles, and a fish-poison is extracted from them.

Study site



The Kruger National Park, South Africs. The Study area in Skukuza is indicated with a rectangle.

This study was conducted between June and September, 2012, close to Renosterkoppies in the Skukuza supersite of the Kruger National Park (KNP), in South Africa, The KNP lies along the borders of Mozambique and Zimbabwe, and covers an area of 19,485 km^2, occupying the region 22°25’ S to 25°32’ S and 30°50’ E to 32°2’ E (Kennedy & Potgieter, 2003). The Skukuza land system consists of mixed broad-leaf and fine-leaf vegetation, on slightly undulating plains and sandy soils, derived from nutrient-poor granitic rock (Shannon *et al.,* 2008). The mean annual precipitation for the Skukuza area is 500-750 mm. The vegetation around Skukuza is generally very dense and falls within the “Sabie River Thickets” ecozone (Venter *et al.,* 2003).

Layout

This project can be separated into three chapters. The first focuses particularly on fire and elephants: how these disturbance factors impact individual *B. maughamii* trees when acting independently and synergistically, and how the trees respond to such disturbance (i.e. how resilient they are). The second chapter focuses on creating a demographic profile of the *B. maughamii* population, identifying where the population experiences demographic bottlenecks, and determining how the population persists in the face of such bottlenecks. The third chapter deals with recruitment dynamics and focuses particularly on fruit and seed dispersal. Each chapter is presented with its own introduction, methods, results and discussion. The overall conclusion will incorporate the main findings in each chapter, providing a broad synthesis.

CHAPTER ONE

Introduction

In savanna ecosystems, disturbances such as fire and herbivory maintain the dynamic balance between tree and grass cover (Higgins *et al.*, 2000; Hoffmann *et al.*, 2003; Sankaran *et al.*, 2005; Scholes & Archer, 1997). Long annual dry seasons, combined with the rapid accumulation of highly flammable grassy biomass, create conditions conducive to frequent fires (Archibald *et al.*, 2009). These fires are intense enough to cause "topkill" (the complete death of a plant's aerial biomass), and small trees are repeatedly caught in the "fire trap". Frequent fires keep trees in reduced, often non-reproductive stages, preventing recruitment into adult size-classes (Hoffmann *et al.*, 2003; Hoffman *et al.*, 2009). Fires are of relatively low intensity and will therefore affect tree recruitment rather than adult survival (Gignoux *et al.,* 1997; Hofmeyr & Echardt, n. d.).

Megaherbivores such as African elephants (*Loxodonta africana*) can have a dramatic destructive effect on woody vegetation, causing significant backward height transitions and preventing recruitment into larger size classes. They also cause mortality of established trees (Jacobs & Biggs, 2002). Elephants are selective when it comes to utilising certain species as well as plant parts, such as roots, leaves, fruit or bark, during feeding or as part of aggressive behavioral displays (Hofmeyr & Eckardt, n. d.) and have been shown to target and over-utilize certain species (Barnes *et al.,* 1994; O'Connor *et al.*, 2007; Shannon *et al.,* 2008). Utilisation includes breaking leaves and branches off trees, pushing trees over entirely and stripping bark from the main stems (Scholes *et al.,* 2002). In isolation, bark stripping does not seem to cause death in large trees, unless the tree is almost completely ring-barked (MacGregor & O'Connor, 2004). Elephants typically do not ring-bark trees entirely, but even the removal of small areas of bark increase a tree's susceptibility to fire damage

(Moncrieff *et al.,* 2008). Guy (1989) postulated that the wood-boring beetles, which invade the exposed wood, create burrows and fissures that ventilate fires, exacerbating the damage.

Fires in the KNP kill small trees, and elephants directly impact medium-sized trees, but when elephants and fire act synergistically, they kill trees larger than either could kill individually (Dublin *et al.* 1990; Holdo, 2005; Midgley *et al.,* 2010). This significantly decreases population size. In a population where large trees are dying and smaller trees are stuck in the fire trap, sexual reproduction is reduced, as seed production is positively related to plant size (Hoffmann, 1998). Nefabas and Gambiza (2007) propose that there are three key adaptations that allow woody plants to survive these disturbances in savanna systems, thus maintaining healthy populations: some species rely on thick bark for protection, some species have very fast growth rates, so grow tall enough for apical buds to escape being scorched in the fire trap, and other species rely on the ability to resprout after disturbance.

Elephants target and over-utilise large trees in the KNP, either causing direct mortality or increasing susceptibility to fire damage (Shannon *et al.,* 2008). There is concern that the large *B. maughamii* trees, abundant in the Skukuza area of the KNP, may also be subject to over-utilisation. The aim of this chapter is to determine how *B. maughamii* trees are affected by elephant utilisation and fire, independently or synergistically, and how the trees respond. Based on this, it will be easier to determine whether the population is coping in a high disturbance system or whether the concern expressed is warranted.

The insulating capacity of bark protects cambial tissue from heat induced mortality, and bark thickness is the most important variable for protection (Eriksson *et al.,* 2003). Tree stem survival is thus strongly dependent on bark thickness. To determine whether the bark of *B. maughamii* trees offers sufficient protection from fire, bark thickness will be measured and compared with other known fire-sensitive, thin-barked trees and thick-barked tolerators. *B. maughamii* trees grow very slowly (www.plantzafrica.com; Williams *et al.,* 2005), so reaching a sufficient fire-escape height between short fire-free intervals is unlikely. As bark thickness is largely dependent on stem diameter (Borger, 1973; Cunningham, 2001; Hoffmann *et al*., 2003; Hoffmann & Solbrig, 2003; Uhl & Kauffman, 1990), large adults may have sufficiently thick bark to offer protection from fire, but small trees may not. The large trees have fluted trunks and tessellated bark (the surface is marked by regular square or oblong plates or blocks (Junikka, 1994), which becomes rougher with age (Williams *et al*., 2005). These traits prevent large strips of bark being torn off at once, and the canopies of large trees are often beyond the reach of elephants, so are likely well protected from elephant utilisation. Trees in intermediate size classes are unfluted, have smoother bark and are not tall enough to avoid canopy breakage, so are likely very vulnerable.

Methods

Resilience to disturbance

Ten plots in the granitic supersite near Skukuza in the KNP were selected and all were in crest regions with red or brown sandy soil and broad-leaved vegetation, to control for soil and nutrient variation. Each plot sampled was four hectares in size. A total of 333 *B. maughamii* trees were tagged and their GPS positions were recorded for long-term study. All trees were assessed for damage, but only trees over three meters tall were assessed for elephant utilisation, because damage to smaller trees could be attributed to other herbivores. Elephant utilisation was divided into three categories: "breaking", "stripping" and "toppling". The percentage of the canopy that was broken was estimated, and to determine how plants respond to such utilisation, any new growth from broken points was recorded. Where stripping of bark had occurred, the percentage of the area below three meters stripped was estimated, and to determine whether exposed wood was invaded by boring beetles and had experienced fire damage, the percentage of the stripped area affected by borers or fire was estimated. Where bark regrowth had taken place around the stripped area, the percentage was estimated, to give some indication of how the trees recover from damage. Finally, basal resprouts growing from toppled and top-killed trees were noted.

Bark thickness

Bark thickness measurements were done on 29 randomly selected adult trees in the supersite and Skukuza staff village. A bark-punch was used to core into the trunk and remove a small section of bark, so that the thickness could be measured with callipers. To determine whether fluting influences bark thickness, measurements were taken from the outer edges and inner folds of the flutes as well as from flat parts (see Figure 1.1). Unfluted trees only had flat parts from which to measure bark thickness. Hempson *et al.* (in prep.) provided stem diameter and bark thickness measurements of *Acacia nigrescens*, *Sclerocarya birrea*, *Dichrostachys cinerea*, *Acacia grandicornuta*, *Terminalia sericea* and *Ziziphus mucronata*, which were used in bark thickness comparisons.

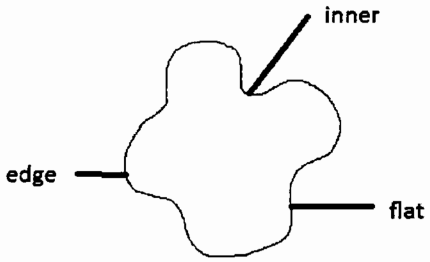


Figure 1.1: Schematic of a fluted *B. maughamii* stem, indicating where bark thickness measurements were taken.

Analyses

The trees were divided into diameter size classes (□ 2 cm, 2-5 cm, 5-10 cm, 10-20 cm, □20 cm), and breaking was divided into six usage classes: 0 %, 1-10 %, 11-25 %, 26-50 %, 51-75 %, and 76-100 %. A stacked bar graph was created to show how the proportion of trees in each diameter size was affected by breaking. To assess utilisation, the forms of utilisation (breaking, stripping and toppling), response of trees over three meters in height, and percentage of trees in each response category were tabulated. To test if flutedness influenced bark thickness, the mean relative thickness of edge, flat and inner bark was found by dividing bark thickness by stem diameter and calculating the average. The distributions were tested for normality using Statistica, and log-transformed to run an ANOVA. Logged bark thickness was plotted against logged stem diameter and linear regressions were done to compare bark thickness across different savanna species. The mean relative bark thickness at a five centimetre diameter, slope, and intercept was recorded for each species and tested for significance in Statistica.

Results

Elephant utilisation and the response of *B. maughamii* trees

In the smallest size class, a large proportion of trees is completely undamaged, but trees in the three intermediate size classes experienced extensive breaking. Damage does not appear to accumulate, because the trees in the three intermediate size classes were damaged to a similar extent, despite their increasing sizes and the trees in the largest size class were less severely broken in the three intermediate size classes.

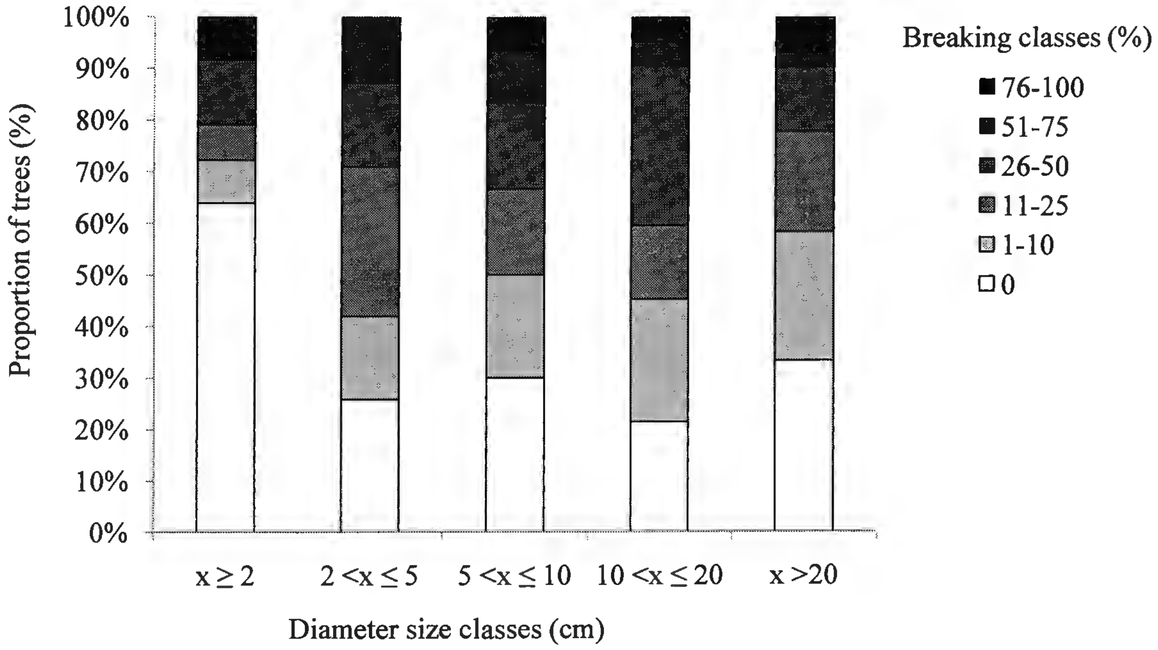


Figure 1.2: The proportion of trees in each diameter size class (2 cm, 2-5 cm, 5-10 cm, 10-20 cm, □20 cm) that experienced some form of breaking. Breaking was separated into breaking classes: 0%; 1-10%; 11-25%; 26-50%; 51-75% and 76-100%.

Almost all bark stripping can be attributed to elephants, which appear to target the largest trees. Despite often having fluted stems, large trees (with diameters greater than 20 cm) experience extensive stripping, whereas trees with diameters below 10 cm experience very little.

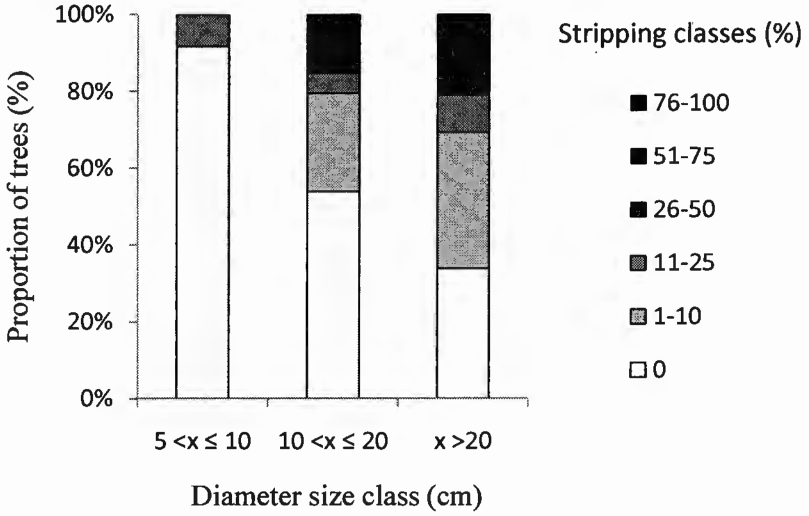


Figure 1.3: The proportion of trees over three meters tall in each diameter size class (5-10 cm, 10-20 cm, □20 cm) that experienced bark stripping. Stripping was separated into stripping classes: 0%; 1-10%; 11-25%; 26-50%; 51-75% and 76-100%.

B. maughamii trees are heavily utilised by elephants. Of the trees over three meters tall sampled, 6.7% were toppled, 51.9% of trees experienced bark stripping and 65.2% of trees experienced some breaking. Despite the extensive breaking in intermediate sized trees and stripping in large trees, the species is able to cope, due to its capacity to resprout. Seventy-five percent of the broken trees resprouted epicormically and all the toppled trees resprouted basally.

The response of *B. maughamii* trees to fire and wood-boring beetles

Six trees suffered topkill by fires, but all survived by resprouting basally. Forty-four percent of trees that had experienced bark stripping were able to regrow some of the removed bark, but on average only 4.02% of the stripped area was covered by new bark. Ten percent of stripped trees with exposed wood experienced borer damage, but on average only 2.68% of the exposed areas were damaged. Slightly more trees (17.1%) experienced fire damage, but an average of only 4.63% of the exposed areas were burnt.

Table 1.1: Summary of the utilisation for all *B. maughamii* trees over three metres tall, found in the ten surveyed sites. Response values are expressed as percentages of trees affected by the overlying condition (e.g. 100% of the 6.7% toppled *B. maughamii* trees were alive). Sample sizes given in parentheses.

Condition	Response	Percentage
Toppled		6.7 (9)
	Alive	100.0 (9)
	Basal resprouting	100.0 (9)
Broken		65.2 (88)
	Epicormic resprouting	75.0 (66)
Stripped		51.9 (70)
	Bark regrowth	44.3 (31)
	Fire damage	17.1 (12)
	Borer damage	10.0 (7)

Bark characteristics

In all species, bark thickness increases with stem diameter, but bark thickness varied among species. At a 5 cm stem diameter, bark is only 1.3 mm thick in *B. maughamii*, which is extremely thin relative to other sampled species, all of which have bark over 3 mm thick.

Table 1.2: A summary of the regression analyses of log transformed bark thickness and stem diameter of six woody plant species found in the Skukuza area of the Kruger National Park, South Africa.

Tree species	Slope	Mean b.t. (mm) at 5cm stem diameter	Intercept	n	P-value
Sclerocarya birrea	0.50	4.38	0.06	64	0.562
Acacia nigrescens	0.64	4.82	-0.79	55	0.000
Acacia grandicornuta	0.82	4.41	-1.74	56	0.000
Dichrostachys cinerea	0.72	3.86	-1.73	55	0.000
Balanites maughamii	0.58	1.30	-1.42	29	0.000
Ziziphus mucronata	0.71	3.24	-1.63	48	0.000

Mean b.t (mm) is the bark thickness at a 5 cm stem diameter.
Stem diameter and bark thickness were log transformed to determine values for slope, intercept and P-value.

The slopes of the lines relating bark thickness to stem diameter were also variable. *A. grandicornuta, D. cinerea* and *Ziziphus mucronata* have steep slopes (0.82, 0.72 and 0.71 respectively) and therefore have high rates of increase in bark thickness associated with increases in stem diameter, where *A. nigrescens, S. birrea* and *B. maughamii* have gentler slopes (0.64, 0.58 and 0.50 respectively) and therefore, slower rates of increase in bark thickness. No significant difference was noted between the relative bark thickness on the edge, flat and inner parts of stem flutes (P=0.08098).

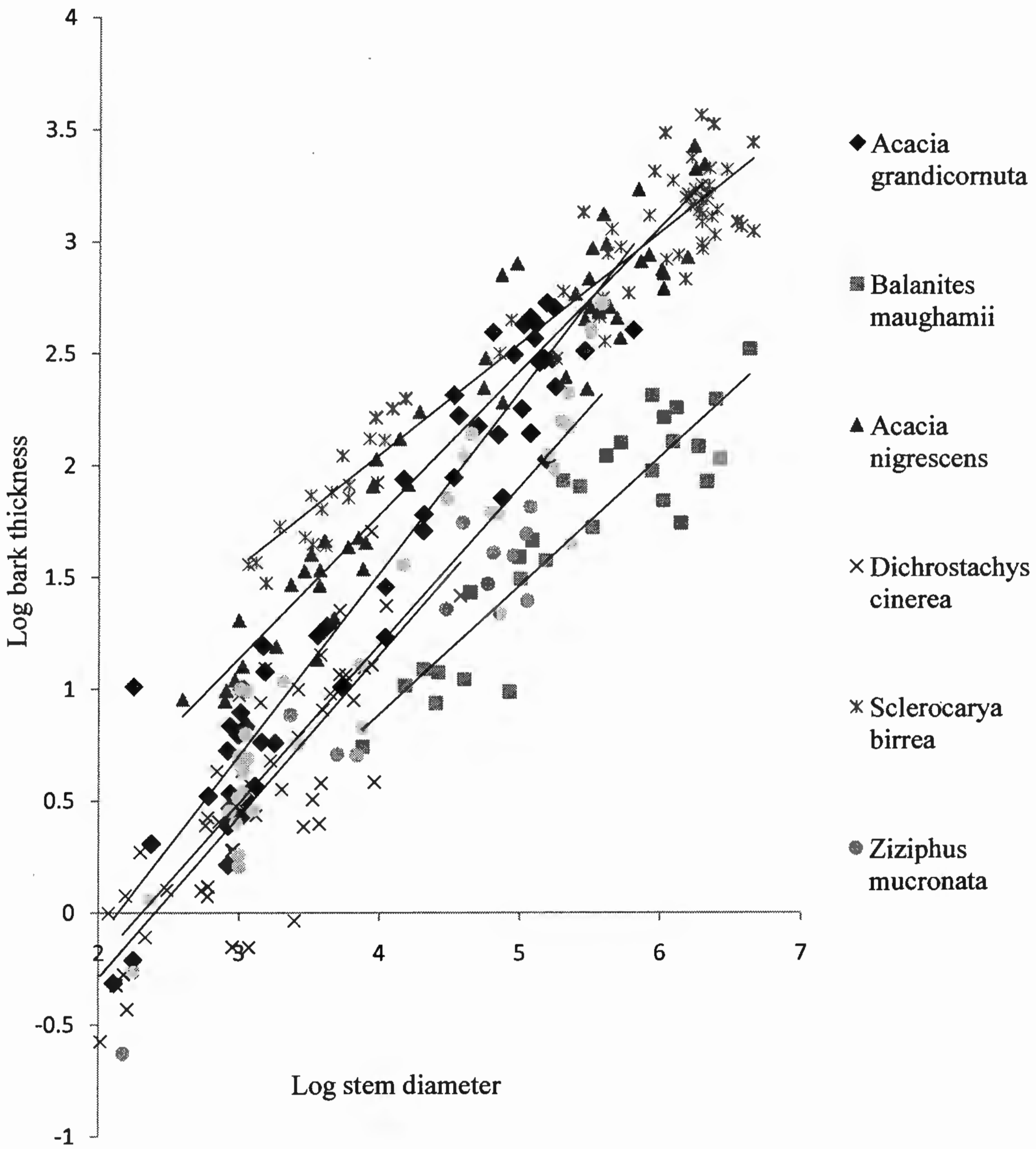


Figure 1.4: Regression analyses of log transformed bark thickness and stem diameter of six woody plant species found in the Skukuza area of the Kruger National Park, South Africa.

Discussion

B. maughamii trees are heavily impacted by elephants, and the trees in intermediate size classes are particularly vulnerable to canopy breakage. These findings are consistent with Midgley *et al.* (2010) who found that elephants directly impact primarily medium-sized trees. Elephants also appear to strip bark selectively off the largest trees, increasing their susceptibility to fire damage. *B. maughamii* trees are weakly defended against fire, with limited recovery of bark over wounds and extremely thin bark. Despite the above, *B. maughamii* trees are relatively resilient, mainly because they are able to resprout vigorously.

Midgley *et al.* (2010) suggest that seedlings are often subject to leaf and stem consumption by browsers and trampling by bulk feeders at a local scale. In this study, damage to *B. maughamii* trees with diameters below two centimetres was not attributed to any one particular disturbance agent, but they were most likely impacted by trampling, herbivory and fire.

As trees age and grow larger, they tend to accumulate damage, which can lead one to over-estimate the extent to which elephants selectively target larger trees. In terms of breaking, *B. maughamii* trees do not appear to accumulate damage, due to their capacity to recover by resprouting (Figure 1.2). They are certainly heavily impacted by elephants, but are fairly resilient because the trees are able to recover from canopy breaking by resprouting epicormically (Table 1.1). The largest trees grow canopies beyond the reach of elephants and other large mammalian herbivores such as giraffes (*Giraffa camelopardelis*) and kudu (*Tragelaphus strepsiceros*), and once this height is reached, they stop accumulating new damage and simultaneously resprout, recovering from old damage. They are also able to recover from toppling and topkill, by vigorous basal resprouting (Table 1.1).

Despite the prediction that the deeply fluted stems would offer protection against extensive stripping by elephants, large trees experienced the most bark stripping (Figure 1.3). This could be a consequence of intense, selective utilisation by elephants, or a consequence of limited bark regrowth over many small strip-wounds that accumulate as the trees age. Flutedness may deter elephants from stripping large pieces of bark at once, but stripping accumulates, because, unlike some savanna species that regrow bark to seal wounds, for example baobabs and sycamore figs (*pers. obs.*), *B. maughamii* compartmentalise and seal off the xylem below the wound rather than covering it, as very little bark regrowth was noted for stripped areas (Table 1.1). Whether bark stripping is a consequence of intense selection or slow accumulation, stripped trees are rendered more vulnerable to damage by boring beetles and fire. Six large trees had experienced topkill due to fire, but besides those, fire damage noted in this study was minimal (Table 1.1), because the sites have not been burnt for some time. Borer-damage in this species is low, possibly because the wood is extremely hard (Sands, 2001). *B. wilsoniana* also has termite-resistant wood and the same may be true for *B. maughamii* wood, though this was not tested.

In the face of fires, tree stem survival is strongly dependent on bark thickness, which is considered to be the critical feature of a plant's resistance to fire (Hempson *et al.,* in prep.) so thick bark would be advantageous in fire-tolerating savanna species (Hoffmann *et al.,* 1998). A thin-barked species could match the ability of a thicker-barked species to resist fire; if it has a faster growth rate within a given fire-free period (Lawes *et al.*, 2011). *B. maughamii* trees, however, have extremely thin bark relative to fire-tolerators, and even to other fire-sensitive savanna species (Figure 4a). In addition, the growth rate and the rate of increase in bark thickness, associated with the increase in stem diameter, is slow (Figure 1.4), suggesting *B. maughamii* is a fire-sensitive species rather than a fire-tolerator. No significant difference was noted in bark thickness on the outer edges and the inner folds of flutes, but the very large trees can allometrically gain bark that is thick enough to provide protection against fires. Small individuals, however, do not.

The most heavily impacted trees in the intermediate size classes are continually damaged and effectively kept trapped in non-reproductive stages, and a potential consequence is that seed production may be reduced, resulting in infrequent recruitment of seedlings. The ability of *B. maughamii* to resprout vigorously is its saving grace, making it a resilient species in the face of frequent and intense disturbance. Trees can survive breaking, stripping and toppling by elephants as well as topkill by fires. The benefits of vegetative reproduction are that cost is lower than that of sexual reproduction (Abrahamson, as cited in Hoffmann, 1998) and vegetative offspring tend to be larger than seedlings of the same age (Hoffmann, 1998). It also buffers populations from the infrequent recruitment of seedlings, and facilitates the maintenance of populations over the short term (Lawes *et al.* 2011).

Recruitment in *B. maughamii* trees could potentially be threatened by disturbance, and to determine how the populations in the KNP fare, their demographies will be considered in a fair amount of detail in the following chapter, in order to determine whether vegetative reproduction is indeed buffering a population that is actually experiencing a recruitment bottleneck.

CHAPTER 2

Introduction

A demographic profile shows the size of a population and the proportion of trees in the different size classes (Midgley *et al.,* 2010), and is the outcome of the balance between recruitment and mortality in a population (Fred Kruger, unpubl.) "Recruitment" refers to the production of genetically new individuals, "transitions" refer to processes which increase or decrease the size of established plants, and "mortality" refers to processes which decrease the size of the population (Midgley *et al.*, 2010). Over time, tree species evolve traits and make trade-offs in response to disturbance regimes, in order to survive. To better understand the demography of a species, it is necessary to identify how these disturbances affect the different life history stages of species (from recruitment through to adult mortality) because trees respond differently to disturbances at different life stages. Demographic profiles are useful, as they can indicate at which stages trees are most susceptible to disturbance, and experience "demographic bottlenecks" (processes or events that kill or prevent reproduction of all but a few individuals in a population). For example, if recruitment were limited, then one could expect few trees in the smallest size classes, and if elephant utilisation was causing mortality of large trees, there would expectedly be few trees in the largest size classes.

In the case of *B. Maughamii* populations in the KNP, however, demographic profiles do not provide sufficient detail to allow all the demographic bottlenecks to be identified. The ability of *B. maughamii* trees to resprout in response to disturbance means that small individuals in the population could be new seedlings (genets) or much older resprouts (ramets) kept back by disturbance. Studying the size class distributions of the population, alone, will not allow one to discern whether trees in the smallest size classes are the products of recruitment or resprouting, so it is impossible to determine the relative importance of recruitment versus resprouting.

The aim of this chapter is to study the demography of the *B. maughamii* population in Skukuza in the KNP, to identify if and where the population experiences demographic bottlenecks, and to assess the relative importance of recruitment versus resprouting in the *B. maughamii* population.

Methods

Demographic profiles

Four plots in the granitic supersite near Skukuza in the Kruger National Park, and one plot within an exclosure, were selected. Each plot was four hectares in size, and was sampled by walking five transects, 20 meters wide and 200 meters long. In these plots, a total of 350 *B. maughamii* trees were sampled and their GPS positions recorded. Trees were also tagged for future long-term study. For each tree, the maximum diameter and height were recorded. In some resprouting species the extent of resprouting can be extensive, making it difficult to determine where one individual ends and the next begins (Kruger *et al.,* 1997). To get around this complication when considering resprouting species, they developed an arbitrary working definition: any connected stems within a radius of 1/10 of the height of the main canopy stem constituted the same "individual". The same definition was used in this study. Any stem under 0.5 m tall was considered a "regeneration individual", regardless of whether it was a seedling (genet) or a sprout (ramet).

Recruitment dynamics

In order to determine the relative importance of seedling recruitment *versus* resprouting, three sites were selected and in each, *B. maughamii* trees below 0.5 m in height were excavated to a depth of 20 cm, to determine whether the plant was a ramet or a genet. "Genet" refers to genetically new individuals and can include seedlings and "gullivers" (Appendix: Image 4). The term "gulliver" is used to describe an individual that has been knocked back by disturbance a number of times, but has resprouted (Bond & van Wilgen, 1996). As a general rule, if the 20cm depth had been reached and a lateral root was not noted, the tree was classified as a genet. If a lateral root was found, the tree was classified as a ramet. Around each of three adult trees, a 2 m area was excavated to determine whether small plants in the surrounding area were genets or root suckers (Appendix: Image 3)

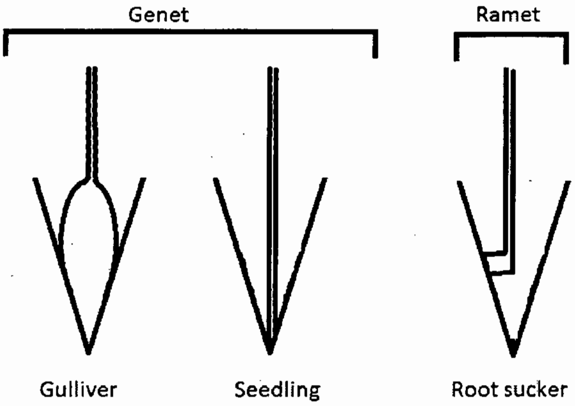


Figure 2.1: The general rule: If no lateral root was noted at a 20 cm depth, the tree was classified a genet. If a lateral root was found, the tree was classified a ramet.

Analysis

All demographic profiles were assessed by creating frequency distributions showing the relative proportions of trees in five biologically meaningful diameter size classes: <2 cm, 2-5 cm, 5-10 cm, 10-20 cm and □20 cm. This was done for each of the four sites within the Skukuza supersite, and also for the exclosure site. The demographic profiles of the whole supersite (combining the four sites) and exclosure were then plotted together for comparison. In these demographic profiles, no distinction was made between resprouting stems and germinants from seed, as all were considered regeneration individuals. The demographic profile of the exclosure site was then plotted with and without ramets. For the excavated trees in the broadleaf supersite, bottomland river site and bottomland exclosure, the proportion of seedlings, gullivers and ramets were plotted on a bar graph.

Results

Within the Skukuza supersite, at sites A and D, the frequency distributions have reverse J-shaped curves, where the greatest proportion of trees are in the smallest diameter size class, and the second greatest proportions of trees are found in the largest diameter size class (>20 cm). The intermediate size classes have few trees. Site C also has the greatest proportion of trees in the smallest size class, but few trees in all the other size classes. Site B has the smallest proportion of trees in the smallest size class, and as diameter size classes increase, so too do the proportion of trees in them. The population in the exclosure also has a reverse j-shaped distribution.

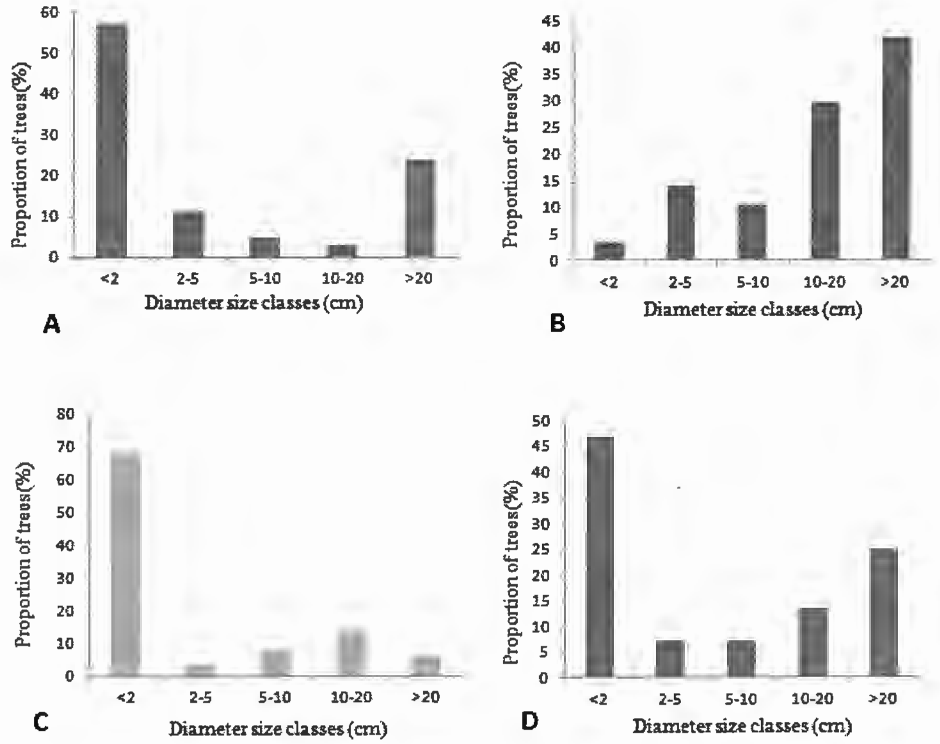


Figure 2.2: The demographic profiles of four individual sites sampled within the Skukuza supersite. In each site (A, B, C, and D) the trees were arranged into diameter size classes (cm) and plotted against the proportion of trees (%) sampled in that site.

When sites A, B, C and D are combined, representing the supersite population as a whole, the population has a reverse J-shaped distribution. The exclosure site is similar, but has fewer trees in the smallest diameter size class than the supersite population. In the 2-5 cm and 5-10 cm diameter size classes, the exclosure has a greater proportion of trees than the supersite. In both the supersite and exclosure, the proportion of trees in the largest size class is very similar.

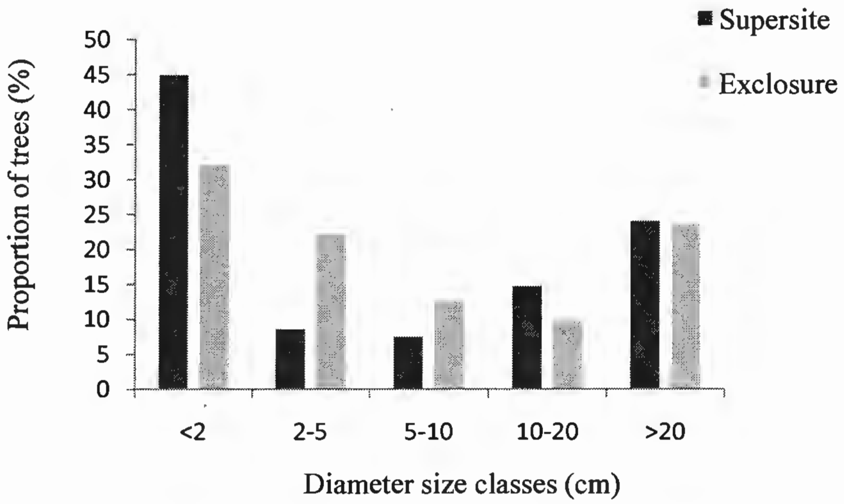


Figure 2.3: The demographic profile of the four sites sampled within the Skukuza supersite, combined, compared to the population in the large mammal exclosure site, Skukuza, Kruger National Park, South Africa.

When the demographic profile of the exclosure population is plotted with ramets included, the population has a reverse J-shaped distribution, but when plotted without ramets, the <2cm size class has lowest proportion of trees, and no longer has the reverse J-shaped distribution.

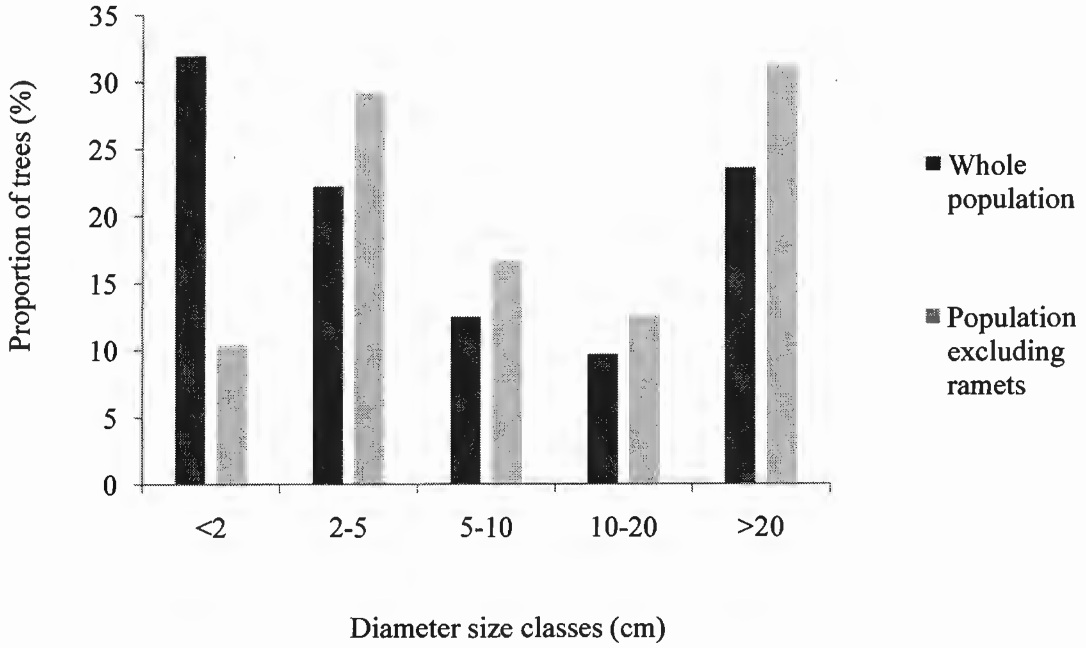


Figure 2.4: The demographic profile of the large mammal exclosure site. The trees sampled in the site were arranged into diameter size classes (cm) and plotted against the proportion of trees (%).

The excavations of trees below 0.5m tall, in the in the broadleaf supersite, bottomland river site and bottomland exclosure site revealed that a number of trees in the <2cm and 2-5cm diameter size classes, were ramets and not genets. The excavations of the three 2 m plots around adult trees supported this finding, as all surrounding small trees were connected to the "parent tree" *via* extensive root systems (See Appendix: Images 1-4). In the supersite, 60% of the population consists of genets (where 40% are seedlings and 20% are gullivers) and 40% of the population consists of ramets (40% are root suckers). In the bottomland river site, only genets were noted, where 43.3% are seedlings and 56.6% are gullivers. In the exclosure site, only ramets were found (100%).

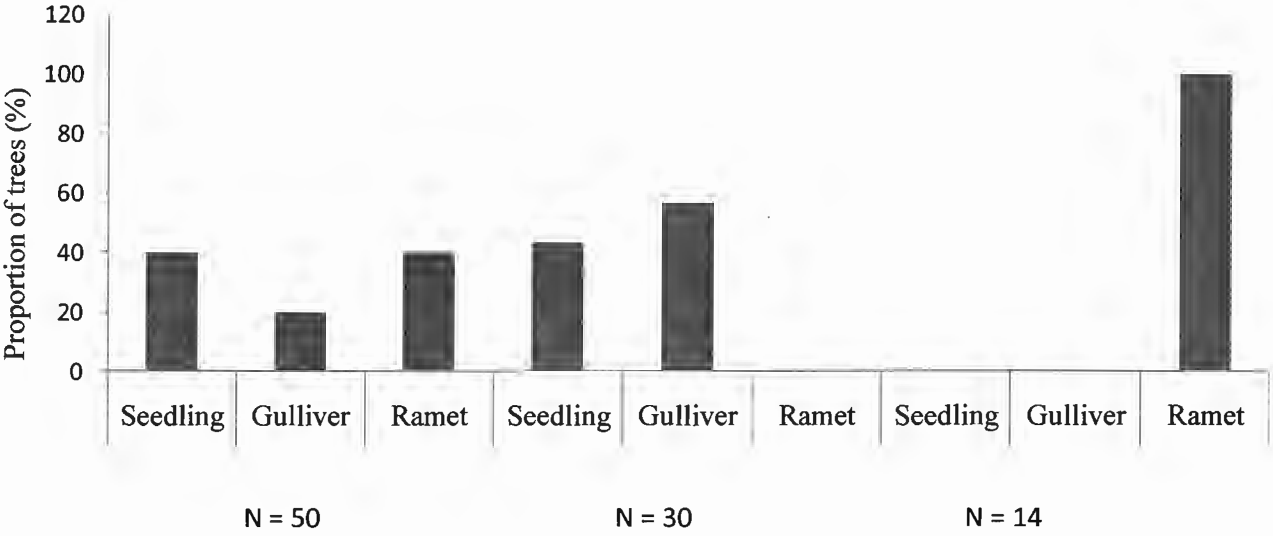


Figure 2.5: The proportion of excavated seedlings, gullivers and ramets in the broadleaf supersite, bottomland river site and bottomland exclosure.

Discussion

When analysing the demographic profiles of the *B. maughamii* populations in the Skukuza supersite and exclosure, recruitment and transition through size classes appears to be successful, due to the large proportions of trees in the smallest size classes. Yet, when regeneration-individuals are excavated, it becomes clear that the population in the exclosure experiences a severe demographic bottleneck somewhere between recruitment and seedling establishment, because no seedlings were found. Ramets, functionally, replace seedlings in the large mammal exclosure, but are not genetically new individuals, and it was found that ramets were "root suckers" - defined by Hoffmann (1998) as new stems originating from root buds some distance from the parent stem, and not simply disturbance-induced basal resprouts.

The occurrence of reverse J-shaped frequency distributions in the sites within the supersite indicates a high density of trees in the smallest diameter size classes, and fairly heavy exploitation in intermediate classes (Figure 2.2), but, typically, populations with steady recruitment and transition through size classes have reverse-J shaped distributions (Midgley & Bond, 2001). Both the supersite population as a whole and the exclosure site therefore have steady recruitment and transition through size classes (Figure 2.2). The proportion of the population made up of large trees in both the supersite and exclosure are similar, yet in the exclosure, elephants have been excluded for at least c.a. 30 years, which suggests mortality of large trees in the supersite cannot be blamed entirely on elephants. Recruitment appears to be stronger in the supersite too, with a greater proportion of trees in the smallest diameter size class (Figure 2.2).

When ramets are excluded from the demographic profile in the exclosure, the lack of seedlings in the population is evident (Figure 2.3), but transitions into larger size classes still take place, because ramets functionally replace seedlings. Excavations revealed that ramets were not disturbance-induced basal resprouts, but root suckers produced by larger trees (Appendix: Images 2 and 3). In the exclosure, fire has been absent for at least ten years, and elephants c.a. 30 years, but trees produce extensive root suckers, and so do trees in the supersite where disturbance is common. The development of root suckers therefore occurs independently of disturbance. Within the exclosure, all regeneration individuals (under 0.5 m tall) were ramets (Figure 2.4). The river site had seedlings and gullivers, but no root suckers. Some gullivers may actually have been root suckers too, but it was simply not possible to tell when excavating to 20 cm depths.

Although there is seedling recruitment in some *B. maughamii* populations (supersite and river site), a great proportion of small trees are ramets, not genets. *B. maughamii* trees are vigorous resprouters, epicormically, basally, and as has now been observed, via root suckers, which brings into question the importance of sexual reproduction. The advantage of vegetative reproduction is that, once *B. maughamii* trees establish, they are able recover from fire damage, breaking, toppling and topkill. Clonal reproduction can have consequences over the long term if sexual reproduction is limited, for example infertility due to mutations that accumulate (Dorken & Eckert, 2001). *B. maughamii* appears to be bet-hedging, by relying on clonal reproduction for survival, and sexual reproduction to ensure transmission of genetic variation and maintain high genetic diversity in the population (Dorken & Eckert, 2001).

The lack of seedlings in the exclosure indicates that the *B. maughamii* population is experiencing a severe bottleneck somewhere between recruitment and seedling establishment. The only difference between the sites outside and inside the exclosure is the presence of large mammals and the time since the last burn. Therefore, it is likely that either fire or large mammals play a role in the recruitment process. To determine the relative importance of resprouting *versus* recruitment, it is necessary that a more detailed study of the recruitment process be carried out. This will also help in determining exactly where the bottleneck occurs.

CHAPTER 3:

"Look into the seeds of time and say which grain will grow and which will not" –Macbeth.

Introduction

When *B. maughamii* populations are isolated from fire and elephants for a long period of time, they experience a bottleneck somewhere between recruitment and seedling establishment (chapter 2), which could potentially be any of the following: 1) seed set limitation due to pollinator failure in outcrossing individuals, 2) seed limitation due to seed predation pre- and post-dispersal, 3) seed dispersal limitation in zoochorous species and 4) germination limitation due to lack of appropriate germination cues. Very little has been done on *B. maughamii* pollination, so this will not be considered, but the fate of *B. maughamii* fruit will be followed from the stage where the fruit leave the tree, to the stage where seeds germinate. Determining the survival rate of seeds at each stage is important for understanding plant fitness, as it is the surviving seeds that drive the recruitment of plants (Levey & Byrne, 1993).

Primary dispersal refers to the movement of seeds from the parent plant to a surface, and secondary dispersal includes subsequent movements (Chambers & MacMahon, 1994). By acting as seed vectors, animals can play an essential role in the reproductive cycle of a plant (Hererra, 1995). Animals may move seeds passively (seed "hitch-hikers" attach to fur, e.g. burrs, or are incidentally consumed with other foods), or actively (selectively eating fruit, or scatter- and larder-hoarding seeds). The advantages of dispersal are: 1) Seedlings can colonise new, potentially suitable sites. Dirzo and Dominguez, (1986) found that reproductive success of offspring increase as they are located further away from their parent plant. This is referred to as the "colonization hypothesis", 2) Competition among sibling seedlings is reduced, 3) Parent-offspring competition is reduced, and 4) the risk of offspring predation is reduced, because seed predators and herbivores often concentrate their activities where resources are common (Howe & Smallwood, 1986. Platt and Hermann (1986) refer to this as the "escape hypothesis".

A number of animal groups have been found to actively move seeds to favourable microsites without killing them (Vander Wall *et al.*, 2005). Mutualistic interactions between vascular plants and frugivorous animals have been well documented and have occurred for over 70 million years (Fleming, 1986). Many plants that depend on animals for primary dispersal, produce propagules (seeds or fruit) that have evolved morphologically in response to animal behaviour and morphology (Stiles, 1992). For example, fruit dispersed by mammalian frugivores must have heavily protected seeds, to prevent the seed being crushed during mastication. For a propagule to potentially pass, unharmed, through the digestive tract of a larger mammal, it must fit into the mouth and throat of that animal (Stiles, 1992). Gautier-Hion *et al.* (1985) suggest that fruit dispersed exclusively by African elephants are typically large, indehiscent, thick-husked and dull in colour, with fibrous pulp. This description fits *B. maughamii* fruit, which are large and heavy, with a thin, firm exocarp, a fibrous, oily mesocarp, and a hard, woody endocarp about six millimetres thick. Elephants have been observed eating the fruit so it is possible that *B. maughamii* trees rely on elephants for dispersal. Unlike mammals, seed dispersal by rodents is limited by what the hoarder can lift, not swallow, because they gnaw seeds to open them (Hallwachs, 1986).

Section 1

The role of elephants and the fate of fruit

African elephants have been present in Africa for over 50 million years and Cochrane (2003) believes that plant-elephant relationships are common. A tree species that appears to depend on the African elephant for dispersal is *Balanites wilsoniana* (Chapman *et al.*, 1992; Cochrane, 2003; Dawe, 1906; Lieberman *et al.*, 1987). The fruit are large, have a hard, fibrous endocarp up to one centimeter thick, and each fruit contains a single large seed (Chapman *et al.,* 1992). They fall to the ground under the parent tree when they are ripe and are eaten by elephants, which disperse the seeds over great distances (Stoner *et al.*, 2007). Dawe (1906) found that some seeds pass through the gut of elephants undigested, leaving them cleared of fruit pulp, but still intact. It was suspected that passage through an elephant weakens the seed coat, increasing the probability of seed germination. Such a relationship exists between the Marula tree (*Sclerocarya birrea*) and the African elephant. The lignified endocarp of a fruit contains several seeds, each within its own locule, sealed by an operculum. Many animal species eat the Marula fruit, but Midgley *et al.* (2012) propose that African elephants are the legitimate primary dispersers of the seeds, because mastication by elephants physically loosens the opercula, which stimulates germination. No other frugivores have the jaw strength to do so. Midgley *et al* (2012) suspect that through mastication, elephants exert a force of about 2.7kN. Chapman *et al.* (1992) found that the passage of *B. wilsoniana* seeds through elephants significantly increases the probability of germination, but the mechanism facilitating germination was not described. In the Kibale Forest Reserve, in western Uganda, Chapman *et al.*, (1992) and Cochrane (2003) found that where elephants were rare, few seedlings were found, and only under conspecific adult trees, but where elephants were common, many *B. wilsoniana* seedlings were found growing some distance from large conspecific trees. They also found that very few of the fruit under parent trees appeared to be capable of germination and survival.

The long term maintenance of populations of tree species such as *Sclerocarya birrea* and *Balanites wilsoniana* may depend, in part, on the survival of the animals that facilitate dispersal. Therefore, determining the existence of such tree-animal disperser relationships is important. Understanding the extent to which *B. maughamii* trees depend on animals for dispersal and continued population regeneration, will also provide insight into the current spatial pattern and geographic range of the species.

The aim of this section in the chapter is to analyse the role that elephants play, both as fruit consumers and seed dispersers. It is hypothesised that germination is facilitated when seeds pass through an elephant. The mechanism hypothesised, is that the hard endocarp around the seed is physically compromised rather than chemically dissolved. Elephants exert a forward and horizontal shearing force during mastication and apply a grinding force by moving the broad surfaces of the teeth, with roughly parallel transverse enamel ridges, over one another (Maglio, 1972). This rolling, grinding action would be sufficient to split the endocarp and remove the fruit pulp without crushing the seed. To test the germination hypothesis, the force required to split the apical flanges, but not crush the seed, will be determined and seeds will be crushed with this force to mimic an elephant bite. These split seeds, along with seeds from elephant dung and seeds from under the parent tree, will be planted and germination rates will be noted.

Methods

B. maughamii fruit were collected under trees in and around the Skukuza staff village and fed to elephants at an elephant sanctuary. The elephants were conditioned to follow instructions, and after being encouraged to try the fruit, they consumed fruit willingly (Appendix: Image 5). Six elephants were fed 60 fruit each and, for the next 48 hours, most of the dung was collected. Any whole seeds found were collected for germination experiments.

B. maughamii fruit collected under trees were taken back to the Department of Mechanical Engineering at the University of Cape Town (UCT), South Africa, where a Zwick (Zwick, Germany) 1484 200-kN load cell was used to determine the compressive force required to split the flanges, but not crush the endocarp and damage the seed. A seed cleared of fruit was placed on the lower surface of the machine, and the head of the machine was lowered until it was against the seed. The equipment then applied a steadily increasing pressure until there was an abrupt change in displacement of the seed. The force at that point was recorded. This was done for 20 seeds from a 2011 batch and 10 from the 2012 batch, and graphs showing Force (N) plotted against displacement (mm) were produced. The average force required to split the flanges was calculated and 80% of that force was then applied to 20 seeds in the 2011 batch. For the 2011 batch, 20 seeds were also crushed to breaking point. The force required to split flanges was then compared with the force Midgley *et al.* (2012) estimated for the bite of an elephant.

For germination trials, 50 elephant dung seeds, 20 seeds crushed to 80% of the break force, 20 seeds crushed to breaking, 20 seeds with fruit intact, and 40 seeds cleared of fruit, were planted from a 2011 batch. The germination trial was continued in a greenhouse for 74 days, from the 13th of August 2012 to the 25th of October 2012. Seeds were planted in 20 cm x 10 cm trays, in river sand, and watered daily.

Results

No crushed or compressed seeds in the treatment group germinated, despite being crushed to mimic the bite force of an elephant. Many seeds collected from elephant dung germinated, and did so more rapidly than seeds in the control group, with fruit cleaned off.

Table 3.1.1: Germination trials with seeds found in 2011, in the Skukuza area of the KNP, South Africa.

	Treatment			Control	
	elephant dung	crushed to crack	compressed to 80% of break force	flesh cleaned off	fruit intact
Germinated	39/50	0/20	0/25	3/40	0/20
Proportions (%)	78	0	0	10	0

The mean force (N) ± SD required for splitting apical flanges but keep the seed intact was 1950 ± 320N for 2011 and 2012 seeds combined.

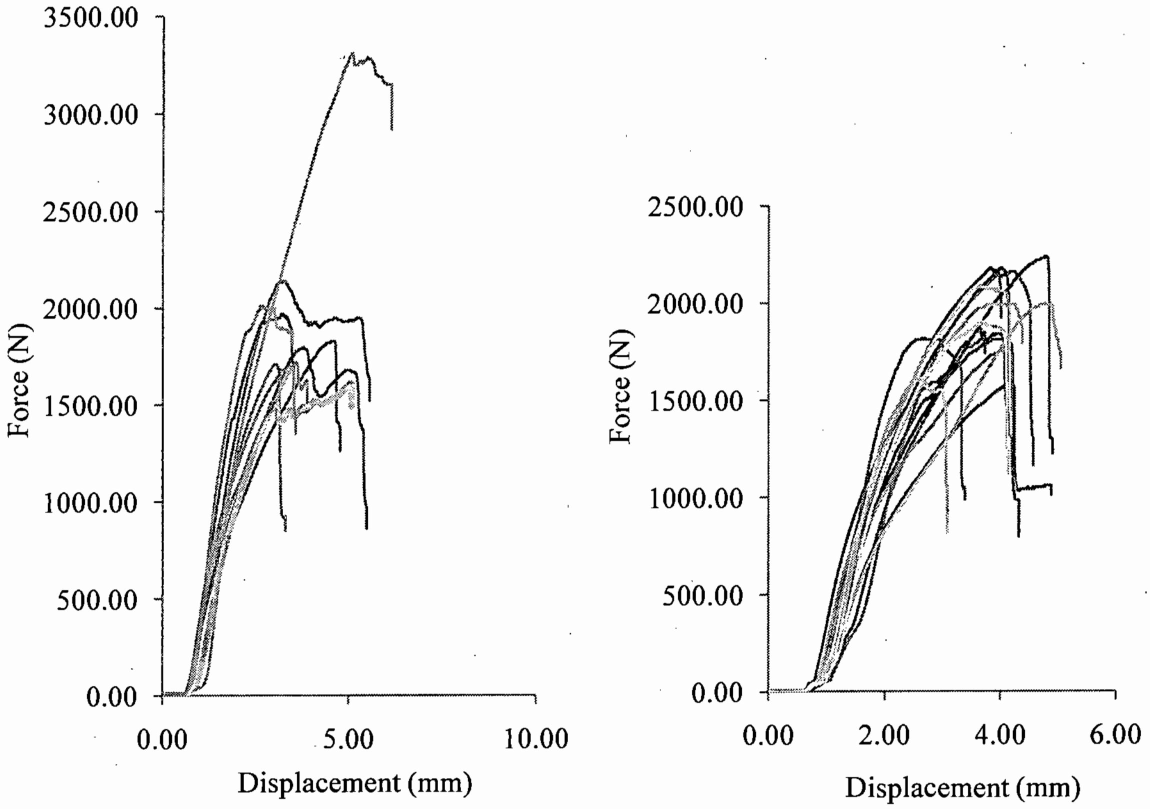


Figure 3.1.1: Force (N) and displacement (mm) of seeds compressed to the point where apical flanges split, but the seed remained intact. Left: 2012 seeds. Right: 2011 seeds.

Discussion

B. maughamii endocarps are extremely strong, but during mastication, elephants are able to crush through them, destroying seeds entirely. Despite this, many seeds survive, because elephants chew the fruit by grinding and rolling them, which removes the fruit pulp, but leaves the endocarp intact. Seeds that pass though elephants germinate more successfully and rapidly than seeds collected under parent trees, and in the absence of elephants, recruitment is limited. Seeds do not receive a germination cue, and are not moved to favourable microsites, leaving them vulnerable to predation.

Seeds can resist almost 2000 N of force on average, before the endocarp cracks, yet elephants are capable of destroying seeds entirely during mastication. The way in which elephants feed typically prevents this, because most fruit are ground between teeth with a rolling action to remove pulp, and then the seeds are swallowed whole, along with the pulp. Seeds are then excreted intact in the dung. Germination is facilitated when seeds pass through elephants, but whether mastication alone is the most important germination cue is uncertain, as seeds crushed to mimic an elephant bite did not germinate. Trials may have to be repeated, to provide more conclusive support for the mastication hypothesis.

Chapman *et al.* (1992) found that in the Kibale forest in Uganda, where elephants were rare, few *Balanites* seedlings were found, and were only under conspecific adult trees. A similar situation was noted in the KNP exclosure. Where elephants were absent, seedlings were absent, so evidence suggests that elephants play an important role in recruitment. Not only do elephants disperse seeds over great distances, away from conspecific parent trees (Stoner *et al.*, 2007), they increase the probability and rate of germination. Evidence suggests that where elephants are absent, the *B. maughamii* population experiences recruitment bottlenecks due to two hurdles: 1) seed dispersal limitation because the dispersal mutualist is absent, and

2) germination limitation due to lack of appropriate germination cues, supplied by the elephants.

According to Bond (1994), species which cannot resprout (seed limited) are the most likely to face extinction in the face of mutualist extinctions. Traits that lower the risk of extinction include: 1) vegetative propagation, 2) long life spans and 3) the capacity to vegetatively resprout after disturbances. The risk of extinction is increased if a mutualism fails in a species where dispersal is obligatory to cue germination (Bond, 1994). Such cues could involve the disperser transporting a seed to a safe site where it evades predation, or as appears to be the case with *Balanites maughamii* and *Sclerocarya birrea*, to break open the hard endocarp around the seed, facilitating germination.

There are consequences when dispersal mutualisms fail. During the Pleistocene era, large mammals such as gomphotheres, ground sloths, glyptodonts and equids (mixotoxodon and toxodon) were common in the neotropics, and Janzen and Martin (1982) suggest that through frugivory, they were important dispersers of seeds. Plants with megafaunal fruit could have had their large seeds dispersed over great distances by the now extinct frugivores (which included at least 13 genera with body masses of over 1000 Kg). Utilizing these dispersers, plants could escape the trade-off between seed size and dispersal distance, but for many species, this trade off left them ecologically anachronistic when the major dispersers disappeaedr. “Anachronic dispersal syndromes”, are defined as “dispersal syndromes with fruit traits and phenological patterns best explained by interactions with extinct animals”.

It is important to understand the demographies of trees, in order to determine whether they are at risk of becoming ecologically anachronistic. That way, species which are most at risk can receive the most focus in terms of conservation efforts. However, determining the risk that the *B. maughamii* population faces is complicated by the fact that risks change when being considered over the short and long term. *B. maughamii* relies on elephants to disperse seeds and provide a germination cue, so in the absence of elephants, recruitment may be greatly limited. To compensate for limited dispersal and germination, the trees are able to reproduce vegetatively, which fills the "recruitment gap" and maintains the population. This is certainly advantageous for short-term survival of the population, but over the long term, Gene flow between conspecific populations is important for maintaining genetic diversity (Levin, 1982) so limited sexual reproduction can lead to low genetic variability, the accumulation of deleterious mutations, and infertility (Dorken & Eckert, 2001).

Over the short term, *B. maughamii* populations in the KNP are demographically resilient, and the long term risk of limited sexual reproduction due to a recruitment bottleneck will only really become a problem if elephants are absent. There seems little chance of elephants in the KNP going extinct, with the current population well over the KNP's carrying capacity. *B. maughamii* populations are more likely to face a recruitment bottleneck as the result of extensive and increasing elephant utilisation of intermediate sized trees that have not reached sexual maturity. If fewer trees are producing seeds, then seed set becomes smaller. Fewer seedlings survive and eventually the same problem of limited sexual reproduction, leads to low genetic variability.

Section 2

The role of rodents and the fate of seeds

Post-dispersal seed removal may end in seed predation, but can also represent the next step in a multistep seed dispersal process (Vander Wall *et al.*, 2005). In the past, seed removal was often considered a proxy for seed predation, and the fate of seeds were not considered further (see vander Wall *et al.,* 2005 for examples). As a result, the importance of secondary dispersal was often underestimated or overlooked entirely. In the 1980s, studies began to indicate the importance of secondary seed dispersal in plant demography (Chambers & MacMahon, 1994; Stoner *et al.*, 2007; vander Wall, *et al.*, 2005). Chambers and MacMahon (1994) believe that the effect it has in shaping plant communities is as significant as the primary dispersal phase. Primary dispersal typically ensures the colonization of new patches, and predator escape. Secondary dispersal delivers seeds to microsites where seedlings are likely to establish successfully (Vander Wall *et al.*, 2005).

The aim of this part of the study is to determine the role of small mammals as potential secondary seed dispersers or predators, in a *B. maughamii* population.

Methods

Cafeteria experiments

Whole seeds that had been cleaned of fruit by natural processes were collected under actively fruiting trees in and around the Skukuza staff village. Each seed had a small hole drilled into the endocarp, and a rare earth magnet was wedged tightly into the hole. These were used in cafeteria experiments. In a later repetition of the same trials, seeds were once again collected, and each seed had a 10 centimetre fluorescent string glued to it, and was then dipped in UV powder. Fluorescent materials were used to aid in finding seeds after dispersal, and both the glue and the powder were non-toxic, to avoid harming potential seed predators in case of ingestion.

Six sites were selected in the vicinity of the Skukuza staff village, near the golf course and in adjacent areas with natural vegetation, where *B. Maughamii* trees could be found (Figure 3.1.2). At each site, a motion-detecting camera (Bushnell) was set up about one metre off the ground, secured to the trunk of a *B. maughamii* tree, and angled downwards. Ten prepared seeds were then laid out in the focal view of the camera, and the cameras were turned on 24 hours a day. Each camera was set to record 30-second video clips when triggered, and from the video footage, it was possible to record the number of animal visitations, number of seeds removed, seeds predated in situ, and the time spent at each seed station.

Sherman traps were placed at sites two, three, four and six, where rodent activity had been observed on previous camera footage. The traps were placed equidistantly in two concentric circles, at a five and ten meter radius from the focal *B. maughamii* tree. The traps were set out between four and six in the evening, baited with a mixture of peanut butter and oats, and collected between eight and nine the next morning. To assess whether the rodent species observed removing seeds in the video clips was a scatter- or larder-hoarder, a 20 meter radius surrounding the focal *B. maughamii* tree was scanned using a magnetometer as well as a UV torch at night. The magnetometer is effective at locating seeds buried to a depth of four centimetres (Midgley *et al.* 2012). The depth buried, and distance from the focal tree was recorded for any located seed, and where evidence of a seed in a burrow was found, cameras were set up around the burrow, and later the burrow was excavated to recover seeds.

Analysis

Camera footage was analyzed by calculating the number of visits with and without seed action, and proportion of visiting species that interacted with seeds was tabulated, along with the overall time each species spent with the seeds. The proportion of visiting species that interacted with seeds, either by eating then *in situ* or by removing them, was analysed.

Figure 3.2.1: The Skukuza area of the Kruger National Park, Mpumalanga, South Africa. Camera sites are indicated with numbers 1 – 6. The GPS locations are: 1) S. 24.99985 E. 31.57467 2) S. 24.98740 E. 31.57410 3) S. 24.98802 E. 31.57447 4) S. 24.98238 E. 31.58068 5) S. 24.99119 E. 31.60697 6) S. 24.98408 E. 31.57848

Results

The camera traps revealed that seeds from sites two, three, four and six were removed by *Tragelaphus scriptus* (bushbuck), *Loxodonta africana* (African elephant), *Hystrix africaeaustralis* (porcupine), *Aepyceros melampus* (impala), and *Tatera leucogaster* (bushveld gerbil). Two bushveld gerbils were caught in traps at sites three and four, confirming species identity (Appendix: Image 6). Impalas and bushveld gerbils were by far the most common visitors, but where more than half the gerbils interacted with seeds, very few impalas did. Only two elephants were observed visiting seeds, but in both cases, interacted with the seeds, and most porcupine visits involved interaction with seeds. Porcupines spent the longest time with the seeds, because they ate the seeds *in situ*. Gerbils on the other hand, visited frequently but spent much less time on site, because they removed most seeds. Bushbuck, elephants and impalas only consumed low numbers of seeds *in situ.* Of all the seeds used in the cafeteria experiments, the fate of 60 could be determined conclusively. 27 seeds were eaten *in situ, and* 33 seeds were removed.

Table 3.2.1: The number of species observed to visit seeds and interact with seeds, the proportion of visitors that interacted with seeds and the total time spent interacting with seeds.

Species	Total visits	Visits with seed action	Proportion that interacted with seeds	Time spent with seeds (mins)
Bushbuck	3	1	33.3	0.25
Elephant	2	2	100.0	2.92
Porcupine	9	6	66.7	15.05
Impala	111	7	6.3	7.13
Bushveld gerbil	57	33	57.9	8.00

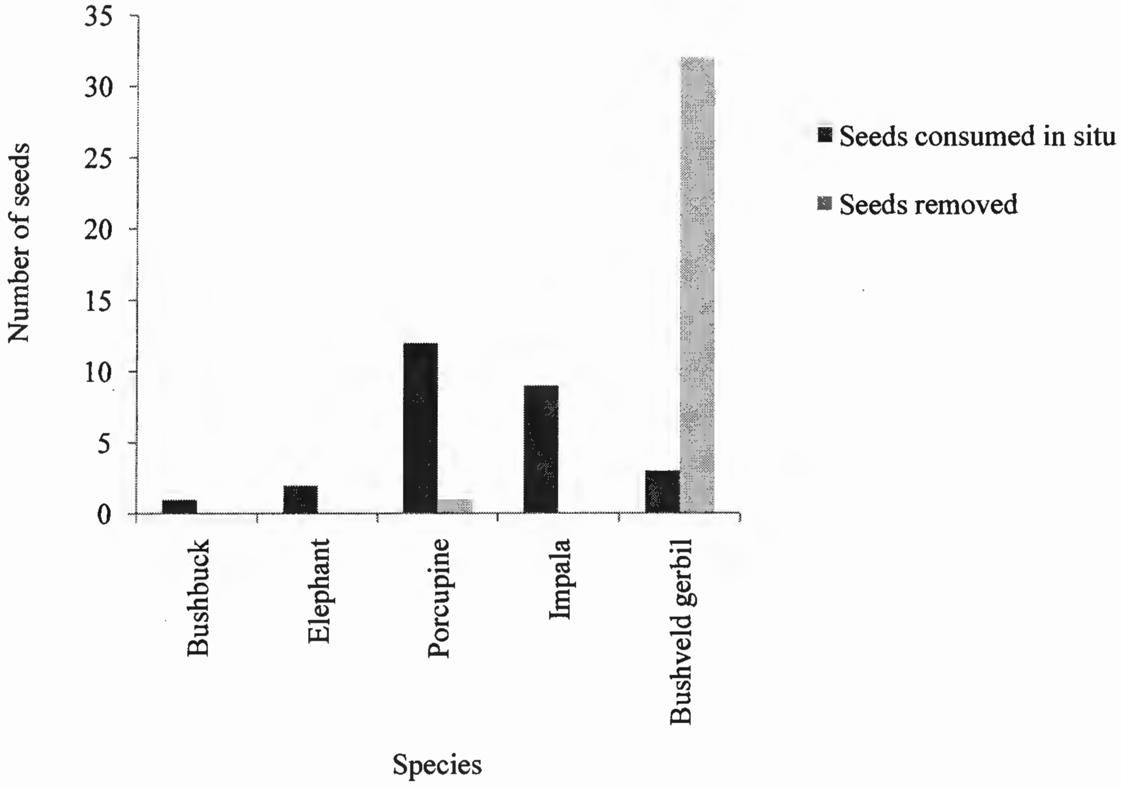


Figure 3.2.2: The number of seeds that bushbuck, elephants, porcupines, impalas and bushveld gerbils were observed to interact with, on camera, either by eating seeds *in situ* or by removing them.

No scatter-hoarded seeds were located with the magnetometer, UV string or fluorescent powder. A single fluorescent string was found at the entrance of a burrow, and consequently, five *T. leucogaster* holes at sites 2, 3 and 4 (found within 10 m of the focal tree) were excavated to locate hoarded seeds, but no seeds were found. At site six, 186 seeds were found in a nest at the bottom of an artificial drainage channel. Of the 186 seeds in the nest, 75 percent had been consumed (Appendix: Image 7). The footage from the camera traps set around the nest in the drainage channel at site six, showed clearly that the nest belonged to two resident bushveld gerbils. They spent a large portion of their time walking on the seed pile, periodically sniffing and nibbling at seeds.

Discussion

A number of non-mutualistic frugivores take advantage of the food resource in the fruit and seeds of *B. maughamii* trees, including bushbuck, elephants, porcupines, impala and bushveld gerbils (Table 3.2.1). Where some species purposefully visit seeds and interact with them (elephants, porcupines and gerbils), others happen to come across the seeds, and sometimes interact with them (bushbuck and impala). With cameras, it was possible to follow the fate of the seeds that bushbuck, elephants, porcupines and impala interacted with, and it can be concluded that they are all seed predators. Porcupines in particular, consumed many seeds *in situ* (Figure 3.2.2), taking some time to gnaw through the tough endocarps to reach the seeds. Besides bushveld gerbils, which quickly removed almost all the seeds they could find (Figure 3.2.2), no other animals observed could be considered significant seed dispersers.

In the KNP, rodents do not hibernate or aestivate during times of food shortage (Pettifer & Nel, 1976), so hoarding (the transport and storing of food) is of great importance to ensure survival. *B. maughamii* seeds are large and ideal for hoarding, because like most large seeds, they have good "keeping quality", more mass, and therefore more calorific content per unit than small seeds. Bushveld gerbils were observed removing many *B. maughamii* seeds, and it seemed likely that they play a role in secondary dispersal. For secondary seed dispersal to occur successfully though, seeds must be moved to favourable microsites, suitable for germination (Vander Wall *et al.*, 2005). Scatter-hoarding refers to the storage of individual food items in separate locations within the animal's home range (Pettifer & Nel, 1976) and is the only process where seeds really stand a chance of surviving and germinating, because not all caches are recovered by rodents, and seeds are buried close to the surface. In the case of larder-hoarding, food is stored in the nest or burrow of an animal (Pettifer & Nel, 1976) so even if they survive predation, the seeds are often buried too deep to germinate (Janzen, 1986) No seeds that gerbils were recorded moving, were relocated, which makes it impossible to conclusively quantify seed predation and survival. However, with 75 percent of seeds in the drainage channel nest of two resident gerbils being consumed, and the small proportion of seeds that survived, being in an unfavourable microsite for germination, it is likely gerbils are seed predators too. Pettifer and Nel (1976) attempted to study the hoarding behavior of bushveld gerbils (*Tatera leucogaster*) in captivity. Gerbils were never observed to larder- or scatter-hoard, but did occasionally carry a seed into the provided nest box, sometimes abandoning it half-eaten, in the nesting material. In almost all cases, gerbils were observed to kick sand over seed piles during or after feeding, until seeds were completely covered, but this was not considered to be scatter- or larder- hoarding.

In *B. maughamii* populations, a recruitment bottleneck exists, and the hurdles identified thus far, are seed dispersal limitations and germination limitations in the absence of elephants, but in all populations, whether elephants are present or not, another hurdle affects recruitment, and it is seed limitation due to seed predation pre- and post- dispersal.

CONCLUSION

B. maughamii trees are heavily impacted by elephants, which strip bark selectively off the largest trees, increasing their susceptibility to fire damage. *B. maughamii* trees are weakly defended against fire, with limited recovery of bark over wounds, and extremely thin bark. Elephants also over-utilise the intermediate size classes, which experience extensive breakage, keeping many trees trapped in non-reproductive stages. A potential consequence thereof is that seed production may be reduced, resulting in infrequent recruitment of seedlings. *B. maughamii* trees can however survive breaking, stripping and toppling by elephants, as well as topkill by fires, because they resprout vigorously in response to damage. Vegetative reproduction buffers the populations from the infrequent recruitment of seedlings, and facilitates the maintenance of populations over the short term.

The demographic profiles of the *B. Maughamii* populations in the Skukuza supersite and exclosure, indicated that recruitment and transition through size classes were successful, due to the large proportions of trees in the smallest size classes. Yet when regeneration-individuals are excavated it became clear that the population in the exclosure was experiencing a severe recruitment bottleneck, because no seedlings were found. Root suckers functionally replace seedlings in the large mammal exclosure, but are not genetically new individuals.

The only difference between the sites outside and inside the exclosure is the presence of large mammals, and in fact, *B. maughamii* relies on elephants to disperse seeds, moving them away from conspecific parent trees, and providing a germination cue. Many seeds taken from elephant dung germinated rapidly. Seeds are extremely strong, and can resist almost 2000 N of force on average, so elephant mastication likely facilitates germination, but whether mastication alone is the most important germination cue is uncertain, as seeds crushed to mimic an elephant bite did not germinate. In the absence of elephants, recruitment may be greatly limited.

In all populations, whether elephants are present or not, another hurdle affects recruitment, and it is seed limitation due to seed predation pre- and post- dispersal. When animals move seeds without consuming and killing them, secondary seed dispersal can potentially occur successfully, and *B. maughamii* seeds are large and ideal for hoarding, because they have good "keeping quality". Cafeteria experiments revealed that bushveld gerbils (*Tatera leucogaster*) were removing many seeds, potentially scatter-hoarding them. However, when following the fate of removed seeds, it became clear that bushveld gerbils are seed predators, which carry food into their nests and burrows, but do not scatter- or larder-hoard. They therefore play no significant role in the secondary dispersal of *B. maughamii seeds.* Extensive predation adds to the recruitment bottleneck

Over the short term, *B. maughamii* populations in the KNP are demographically resilient, because the trees reproduce vegetatively to compensate for limited dispersal and germination. This fills the "recruitment gap" and maintains the population. Over the long term, however, limited sexual reproduction can lead to low genetic variability, the accumulation of deleterious mutations, and infertility. .In the KNP, the long term risk of limited sexual reproduction due to a recruitment bottleneck will only really become a problem for B. maughamii if elephants are absent. There seems little chance of elephants in the KNP going extinct, with the current population well over the carrying capacity of the KNP, so *B. maughamii* populations in the KNP are more likely to face a recruitment bottleneck as the result of extensive and increasing elephant utilisation of intermediate sized trees that have not reached sexual maturity. If fewer trees are producing seeds, then seed set becomes smaller, so fewer seedlings survive, and eventually, the same problem of limited sexual reproduction, leads to low genetic variability.

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Appendix

Image 1: ***B. maughamii*** **seed with 5 apical flanges.**

Image 2: Ramets.

Image 3: Ramets produced by large adult trees.

Image 4: Left: gulliver. Right: excavated seedlings.

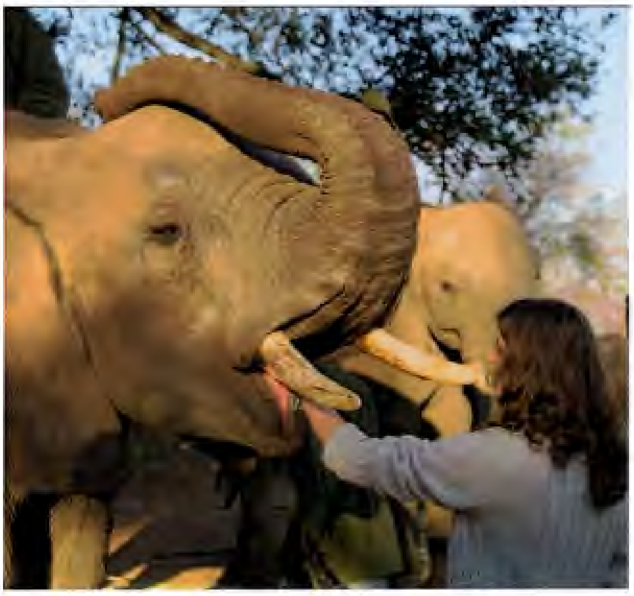

Image 5: *B. maughamii* seeds being fed to an elephant.

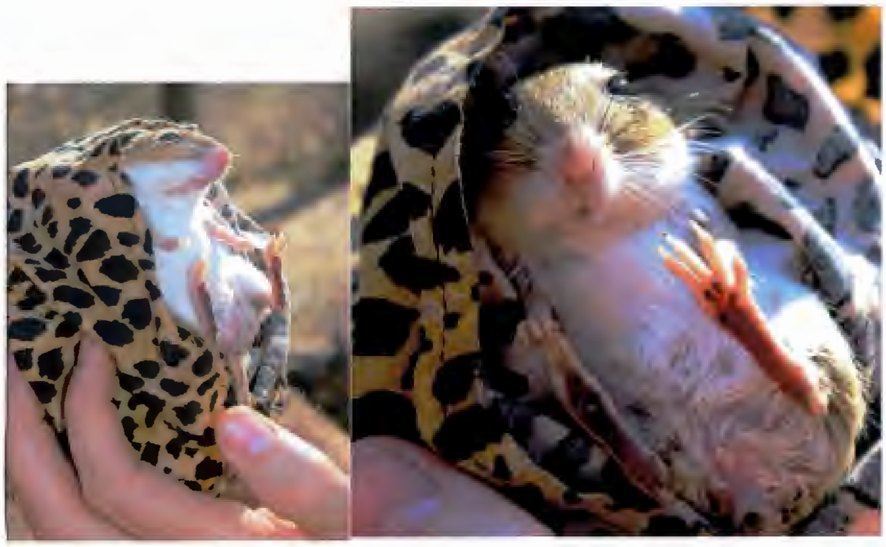

Image 6: *Tatera leucogaster* caught in a Sherman trap at site 4.

Image 7: *Tatera leucogaster* nest in a drainage basin. The majority of hoarded seeds within the nest were consumed.