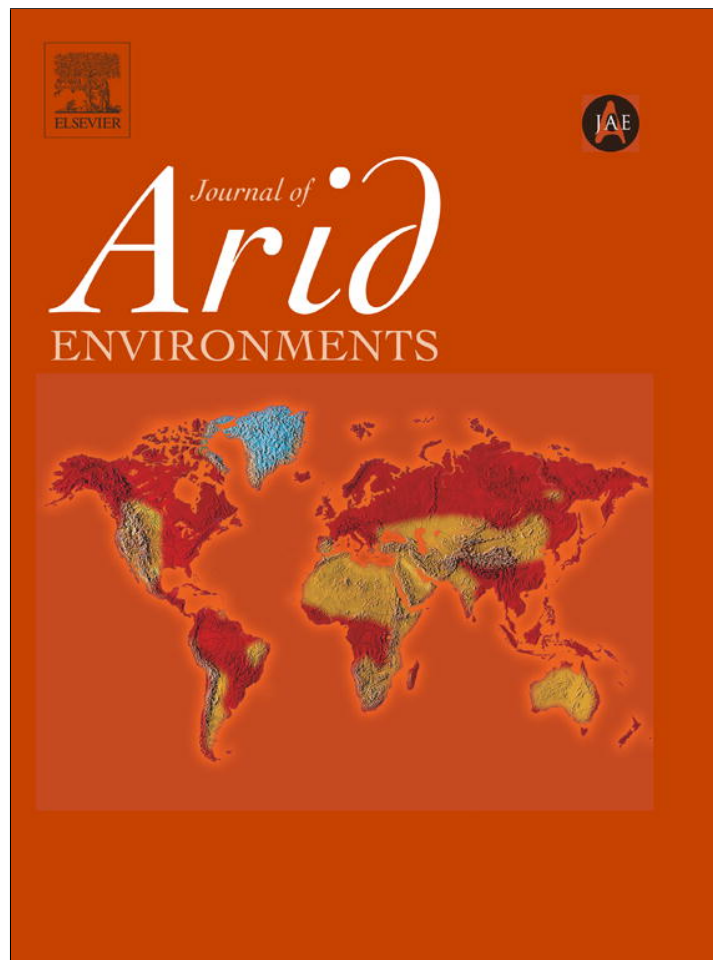


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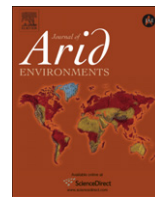
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## Where are the young baobabs? Factors affecting regeneration of *Adansonia digitata* L. in a communally managed region of southern Africa

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## ABSTRACT

Large baobabs are prominent in many African savannas, but the apparent lack of young trees suggests that recruitment is limited and possibly episodic. This study aims to determine if recruitment was seed or establishment (microsite) limited. From five annual seed crops, baobab seed consistently exhibits high viability (>89%) and a field trial shows they form persistent soil seed banks. Seed production is substantial ( $5500 \pm 2334$  seed/ha) and thus recruitment does not appear to be seed limited. In closed plots (excluding livestock) 6.33% of seeds emerged after  $328 \pm 28$  (mean  $\pm$  SE) days and of these 94.4% died within  $21 \pm 5$  days of moisture stress and insect browsing. In open plots (exposed to livestock) 2% of seeds emerged after  $377 \pm 5$  days and all died within  $12 \pm 5$  days from goat browsing. Planted sapling survival in closed plots (65%) was much higher than in open plots (10%), with an average time to death of  $10.45 \pm 0.97$  and  $4.33 \pm 0.45$  months respectively. Hence seedling establishment is poor in response to infrequent rainfall and survival of seedlings and saplings, that do manage to persist, is further hampered by high livestock numbers. Recruitment is thus microsite limited in communal lands. Planting and protection from livestock is required to overcome the recruitment bottleneck.

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## 1. Introduction

Baobabs (*Adansonia digitata* L.) are large, distinctive, iconic trees, and the only species of the genus that is found, occurring naturally, on the African continent (Baum, 1995a). Across the continent, baobab trees are utilized for a wide variety of products including food, fibre and medicine and in this way provide an invaluable resource to many rural people (Sidibe and Williams, 2002; Wickens and Lowe, 2008). It is thus essential that the resource is managed sustainably to ensure its long-term persistence and productivity.

Poor baobab recruitment is commonly reported for many landscapes across Africa with many populations having bell-shaped or positively skewed stem diameter size-class distribution (SCD) curves (Assogbadjo et al., 2005; Chirwa et al., 2006; Dhillion and Gustad, 2004; Edkins et al., 2007; Hofmeyr, 2003; Venter and Witkowski, 2010). In surveys done by Chirwa et al. (2006) in Malawi, Hofmeyr (2003) in the Kruger National Park and Venter

and Witkowski (2010) in South Africa, no baobab seedlings were found. In some West African villages baobab seedlings are planted and actively protected from livestock, but outside villages there is poor recruitment (Assogbadjo et al., 2005; Dhillion and Gustad, 2004; Schumann et al., 2012). In South Africa, Venter (2012) found fewer juvenile and sub-adult (<100 cm dbh) relative to adult baobabs in human-modified areas (villages and fields) than in adjacent more natural areas (plains and rocky outcrops). Here, unlike West Africa, baobab seedlings are not actively planted or protected (Venter and Witkowski, 2012). The apparent lack of young baobabs in many populations has repeatedly led to the often-asked question, “where are the young baobabs?”

A wide range of variables can affect the success of baobab recruitment. Recruitment could be 1) seed limited, i.e. not enough viable seed available; or 2) establishment (microsite) limited, where emerging seedlings do not survive because of external factors associated with its environment (Eriksson and Ehrlén, 1992).

In general annual baobab fruit production is substantial, even though it varies considerably from year to year (Assogbadjo et al., 2005; Venter and Witkowski, 2011). Nonetheless, little is known about the viability and persistence of seeds within field conditions, or the factors that limit seedling establishment (Wilson and

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Witkowski, 1998). Drought, fire and livestock browsing have frequently been mentioned as causes of poor recruitment (Dhillon and Gustad, 2004); while De Smedt et al. (2012) and Cuni Sanchez et al. (2011a, 2011b) have described the mechanisms used by seedlings to cope with drought stress, however no field studies have been done on seedling survival.

Percentage germination of *A. digitata* seeds under nursery conditions ranges from 20 to 57% (Assogbadjo et al., 2010; Danthu et al., 1995). When pre-treated by manual scarification, soaking in sulphuric acid or boiling water, germination can reach 90–100% (Esenowo, 1991; Razanameharizaka et al., 2006). However, in natural conditions germination is described as “extremely poor”, even as low as 0% (De Villiers, 1951). This mismatch between controlled and field results calls for a better understanding of seed fate in the field.

In South Africa, cohorts of baobab trees appear to coincide with good rainfall years and regeneration may only have occurred every 100–150 years (De Villiers, 1951), thus regeneration has been episodic. Venter and Witkowski (2010) reasoned that, as baobabs are long lived trees, reaching at least 1200 years of age (Patrut et al., 2007), populations should survive episodic recruitment even if episodes are separated by many years, even of the order of 100 years. However the environmental context has changed greatly over time as impacts increase within the increasingly human dominated landscapes, particularly in communal lands (Dovie et al., 2005).

The overall objective of the study was to determine whether recruitment was seed limited or microsite limited and how current land management practices affect future persistence. It was predicted that poor recruitment was due to microsite limitation, a result of inadequate moisture and exposure to livestock, rather than seed limitation.

For seed limitation, the following questions were asked:

1. How much seed do baobab populations produce in a season?
2. What proportion of the seed is viable?
3. Do seeds lose viability over time and can they form persistent soil seed banks?

For microsite limitation, the following questions were asked:

4. What is the natural rate of seedling emergence and in the absence of livestock, what are natural seedling survival rates?
5. To what extent does exposure to livestock (goats and cattle) affect seedling and sapling survival rates?
6. Does survival improve with sapling size (one- and three year old) in the absence and in the presence of livestock?

## 2. Materials and methods

### 2.1. Study area

Seed collection and study plots were situated in communally managed land in the Limpopo River valley, commonly known as northern Venda, around 22°50'S and 30°45'E. The study area is bordered by Zimbabwe to the north and the Kruger National Park (KNP) to the east (Fig. 1).

The area lies at an altitude of around 400 m above sea level with gently undulating topography and a narrow sandstone ridge running east–west. Soils are derived from sandstone, basalt and aeolian deposits (Venter, 2012). It is a semi-arid summer rainfall area with a mean annual rainfall of between 334 and 423 mm and a high coefficient of variation (CV = 25–40%) (Schulze, 1997). The area is characterized by hot summers (October–March) and mild winters

(April–September) with mean monthly maximum and minimum temperatures of 39.7 °C and 8.5 °C for December and July respectively (Mucina and Rutherford, 2006). It is a frost free area (Schulze, 1997).

The area falls within the Savanna Biome and more specifically within the Mopane and Lowveld Ecoregions (Mucina and Rutherford, 2006). Baobabs are closely associated with vegetation dominated by *Commiphora*, *Grewia* and *Colophospermum mopane* (Venter, 2012). Wild fires seldom occur because of naturally low fuel load. Wildlife is scarce and elephants are now rare visitors. In neighbouring conservation areas and in rocky outcrops, baboons, which eat the fruit (Venter and Witkowski, 2011), are common.

Management and ownership of the land and its resources is determined by local customs and structures (Venter and Witkowski, 2012). Subsistence agriculture and animal husbandry are the main activities (Fig. 2A). The primary management objective is maximization of livestock numbers, thus stocking densities are high and are far above recommended carrying capacities (Dovie et al., 2006).

### 2.2. Study species

Baobab (*A. digitata*, family Malvaceae, subfamily Bombacoideacea (Baum, 1995b)) fruit are large, woody, indehiscent capsules (Fig. 2B). Seeds, within the fruit, are imbedded in a whitish powdery pulp (Fig. 2B). The seeds are non-endopermatic, i.e. the dominant embryo includes two cotyledons (dicotyledonous) and a hypocotyl root axis. Germination is hypogeal (Baum, 1995b). Soon after germination and within the first three months, seedlings develop simple leaves (Fig. 2D), a short stem and a swollen carrot-like tap root, the latter two function as water storage organs (De Smedt et al., 2012). Young plants, which have survived the first winter dry season are referred to as ‘saplings’ (Fig. 2E). Simple leaves may persist for a number of years with 2- and 3-foliolate leaves starting to develop as early as the second year in some nursery plants and the typical 5–7-foliolate palmate leaves in older plants (Wickens and Lowe, 2008). Saplings shed leaves in winter, which flush again in summer, when plant growth continues. Baobabs are deciduous, bearing leaves and flowers in the summer wet season (Baum, 1995b).

### 2.3. Methods

#### 2.3.1. Seed production

Baobab adult tree density (Venter and Witkowski, 2010) and fruit per adult tree (Venter and Witkowski, 2011) have previously been determined for the study area. The data was reported for different land-use types (plains, rocky outcrops, fields and villages) and for three fruit sizes (Fig. 3A): small ( $\pm 10 \times 5$  cm), medium ( $\pm 15 \times 8$  cm) and large ( $\pm 20 \times 10$  cm), measured as diameter length (stalk to tip) and diameter width (midway between stalk and tip).

Forty five fruit, fifteen from each of the above three fruit size-classes ( $15 \times 3 = 45$ ) were dissected and the number of seed within each fruit counted to calculate the mean number of seed per fruit size-class.

Venter and Witkowski (2011) also found that a large proportion of trees in the study area consistently produced less than five fruit a year; these trees were called poor-producers. Therefore only trees that produce more than 5 fruit a year (producers) were included in the calculation.

For each land-use type and each fruit size separately (which were then summed), seed production was determined as follows:

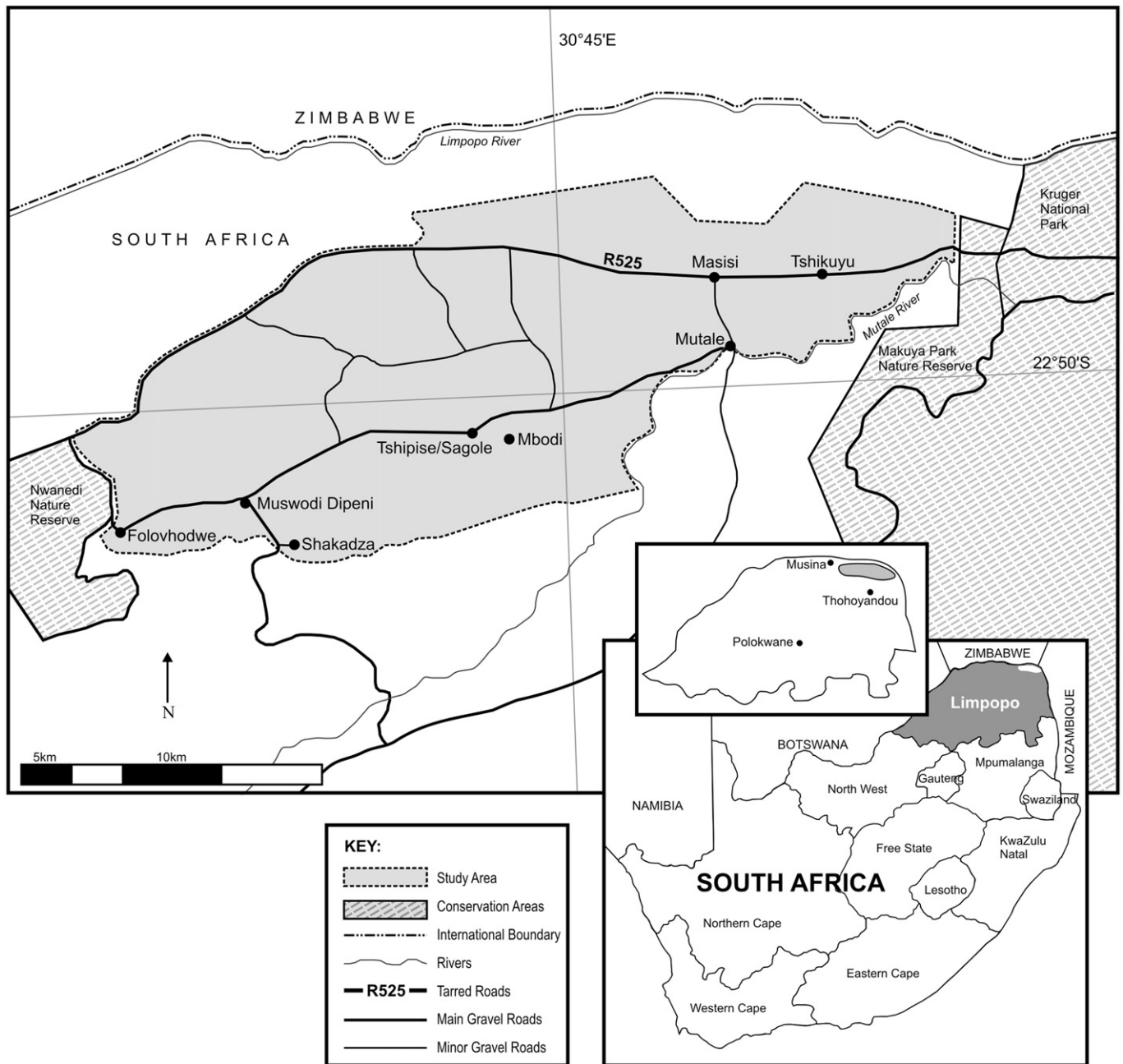


Fig. 1. Map of the northern Venda study area indicating where Muswodipeni, Mbodi and Tshikuyu villages (sites of open and closed plots) are situated.

- $Seed/ha = Adult\ tree\ density \times Proportion\ producers \times Average\ number\ of\ fruit/adult\ tree \times Average\ number\ of\ seed/fruit.$

### 2.3.2. Amount of viable seed produced

The percentage of viable seed for each of the three fruit sizes was determined from a random subsample of 50 seed from each fruit size ( $n = 50 \times 3 = 150$  seeds). The viability of each seed was determined with tetrazolium ( $C_{19}H_{15}ClN_4$ ;  $M = 334.81$  g/mol) following the technique described in MacKay (1972) and Moore (1985). In addition, individual seed mass was measured on a digital scale (0.1 g precision). Once viability of the seed was determined, the predetermined seed mass was allocated to viable and non-viable categories for comparative analysis. If the result showed a difference then viable seeds could easily be screened by mass for future baobab planting programs.

The results of the tetrazolium tests were used to calculate the amount of viable seed produced per hectare for each fruit size separately in each communal land-use type. Results of each fruit size, within each land-use type, were summed to get total viable seed production per hectare per land-use type.

- $Viable\ seed/ha = Seed/ha\ (per\ land-use\ type) \times Percentage\ viable\ seed\ (per\ fruit\ size).$

### 2.3.3. Stored and buried seed viability

Over a six year period from 2005 to 2010 baobab fruit were harvested for commercial purposes from the study area. These fruit were cracked open and seed extracted for oil production. Each year a portion of this seed was put aside and stored in sealed plastic bags in dark, cool ( $\pm 18$  °C) conditions (Fig. 2C). The exact tree and

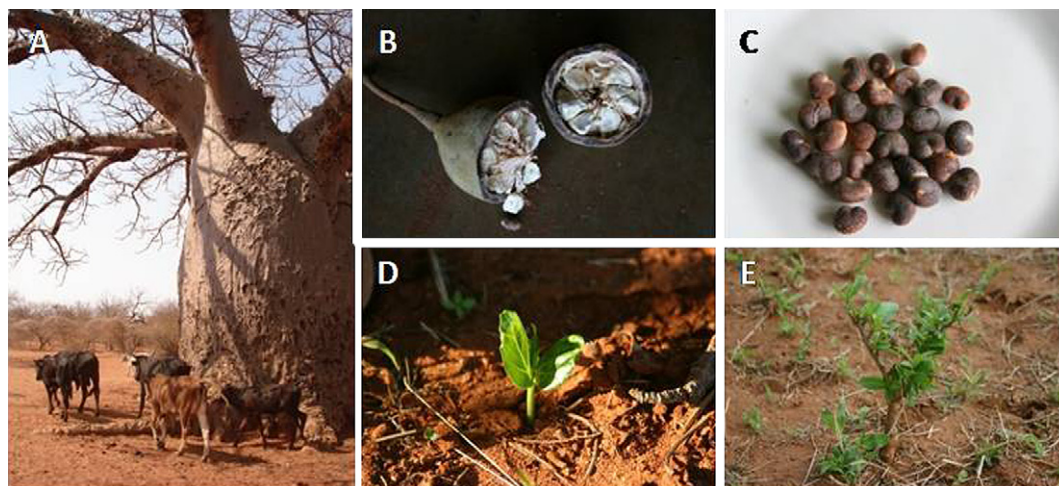


Fig. 2. Photographs of livestock in the study area (A), cut baobab fruit showing pulp (B), stored seed (C), newly emerged seedling (D) and sapling (E).

specific location, from which any one seed came, was not recorded at the time and therefore could not be allocated to land-use type or fruit-size categories used in 2.3.1.

To determine the proportion of viable seed for each year, a sample of one hundred seeds was drawn from each year's store (2005–2009) ( $n = 5 \times 100 = 500$  seeds) and viability tested using tetrazolium (as in 2.3.2). The results were compared between years to determine if there was any change in viability with seed age. Individual seed mass was measured on a digital scale (0.1 g precision) and compared between years. Once it was determined whether the seed was viable or not, the predetermined seed masses were grouped and analysed for differences in mass.

Persistence in the soil was tested by sowing one hundred cleaned (pulp removed) and untreated seed in an enclosed plot of  $5 \times 10$  m in the study area. The plot was cleared of grass and shrubs and enclosed with 12 cm diameter chicken mesh, to exclude livestock. Seeds were planted in a  $30 \text{ cm} \times 30 \text{ cm}$  grid so that they could be individually located. Using a hand trowel, small holes (20 mm deep) were made in the soil into which the seeds ( $\pm 5$  mm in diameter) were sown. After sowing, holes were filled with the soil. No further treatment was applied.

The plot was monitored for seedling emergence every two weeks and rainfall recorded daily. Twenty four months later (two years), the remaining seeds were exhumed, counted, weighed and viability assessed using methods described above (2.3.2). The number of viable seeds recovered would indicate the ability of seed to persist in the soil for two years.

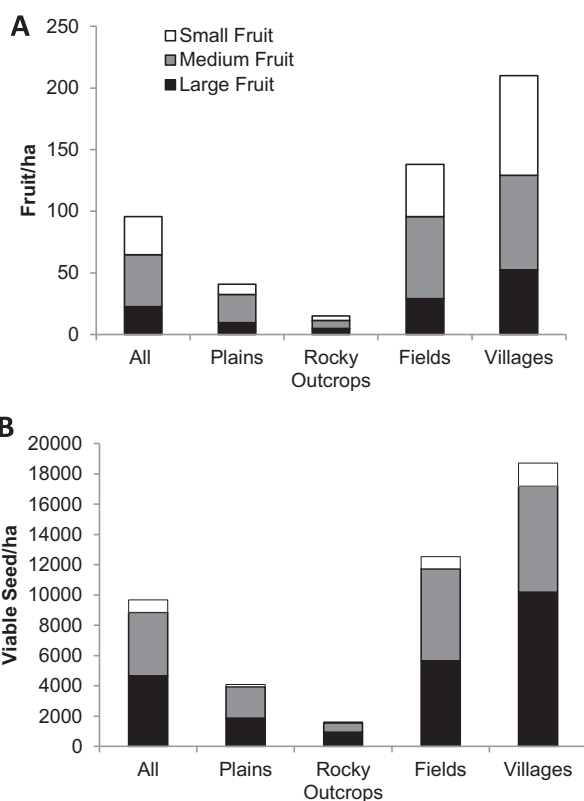


Fig. 3. Three year average baobab fruit production (Venter and Witkowski, 2011; Venter, 2012) (A) and viable seed/ha (B) in communal land-use types.

#### 2.3.4. Seedling emergence and survival in the absence of livestock (closed plots)

In late November 2007, at the beginning of the rainy season, 300 fresh untreated seeds (collected in June/July 2007 from within the study area) were sown in three 'closed' plots with one hundred seeds in each plot ( $100 \times 3 = 300$ ). The closed plots were  $5 \times 10$  m in size and enclosed with 12 cm diameter chicken mesh, to exclude livestock. They were located on the edges of three villages (Muswodi Dipeni, Mbodi and Tshikuyu), where they could easily be reached for monitoring purposes (Fig. 1). Seeds were sown in the same manner as described in 2.3.3. No further treatment was applied. Rainfall was recorded daily.

Plots were visited every one to two weeks for 18 months from November 2007 to April 2009 (i.e. over two growing seasons). At each visit, the position of each seed was noted and checked for seedling emergence. Once seedlings had emerged, they were individually monitored to record insect (usually caterpillar) browse (in the form of leaf and stem damage), moisture stress (wilted leaves and stem) and if the seedling was alive or dead.

#### 2.3.5. Seedling emergence and survival in the presence of livestock (open plots)

At the same time of sowing in 'closed' plots (2.3.4), a further 300 seeds were sown in 'open' plots, 100 in each of three plots ( $100 \times 3 = 300$ ). Each open plot was situated adjacent to the 'closed' plots. These were marked with wooden stakes and not enclosed with mesh (so as to allow livestock to pass freely through the plots).

Sowing and monitoring was done as described in 2.3.3 and 2.3.4. In addition, observations on livestock damage were recorded. Evidence of browsing (torn leaves and torn stem) and trampling (bent or squashed plants) were recorded and the type of animal (goat or cow) that caused the damage was identified by hoof prints in the soil. Mortality resulting from livestock damage was noted and animal type (goat or cow) and the way in which the seedling died (browsed or trampled) was recorded.

#### 2.3.6. Sapling survival in the absence (closed plot) and presence (open plot) of livestock

Sixty 1-year old and sixty 3-year old saplings were planted in the plots described in 2.3.4 and 2.3.5 adjacent to the sown seeds. Ten 1-yr old plants were planted in each of the three 'open' plots (10 × 3) and in each of the three 'closed' plots (10 × 3). Similarly ten 3-yr old plants were planted in each open plot (10 × 3) and each closed plot (10 × 3). Saplings were grown from locally harvested seed and sourced from a nursery within the study area. The local nursery did not keep records on watering regime, but levels of water availability would have exceeded field levels. No additional fertilizers were applied. The plants were in good condition when purchased. Planting took place in November 2007, at the beginning of the rainy season and at the same time as seed sowing (2.3.4, 2.3.5). Holes were dug with a pick and spade to about 20 cm deep and 15 cm in diameter and placed 50 cm apart in rows. Each plant was watered with 2 L of water at planting, no other treatment was applied.

Plots were visited every one to two weeks for 18 months from November 2007 to April 2009 (i.e. over two growing seasons). At each visit, the following was recorded: plant condition (alive or dead); damage (browsed, trampled); agent of damage (goat, cow, insect) and cause of mortality (browsing, trampling, moisture stress, disease). Browsing damage was recorded if leaves had been removed from the stem or if the stem had been severed. Trampling damage was recorded if the stem was bent or the plant was lying horizontal on the ground. Moisture stress was recorded for wilted plants. Hoof prints in the soil were used to identify livestock that had caused damage. Herbivory pattern on the leaves helped distinguish between insect and mammalian browsing.

### 2.4. Data analysis

#### 2.4.1. Seed production

ANOVA followed by Fisher's Least Significant Difference tests (LSD) ( $p < 0.001$ ) was used to test for differences in seed number between small, medium and large sized fruit. To determine the amount of seed produced for the population of baobabs in the study area, the results were used from the formula described in Section 2.3.1.

#### 2.4.2. Amount of viable seed produced

The result of viability testing was used in the formula described in 2.3.2 to determine the amount of viable seed produced in the

study area. In addition, contingency table  $\chi^2$  tested for differences in the proportion of viable seed found between the three fruit sizes and  $t$ -tests were used to test for differences in the mass of viable and non-viable seed.

#### 2.4.3. Stored and buried seed viability

The percentage of viable seed for each of the seed ages was calculated. The number of seed exhumed was given as a percentage of the number of seed that had originally been buried. Similarly the number of viable exhumed seed was given as a percentage of the total number of seed that had been exhumed. Contingency table  $\chi^2$ , ANOVA followed by Fisher's LSD ( $p < 0.001$ ) and  $t$ -tests tested for differences in viability and mass of viable and non-viable seed of different aged seed and seed that had been exhumed.

#### 2.4.4. Seedling emergence and survival in the absence of livestock (closed plots)

For emerging seedlings in closed plots, the percentage of seed that emerged as seedlings and of those, those that survived, were calculated. Days from planting to emergence and days from emergence to death were recorded and mean and SE calculated. Due to very low seedling emergence, the sample size of seedlings was too small to do further statistical analysis or correlations with rainfall. Months in which seedlings emerged and died and causes of death were summarized and presented in a series of figures.

#### 2.4.5. Seedling emergence and survival in the presence of livestock (open plots)

For emerging seedlings in open plots, records and calculations were done as described above (2.4.4).

#### 2.4.6. Sapling survival in the absence (closed plot) and presence (open plot) of livestock

Sapling survival, time to death (months from planting to death) between plots and ages (within plot types) and the interaction between plot and age was compared using  $\chi^2$  contingency tables,  $t$ -tests and a two-way ANOVA respectively. Cause of death and frequency of damage were calculated for each plant and summarized by age and plot type. Sapling survivorship curves and occurrence and frequency of damage were created for plants of different ages in each plot and overlaid with monthly rainfall.

## 3. Results

### 3.1. Seed production

The average annual seed production figure across all land-use types was  $5500 \pm 2338$  seed/ha. Villages and fields had higher densities of baobabs and produced more fruit per tree than plains and rocky outcrops (Venter and Witkowski, 2010, 2011). Thus viable seed production was considerably higher in villages ( $11,139 \pm 1503$  seeds/ha) and fields ( $7458 \pm 1006$  seeds/ha)

**Table 1**

For each fruit-size category the following is given: number of fruit dissected ( $N$ ), seed number/fruit (mean  $\pm$  SE), percentage viable seed, viable seed mass (mean  $\pm$  SE), number of viable seed ( $n$ ) which was used to determine the mean and standard error of the viable seed mass, non-viable seed mass (mean  $\pm$  SE), number of non-viable seed ( $n$ ) which was used to determine the mean and standard error of the non-viable seed mass. Large fruit did not have any non-viable seed, hence no 'n' in the second last column.  $t$ -test compares viable and non-viable seed mass.

Fruit size category	$N$	Seed/fruit	<sup>a</sup> Viable seed (%)	Viable seed mass (g)	$n$ viable seed	Non-viable seed mass (g)	$n$ non-viable seed	$t$ -test $t$
Small Fruit	15	24.40 $\pm$ 1.23 <sup>a</sup>	78	0.41 $\pm$ 0.01 <sup>aB</sup>	39	0.22 $\pm$ 0.02 <sup>aA</sup>	11	10.8847
Medium Fruit	15	96.93 $\pm$ 4.25 <sup>b</sup>	94	0.61 $\pm$ 0.01 <sup>cB</sup>	47	0.43 $\pm$ 0.03 <sup>bA</sup>	3	6.5407
Large Fruit	15	194.47 $\pm$ 6.96 <sup>c</sup>	100	0.54 $\pm$ 0.01 <sup>b</sup>	50	–	–	–

a, b, c indicate significant differences within each column and A, B within rows ( $p < 0.05$ ).

$t$ -test results are between viable and non-viable seed within fruit sizes (A, B).

<sup>a</sup> % viable seed based on a sample of 50 seeds from each fruit size.

**Table 2**  
Percentage of viable seed and mass of viable and non-viable fresh, stored (all from harvested fruit) and persistent seed bank seeds. *t*-test compares viable and non-viable seed mass.

Source of seeds (seed age: years)	Viable seed (%)	Viable seed mass (g)		Non-viable seed mass (g)		<i>t</i> -tests	
		Mean ± SE	<i>n</i>	Mean ± SE	<i>n</i>	<i>t</i>	<i>p</i>
Fruit 2010 (fresh)	91	0.54 ± 0.01 <sup>Cb</sup>	136	0.26 ± 0.03 <sup>Aa</sup>	14	10.8934	<0.001
Fruit 2009 (1 year old)	94	0.48 ± 0.01 <sup>Bb</sup>	94	0.32 ± 0.03 <sup>Aa</sup>	6	4.7411	<0.001
Fruit 2008 (2 years old)	89	0.60 ± 0.01 <sup>Eb</sup>	89	0.35 ± 0.03 <sup>Aa</sup>	11	9.2953	<0.001
Fruit 2007 (3 years old)	99	0.47 ± 0.01 <sup>B</sup>	99	0.50 <sup>A</sup>	1	–	–
Fruit 2006 (4 years old)	98	0.56 ± 0.01 <sup>Db</sup>	98	0.30 ± 0.00 <sup>Aa</sup>	2	3.3991	<0.001
Fruit 2005 (5 years old)	96	0.47 ± 0.01 <sup>Bb</sup>	96	0.32 ± 0.20 <sup>Aa</sup>	4	2.7470	0.007
Seed bank seed (2 years)	97	0.42 ± 0.01 <sup>A</sup>	33	0.40 <sup>A</sup>	1	–	–

A, B, C indicate significant differences within each column (*p* < 0.05) and a, b within rows.

compared to plains (2440 ± 360 seeds/ha) and rocky outcrops (964 ± 153 seeds/ha) (Fig. 3), the latter site was also impacted by heavy baboon fruit damage. The number of seed/fruit increased significantly with each increase in fruit size ( $F_{2,42} = 320.75$ ,  $p < 0.0001$ ) (Table 1).

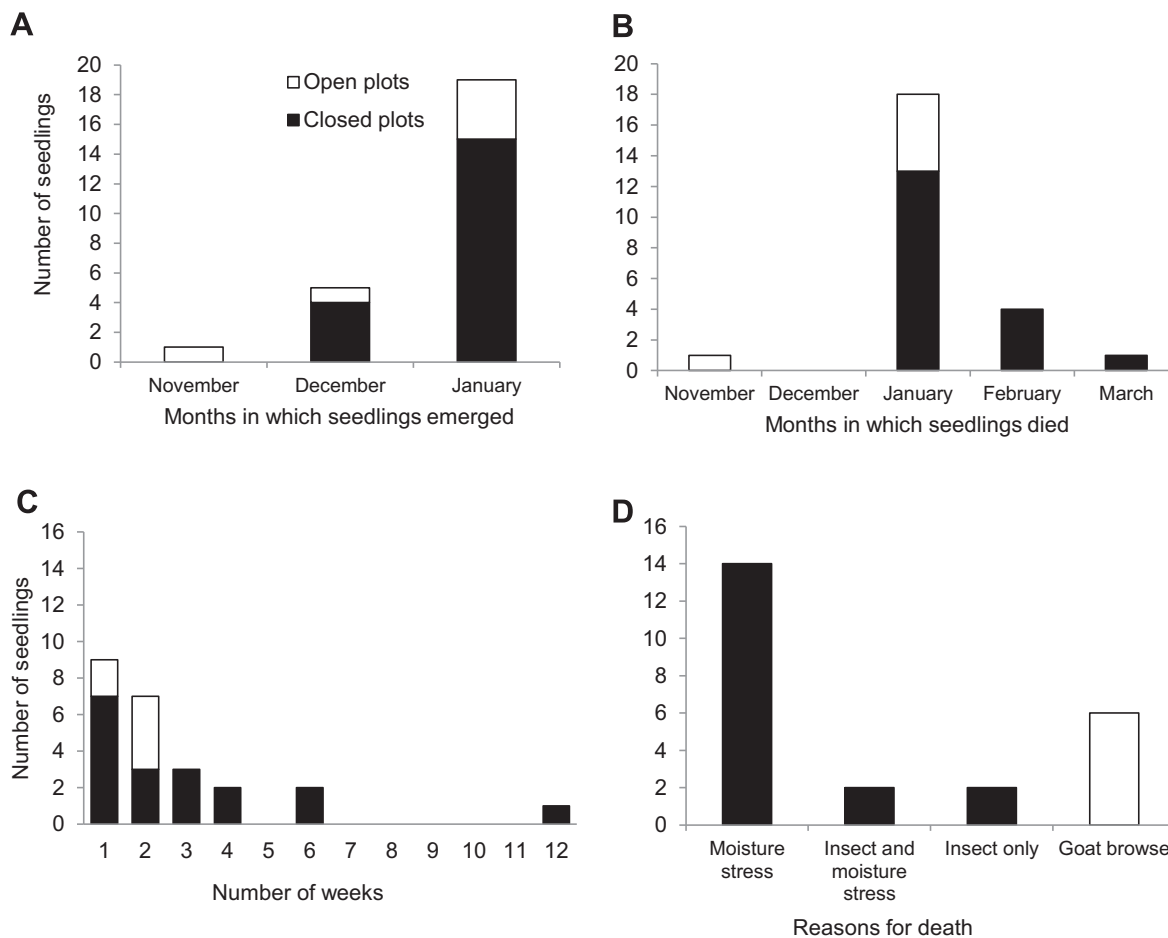
### 3.2. Amount of viable seed produced

Proportion of viable seed and mass of viable seed and non-viable seed increased as fruit size increased ( $\chi^2 = 15.28$ ,  $df = 2$ ,  $p < 0.001$ ;  $F_{2,133} = 105.23$ ,  $p < 0.0001$ ;  $t = -4.56$ ,  $df = 12$ ,  $p < 0.001$ ;  $F_{2,42} = 180.16$ ,  $p < 0.0001$ , respectively) (Table 1). Viable seed was heavier than non-viable seed for both small and medium sized fruit (Table 1).

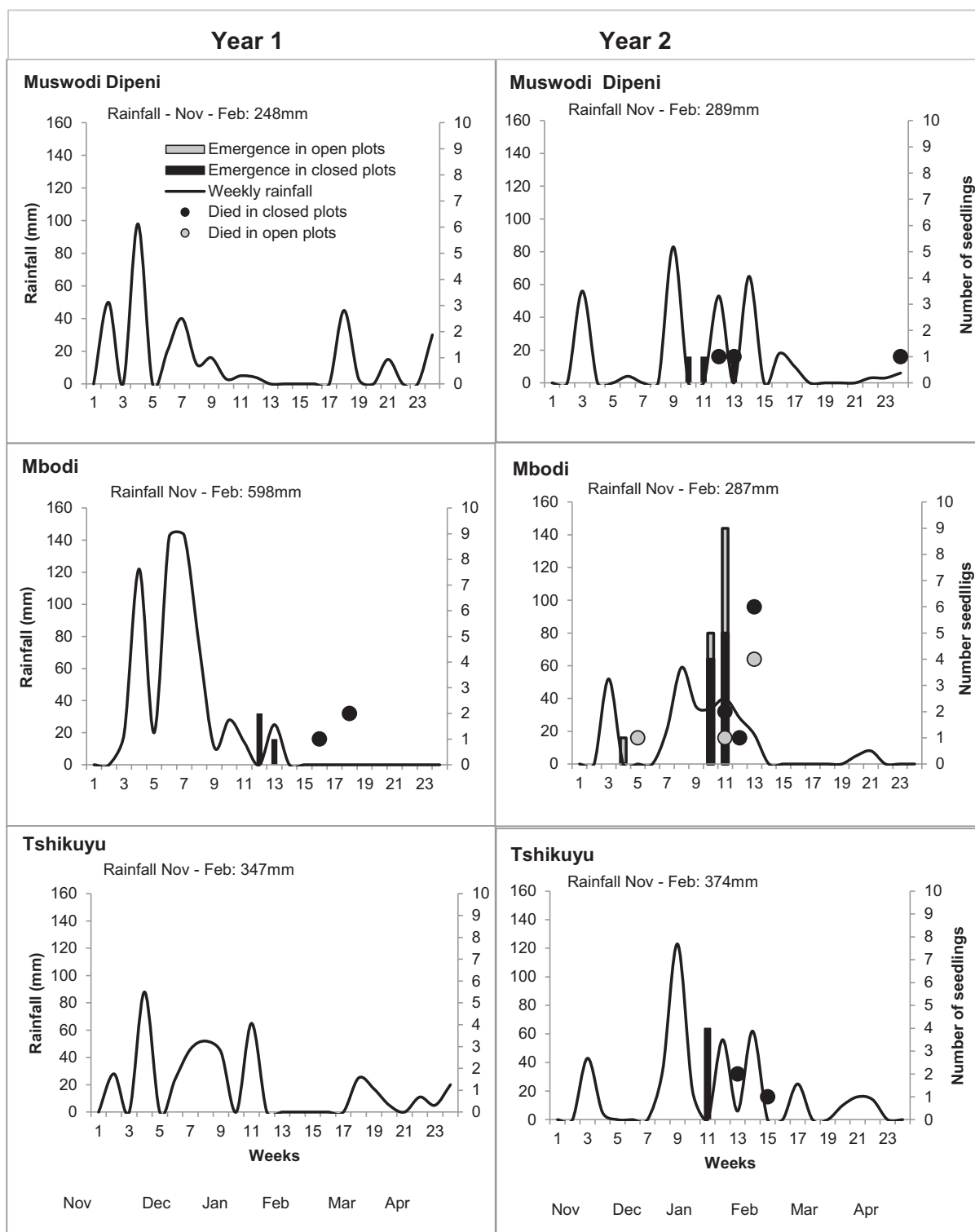
### 3.3. Stored and buried seed viability

The proportion of viable seed differed between seed ages ( $\chi^2 = 15.23$ ,  $df = 5$ ,  $p < 0.001$ ) (Table 2). Across all seed ages, non-viable seed was significantly lighter than viable seed (Table 2). Non-viable seed mass did not differ between seed ages, but viable seed mass did ( $F_{5,32} = 1.64$ ,  $p = 0.1791$ ,  $F_{5,606} = 35.43$ ,  $p < 0.0001$ ). The recorded differences in (a) percentage seed viability and (b) seed mass of viable seeds between the fruit crop years (2005–10) may be due to variation in seed source (sizes of fruit or specific collection area) rather than seed age *per se*.

Thirty four of the one hundred seeds (34%) that were sown were exhumed still intact, of which 97% (Table 2) were viable. Three seeds emerged as seedlings during the trial. The remainder (63%),



**Fig. 4.** Months in which seedlings emerged (A) and died (B), weeks to death (C) and reasons for death (D) in open (white bars) and closed (protected from livestock damage) (black bars) plots.



**Fig. 5.** Weekly rainfall, seedling emergence (bars) and seedling mortality (circles) for closed (black fill) and open plots (grey fill) for 24 weeks over two summer seasons (Year 1: November 2007–April 2008 and Year 2: November 2008–April 2009) at three sites: Muswodi Dipeni, Mbodi and Tshikuyu. No seedlings emerged (or died) at Muswodi Dipeni and Tshikuyu villages, Venda, South Africa in Year 1. Left Y-axis indicates rainfall and right Y-axis indicates all remaining variables.

i.e. seeds that had ‘disappeared’, could have been eaten, decomposed, germinated and died without emerging above the soil surface or emerged and eaten between observation intervals. Viable exhumed seed from the persistent seed bank were significantly lighter in mass than viable stored seed of all seed ages ( $F_{6,637} = 36.32, p < 0.0001$ ) (Table 2).

### 3.4. Seedling emergence and survival in the absence of livestock (closed plots)

In closed plots, 19 seedlings emerged (6.33%) and of these 1 survived (5.56%). Emergence was staggered over two growing seasons ( $328 \pm 28$  days to emergence), but most seeds were



dormant over the first season and emerged in the second. Hence natural germination rates appear to be very slow. Seedlings emergence was limited to December and January (Fig. 4A) and mortality occurred in January, February and March (Fig. 4B). The month of January had the highest seedling emergence and the highest seedling mortality (Fig. 4A and B). Most seedlings died within three weeks of emergence (Fig. 4C) with an average time from emergence to death of  $21 \pm 5$  days. Seedlings in closed plots died mostly from moisture stress and some from insect browsing (mostly caterpillars) (Fig. 4D). Fig. 5 shows weekly rainfall with timing of seedling emergence and mortality and how erratic rainfall, at a critical growing period, may have resulted in moisture stress leading to seedling mortality.

### 3.5. Seedling emergence and survival in the presence of livestock (open plots)

In open plots, 6 seedlings emerged (2%) and none survived (0%). Emergence took place in November, December and January,  $377 \pm 5$  days after planting (Fig. 4A). All seedlings died of goat browsing within two weeks (Fig. 4C and D), with an average time to death of  $12 \pm 1$  days. Fig. 5 shows weekly rainfall and timing of seedling emergence and mortality.

### 3.6. Sapling survival in the absence (closed plot) and presence (open plot) of livestock

#### 3.6.1. The effect of livestock on sapling survival

Results show that saplings that are protected from livestock have a better chance of survival than those exposed to livestock. Sapling survival in closed plots (65%) was significantly higher than in open plots (10%) ( $\chi^2 = 38.72$ ,  $df = 1$ ,  $p < 0.0001$ ) and 'average time to death' of saplings in closed plots was significantly longer ( $10.45 \pm 0.97$  months) than in open plots ( $4.33 \pm 0.45$  months) ( $t = -6.47$ ,  $df = 73$ ,  $p < 0.0001$ ). The results from a two-way ANOVA indicated that there was no significant interaction between open and closed plots and sapling age in 'time to death' ( $F_{1,73} = 0.18$ ,  $p = 0.6725$ ).

#### 3.6.2. One- and three-year old sapling survival in closed plots (livestock excluded)

In closed plots the survival of three-year old saplings (87%) was significantly greater than one-year old saplings (47%) ( $\chi^2 = 47.73$ ,  $df = 1$ ,  $p < 0.0001$ ). Time to death of three-year old saplings tended to be longer ( $12.2 \pm 0.49$  months) than one-year old saplings ( $9.9 \pm 1.24$  months). Fig. 7 indicates that in closed plots moisture stress, soon after planting and just before the rains, was the main cause of mortality of both one- and three-year old saplings (Fig. 6). In Mbodi village stems dried out and withered back so that the underground tuber was the only part of the plant which remained alive during winter. In Tshikuyu many stems managed to survive above ground during winter, but developed a black-coloured bacterial infection which could not be identified by plant pathologists. Although 13% of deaths are attributed to disease, not all diseased plants died. Insect browsing increased during the rains in response to leaf growth, and was responsible for more deaths (31%) than disease (Fig. 6).

#### 3.6.3. One- and three-year old sapling survival in open plots (livestock present)

In open plots, survival of three-year old saplings (13%) was significantly better than one-year old saplings (7%) ( $\chi^2 = 31.48$ ,  $df = 1$ ,  $p < 0.0001$ ). Repeated livestock browsing and trampling was responsible for 86% and 100% of deaths of one- and three-year old saplings respectively, while moisture stress accounted for the

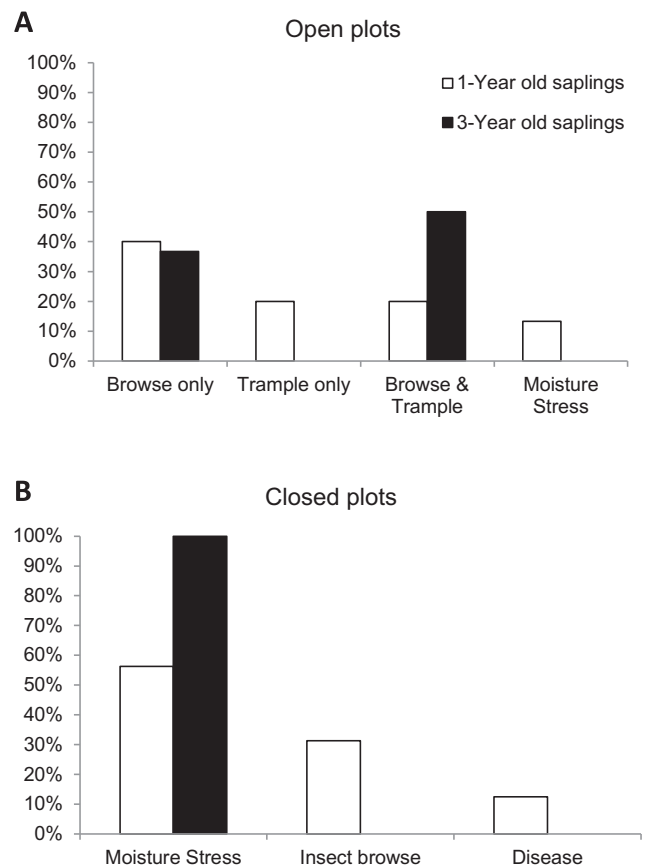


Fig. 6. Causes of damage and mortality in open (A) and closed (B) plots for one- (white bars) and three-year old (black bars) baobab saplings.

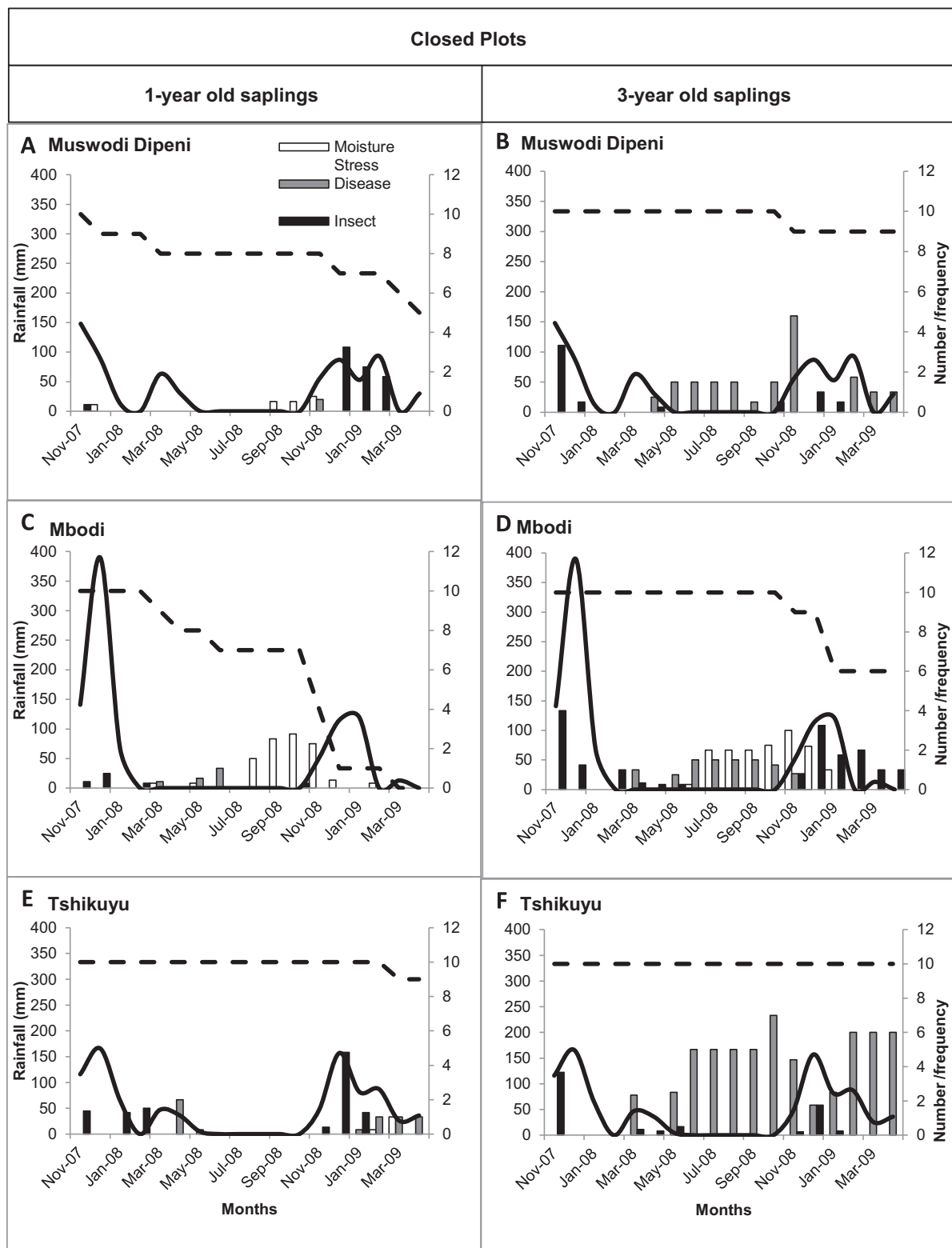
remaining 14% of deaths of one-year old saplings (Fig. 6). Time to death of three-year old saplings tended to be longer ( $5.06 \pm 0.61$  months) than one-year old saplings ( $3.66 \pm 0.65$  months) (Table 3).

Fig. 8 indicates that browsing by goats occurred mostly in the first year and soon after planting. After being browsed, plants flushed more leaves and were then browsed again. Many plants died after the second browsing event, probably due to depletion of stored reserves. During the dry season, plants lack leaves, so browsing seldom occurs. Browsing did not coincide with rainfall in the second year because the plants were so badly trampled that they barely showed above the ground. Trampling took place throughout the year regardless of whether plants had leaves or not. Trampling was more frequent in Tshikuyu village because a cattle path developed through the plot. Trampling often broke the stem and saplings regenerated (resprouted) from their underground tuber.

Saplings were more susceptible to goat browsing than trampling and died more quickly when only browsed than when only trampled (Table 3). Three-year old saplings appeared to be less resilient to the combination of browsing and trampling than one-year old saplings. Saplings that survived were only browsed once and managed to survive repeated trampling events (Table 3).

## 4. Discussion

The total number of available seed is determined by a species' adult abundance and fecundity (Muller-Landau et al., 2002). Baobab fruit production is highly variable in space (Assogbadjo et al., 2005) and time (CV = 44.7 over three years (Venter and Witkowski, 2011)). Furthermore, this study has shown that



**Fig. 7.** Monthly rainfall (solid line) and survivorship (dashed line) curves, occurrence (timing) and frequency (number of plants affected per month) from moisture stress (white bars), disease (grey bars) and insect browsing (black bars) during the period November 2007–April 2009 for one- (A, C, E) and three-year old (B, D, F) baobab saplings in closed plots at Muswodipeni (A, B), Mbodi (C, D) and Tshikuyu (E, F) villages, Venda, South Africa. Left Y-axis indicates rainfall and right Y-axis indicates all remaining variables.

baobabs in human-modified areas (villages and fields) produce more seed than in more natural areas (plains and rocky outcrops). In human-modified areas, higher adult tree density and higher fruit production, possibly aided by sparse ground cover and dripping

water taps, result in substantial seed production in the order of  $10^4$  seeds/ha per annum. This is not the case in West Africa where harvesting of leaves results in very poor fruit production in villages (Schumann et al., 2010). However in natural landscapes both lower

**Table 3.** The number of one- and three-year old baobab saplings in open plots that were browsed and trampled (first column), average number of times damage was recorded (second column) and time to death (third column). Browsing was caused by goats and trampling by cows.

	1-year old				3-year old			
	Number of plants	Browse (mean ± SE)	Trample (mean ± SE)	Time to death (months)	Number of plants	Browse (mean ± SE)	Trample (mean ± SE)	Time to death (months)
<i>Damage to plants that survived</i>								
Browsing only	0	–	–	–	0	–	–	–
Trampling only	1	–	32.0 ± 0.0	–	0	–	–	–
Browsing & trampling	1	1.0 ± 0.0	35.0 ± 0.0	–	4	1.0 ± 0.0	39.3 ± 3.66	–
<b>Total survival</b>	<b>2 (7%)</b>				<b>4 (13%)</b>			
<i>Damage to plants that died</i>								
Browsing only	12	2.13 ± 0.33	–	2.50 ± 0.43	11	4.0 ± 0.81	–	4.41 ± 0.92
Trampling only	6	–	8.0 ± 4.64	3.17 ± 0.40	0	–	–	–
Browsing & trampling	6	2.3 ± 0.98	9.8 ± 5.28	7.50 ± 2.39	15	2.0 ± 0.39	4.1 ± 1.17	5.53 ± 0.82
Moisture stress	4	–	–	2.13 ± 0.72	0	–	–	–
<b>Total mortality</b>	<b>28 (93%)</b>				<b>26 (87%)</b>			
<b>Average</b>				<b>3.66 ± 0.65</b>				<b>5.06 ± 0.61</b>

tree density and lower fruit production/tree resulted in lower seed production, in the order of about  $10^3$  seeds/ha per annum, but still deemed high enough not to be a major attributing factor to poor recruitment. However, in natural areas, where baboons occur, predation of baobab fruit could be a major contributing factor to poor recruitment. When mature fruit (pulp and seed) is eaten the seeds are not destroyed and baboons act as useful seed dispersers, but when immature fruit is eaten the developing seed is destroyed (Pochron, 2005). Baboons are known to reduce fruit production by at least 85% on the ridges and within nature reserves in the study region (Venter and Witkowski, 2011). Furthermore, unpublished data from Skelmwater (long term growth monitoring plot near Musina, South Africa) show that predation of baobab fruit by baboons has resulted in multiple crop failures. Fruit predation may also be a contributing factor to poor recruitment in the Kruger National Park (KNP) and Mana Pools National Park, Zimbabwe, where an absence of saplings has been noted (Hofmeyr, 2003; Swanepoel, 1993). No other fruit predator (other than baboons) has been found in these communal lands, in ongoing (2007–2011) fruit production surveys. The consumption of ripe fruit (containing mature seed) by baboons and other animals such as elephants and eland, may aid scarification and hence may result in more rapid germination of seed. The baobab fruit naturally fall from the trees when ripe in winter if not previously disturbed by baboons. Termites aid in opening these fruit on the ground and releasing the seed. Seedlings have also been observed emerging from under these trees in summer (January), but none of these seedlings persisted into February/March (pers. obs.) as they were eaten by goats. A study on these aspects and the dynamics of the *in situ* seed bank would further enhance our understanding of the recruitment process in communal landscapes.

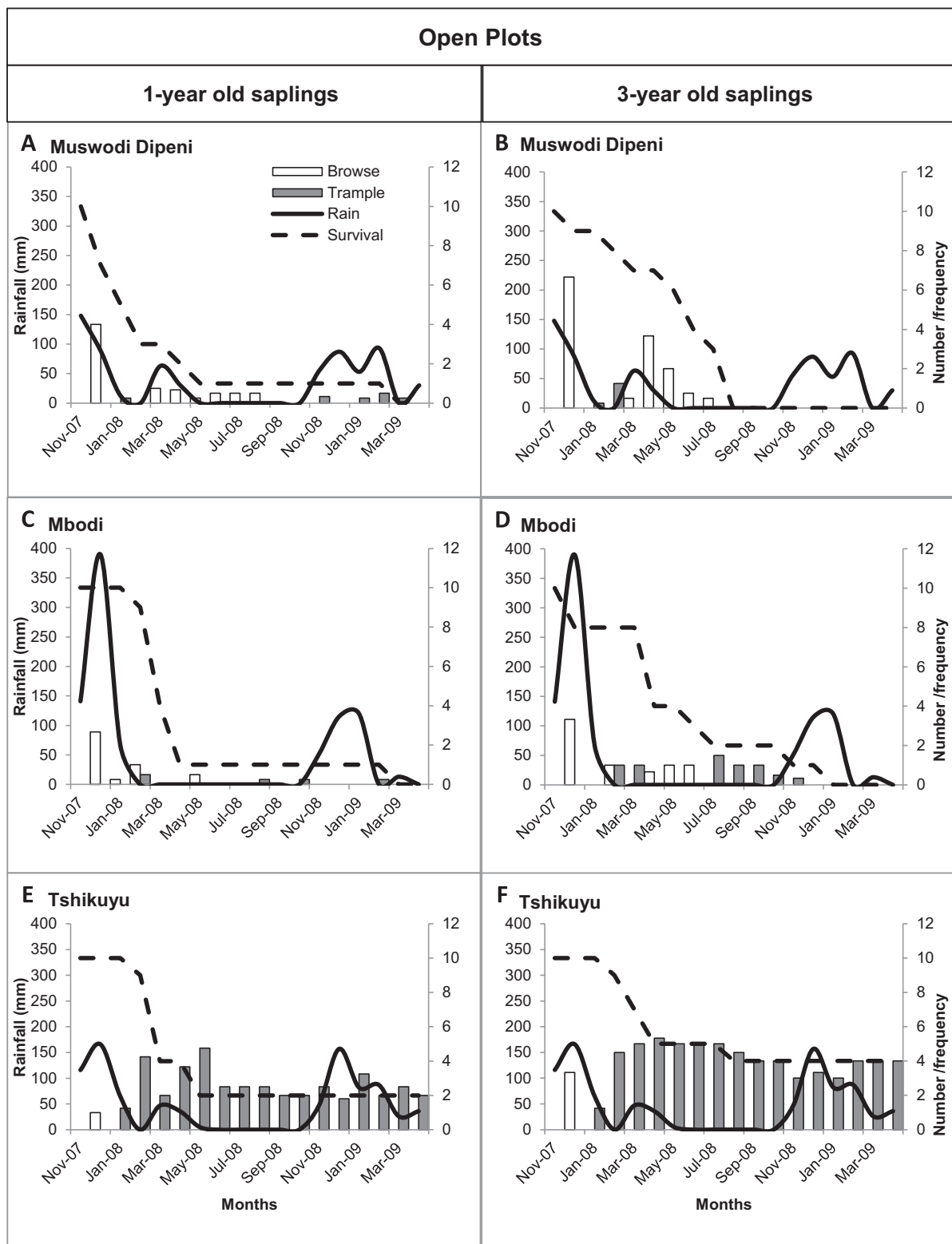
The impact of commercial fruit harvesting on seed limitation needs to be addressed. How many fruit (and hence loss of seeds) can the population endure before it becomes seed limited? To help answer this question a matrix model can be used which would need data on age, fecundity and survival. The results of this study and previous studies will go a long way to helping build such a model. Considering the serious bottleneck affecting baobab recruitment and the increased global interest in baobab fruit products, such a study will be critical to the future conservation of the species.

Seed viability is a crucial component to assessing seed availability. Results from germination experiments in other parts of Africa suggest that across its distribution range baobab trees produce a high proportion of viable seed (over 90%) (Danthu et al., 1995; Esenowo, 1991; Razanameharizaka et al., 2006). It is known that baobab seeds are able to survive for many years under laboratory

conditions, e.g. at 8% moisture and 5 °C, seeds still had a 94% germination success after fifteen years (Wickens and Lowe, 2008). Similarly, in this study, all seeds remained intact (100%) and had high viability ( $\geq 89\%$ ) when stored under 'controlled conditions' (ambient room temperature). Although the seed exhumed from the field had similar high (97%) viabilities, only 34% of the original batch was still present (and intact) after two years and only 3% had emerged as seedlings (Section 3.3). Nonetheless, the availability of viable seeds does not appear to be a significant factor that would limit recruitment. Other semi-arid savanna woody plants such as *Acacia* spp., *Dichrostachys cinerea* (Witkowski and Garner, 2000) and *Burkea africana* (Wilson and Witkowski, 2003), all having seeds with hard seed coats, have been shown to form persistent seed banks. It is known that seeds of some African *Acacia* spp. are able to survive extreme soil surface temperatures ranging from 50 to 70 °C for at least a month (Witkowski and Garner, 2000) but more deeply buried seeds, which have a much more ameliorated temperature range, persist for longer (ETF Witkowski unpublished data). As baobab seeds have a hard impermeable seed coat they are also protected, to a certain extent, from pathogens and predators, and this study has shown that they also form persistent seed banks with 34% of seeds persisting for at least two years. Ninety seven percent of the recovered seeds that were buried for 24 months were still viable, but 63% of seeds that had been buried had disappeared. Some of these seeds may have germinated and then died (Wilson and Witkowski, 1998) or may have been predated (Helm et al., 2011) over the 24 month period. However, substantial annual seed production, high seed viability and 34% of seeds persisting in a soil seed bank after 24 months of burial, suggests that, at least in areas where baboons do not occur, recruitment is not seed limited.

Seeds with an impermeable seed coat will spread germination over a number of years allowing for long-lived seed reserves with germination taking place at the same time each year (Baskin and Baskin, 2001). We found that most seedlings emerged in January, either in the first or second year (Fig. 5). Hofmeyr (2003) noted that baobab seeds staggered their germination over at least three years in nursery conditions in the KNP adjacent to the study region. High fluctuating temperatures are typically required to overcome dormancy in Malvaceae (Baskin and Baskin, 2001). In Southern Africa temperatures start increasing in October and remain high through to April (South African Weather Service). January is the wettest and hottest month of the year and exhibits the lowest diurnal temperature variation which may provide the cue for the observed peak germination in January.

In South Africa, it has been estimated that effective baobab regeneration may only occur every 100–150 years (De Villiers, 1951), i.e. episodic regeneration. Jagged size-class distributions



**Fig. 8.** Monthly rainfall (solid line) and survivorship (dashed line) curves, occurrence (timing) and frequency (number of plants affected per month) from browsing (white bars) and trampling (grey bars) during the period November 2007–April 2009, for one- (A, C, E) and three-year old (B, D, F) baobab saplings in open plots at Muswodi Dipeni (A, B), Mbodi (C, D) and Tshikuyu (E, F) villages, Venda, South Africa. Left Y-axis indicates rainfall and right Y-axis indicates all remaining variables.

(Venter and Witkowski, 2010) could be seen to mirror palaeoclimatic conditions (Huffman, 2010) that may represent poor recruitment during dry periods. By studying rainfall records and young baobabs in the field, De Villiers (1951) suggested that the

then current crop of juveniles might have recruited in 1909, 1918 and 1923. The lack of juveniles below 50 cm dbh in 2006 (Venter and Witkowski, 2010) suggests successful recruitment may not have occurred since 1923.

This study confirmed that seedling establishment is severely hampered by poor and inconsistent rainfall. Over 18 months of observation the majority of seedlings in closed plots survived only three weeks and only one seedling survived the entire period. Poor rainfall is given as the reason for poor baobab seedling survival in many other regions (Chirwa et al., 2006; De Villiers, 1951; Dhillion and Gustad, 2004), but it is more likely that seedling mortality is a result of inconsistent intra-seasonal rainfall rather than low rainfall *per se*. It has been shown with other semi-arid African savanna species, that seedlings need frequent, and not necessarily high rainfall to survive initially (Wilson and Witkowski, 1998). The results of this study show that seedling emergence can occur in years even when early season rainfall is as low as 287 mm (Mbodi: [July–June] 2008/2009) and that in the year that received 589 mm (Mbodi: 2007/2008), seedlings emerged but were unable to survive due to erratic post-emergence rainfall. Rainfall in this area is very seasonal with first rains (>50 mm) in November and last rains (>50 mm) in April. Baobabs have a limited growing season with leaf flush adhering closely to these months (S.M. Venter, unpublished data). Thus it may be important that germination occurs relatively early in the season so that the young plants have enough time to acquire resources to survive the winter, yet inconsistent rainfall and predation hamper survival, and hence resulting in episodic recruitment.

Livestock is often mentioned as a threat to baobab recruitment (Chirwa et al., 2006; Dhillion and Gustad, 2004). Many plants survive herbivory by resprouting (Bond and Midgley, 2001; Helm et al., 2009) and this appears to be a strategy for young baobabs. Soon after germination and within the first few months of growth, baobabs develop an underground tuber (or tap root) in order to support regrowth after browsing or damage (Bond and Midgley, 2001; Wickens, 1982). Dhillion and Gustad (2004) found that once a seedling had established, persistent browsing hampered growth, but did not kill plants. Goats and sheep are associated with poor tree cover in African savannas whereas cattle (as obligate grazers) are not (Groen et al., 2011). Our results show that saplings died more quickly after goat browsing than cattle trampling, but that after repeated damage, of either browsing or trampling, their reserves were too depleted to survive. In conservation areas, goats and cattle are replaced by a variety of wild herbivores such as impala, kudu, eland, zebra and buffalo. Baobab recruitment in conservation areas, such as the KNP, may be hampered by the presence of ungulate browsers and grazers, for similar reasons that marula declined in the KNP (Helm et al., 2009, Helm and Witkowski, 2012).

The study region has a low fire frequency (MacGregor and O'Conner, 2002), so unlike moister areas where fire can greatly impede seedling establishment, fire is unlikely to be a major impediment, although it may reduce the frequency of episodic recruitment events, when moisture levels are sufficiently high that fuel loads can carry a fire.

Baobabs are extremely sensitive to frost, which can cause baobab seedling mortality (Sidibe and Williams, 2002). Thus, in areas where frost does occur the frequency and intensity of frost should be considered. However, where baobabs occur in southern Africa, frost is limited to <20 days a year and in the study area specifically, frost never occurs (Schulze, 1997).

To enhance recruitment, active planting and protection of young seedlings may be required. In parts of West Africa a higher density of baobab seedlings and young trees were found in villages than in surrounding fallows. This was attributed to seed being dispersed in village garbage and the care local people take of baobab seedlings and saplings (Assogbadjo et al., 2005; Dhillion and Gustad, 2004; Duvall, 2007). Interviews conducted in Mali by Dhillion and Gustad (2004) found that 50% of respondents protect naturally germinated

seedlings and 60% had transplanted seedlings for protection. Villagers built barriers to prevent browsing, irrigated seedlings, prepared basin-shaped beds for water collection around seedlings and pruned and cut back surrounding vegetation. These protective actions are motivated by the high value people in West and North Africa place on baobab products (leaves, fruit, bark) and their cultural significance. Baobab leaves are a staple crop in Mali and surrounding areas so the tree, as a food source, is very important (Assogbadjo et al., 2008). In South Africa, local people tend not to protect young plants even though there are two sets of National legislation that protect baobabs, the National Environmental Management and the National Forest Act (Department of Environment Affairs and Tourism, 2004; Department of Water Affairs and Forestry, 1998). This legislation is poorly enforced and unless local people develop a 'baobab culture', as is seen in West Africa, recruitment constraints are likely to hamper future populations.

## 5. Conclusion

The results of this study clearly indicate that baobab recruitment in communally managed land, in the absence of commercial fruit harvesting is microsite limited and not seed limited. The baobab population in the study area is able to produce large quantities of viable seed. Viability tests on stored and exhumed seed indicate that persistent seed banks are formed and can be maintained by annual seed input and staggered germination (mainly in January each year), with each seed crop germinating over a number of years. Thus recruitment is not limited by seed availability.

Baobab recruitment is shown to be severely hampered by microsite conditions. This study showed that poor regeneration is influenced by the lack of consistent rainfall required to support seedling survival. This situation is exacerbated by livestock browsing and trampling, resulting in extremely high rates of seedling and sapling mortality.

Baobab populations could possibly be maintained with low episodic recruitment (Venter and Witkowski, 2010), but if conditions for recruitment do not re-occur, then there may be cause for concern. Climate change models predict that many areas where baobabs occur will get dryer and hotter (Cuni Sanchez et al., 2011a, 2011b). This, in addition to rapidly increasing human and livestock populations, implies that future recruitment events may be even scarcer. A viable adaptation to this long term change is active planting, assisted tree regeneration, protection and monitoring of young plants, in order to maintain baobab populations in these landscapes. Future studies should concentrate on the effects of commercial fruit harvesting on seed availability, natural dispersal and scarification by wild animals and the fate of seed in soil seed banks.

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