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Using a deterministic population model to evaluate population stability and the effects of fruit harvesting and livestock on baobab (*Adansonia digitata* L.) populations in five land-use types

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A B S T R A C T

The subsistence and commercial use of baobab (*Adansonia digitata*) fruit is important to many thousands of marginalized people in the arid tropics of Africa, yet sustainable harvest levels have not previously been studied. Size-class distributions of baobab populations tend to be stable, suggesting high tolerance to fruit harvesting. However, environmental conditions have changed substantially over the last 100 years. Increasing livestock numbers, land modification and climate change are new threats which may affect tolerance to fruit harvesting. To investigate this, a deterministic stage-based population projection matrix model was developed using (a) long term baobab monitoring data from 2 sites, (b) radiocarbon age calculations, (c) extensive field surveys of population structure and fruit (and seed) production, and (d) experimental field trials on seed banks and seedling and sapling survival in relation to the presence of livestock. Projected population growth (λ) was then evaluated for five land-use types (nature reserves, rocky outcrops, plains, fields, and villages) under three levels of livestock (none, moderate and high stocking rates). Response to fruit harvest intensity was tested for each scenario by decreasing seed availability by 10% from 100%. High livestock numbers resulted in baobab population declines, with $\lambda < 1$ in all land-use types. Under moderate and zero livestock numbers, baobab populations in plains, rocky outcrops, villages and fields were able to tolerate between 33% and 90% fruit harvest rates. In nature reserves there was already high predation on immature fruit by baboons, another cause of population decline, with the model showing no tolerance whatsoever to fruit harvesting. These results show that fruit harvesting can be sustainable in production landscapes under moderate livestock levels. However the future is uncertain, as a predicted lowering of rainfall due to climate change is a further concern, with likely negative impacts on fruit yields and recruitment and consequently population projections. Thus active planting and protection of seedlings should take place to mitigate current and future negative impacts facing baobab populations.

1. Introduction

Sustainable utilization means, essentially, that take-off rates should not damage the productive potential of the resource, and that harvesting can be maintained indefinitely (Carter, 1996). The term ‘ecological tolerance’ is used to describe the degree to which plant populations can recover from harvesting (Ticktin, 2004). Many studies have found that the utilization of NTFPs (non-timber forestry products) is unsustainable at current levels of harvest (Hall and Bawa, 1993; Peters, 1996). However, the harvesting of fruit and seed has the least impact on population structure with high degrees of tolerance, except for non-sprouting species. For long-lived tree species, extraction rates of between 86% and 92% are commonly calculated (Bernal, 1998; Zuidema and Boot, 2002; Emanuel et al., 2005). High tolerance levels are attributed to four factors: fruit harvesting does not damage the plant itself; adult trees have high survival potential; recruitment is continuous, even if episodic; and trees are long-lived with extensive reproductive periods.

Baobab fruit are being wild-harvested for commercial and subsistence use in many parts of Africa, and this has become very important to the livelihoods of thousands of marginalized people (Buchmann et al., 2010; Venter and Witkowski, 2013a). Recently the global demand for baobab fruit derivatives, namely fruit powder and seed oil, has grown substantially with exports to Europe, Asia and North America. This has made significant contributions to alleviating poverty and yet sustainable harvest levels have not been evaluated (Gruenwald and Galizia, 2005; Venter and

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Witkowski, 2013a). Due to the long history of human use of baobab fruit, its importance as a subsistence product and the stability of baobab populations, the impact of fruit harvesting has seldom been of concern (Wickens, 1982; Venter and Witkowski, 2010). However, recent changes in the environment, such as land cover and land use changes (Coetzer et al., 2010), increasing livestock numbers and climate change have raised the alarm about the future of baobab populations (Dhillion and Gustad, 2004; Cuni Sanchez et al., 2011; Venter and Witkowski, 2013b).

In many parts of Africa poor baobab recruitment is associated with high livestock numbers (Dhillion and Gustad, 2004; Chirwa et al., 2006). Venter and Witkowski (2013b) found that consumption and trampling by livestock resulted in up to 87% sapling mortality. Poor rainfall and drought are also known to severely reduce recruitment and can lead to adult tree death (Gijsbers et al., 1994; Caplan, 1995; Maranz, 2009; Venter and Witkowski, 2013b). A loss of up to 85% of fruit has been found in areas where baboons predate immature fruit and this, too, may contribute to poor recruitment in some land-use types (Venter and Witkowski, 2011, 2013b). Furthermore, climate change predictions suggest that current suitable habitat for baobab populations in Africa could be reduced by up to an alarming 95% (Cuni Sanchez et al., 2011). In light of these threats, there is clearly a need to re-assess the state of baobab populations and to evaluate the impact that baobab fruit harvesting will have on these populations in the future.

Population projection matrix models can be used to understand plant population dynamics, the importance of different life history processes and to answer 'what if' questions within different scenarios (Desmet et al., 1996; Drechsler et al., 1999; Caswell, 2001). They can be used to assess the impact of different levels of harvesting and determine the maximum harvest intensity that a population can tolerate (Bernal, 1998; Emanuel et al., 2005). The advantage of such models is that they have a standardized form, relatively low data requirements and can quantitatively predict the direction of population change in response to changes in fecundity, growth and survival (Desmet et al., 1996; Caswell, 2001).

A study aimed at assessing the sustainability of baobab fruit harvesting was initiated in 2006. This study evaluated population size, fruit production, phenology, recruitment and socio-economic

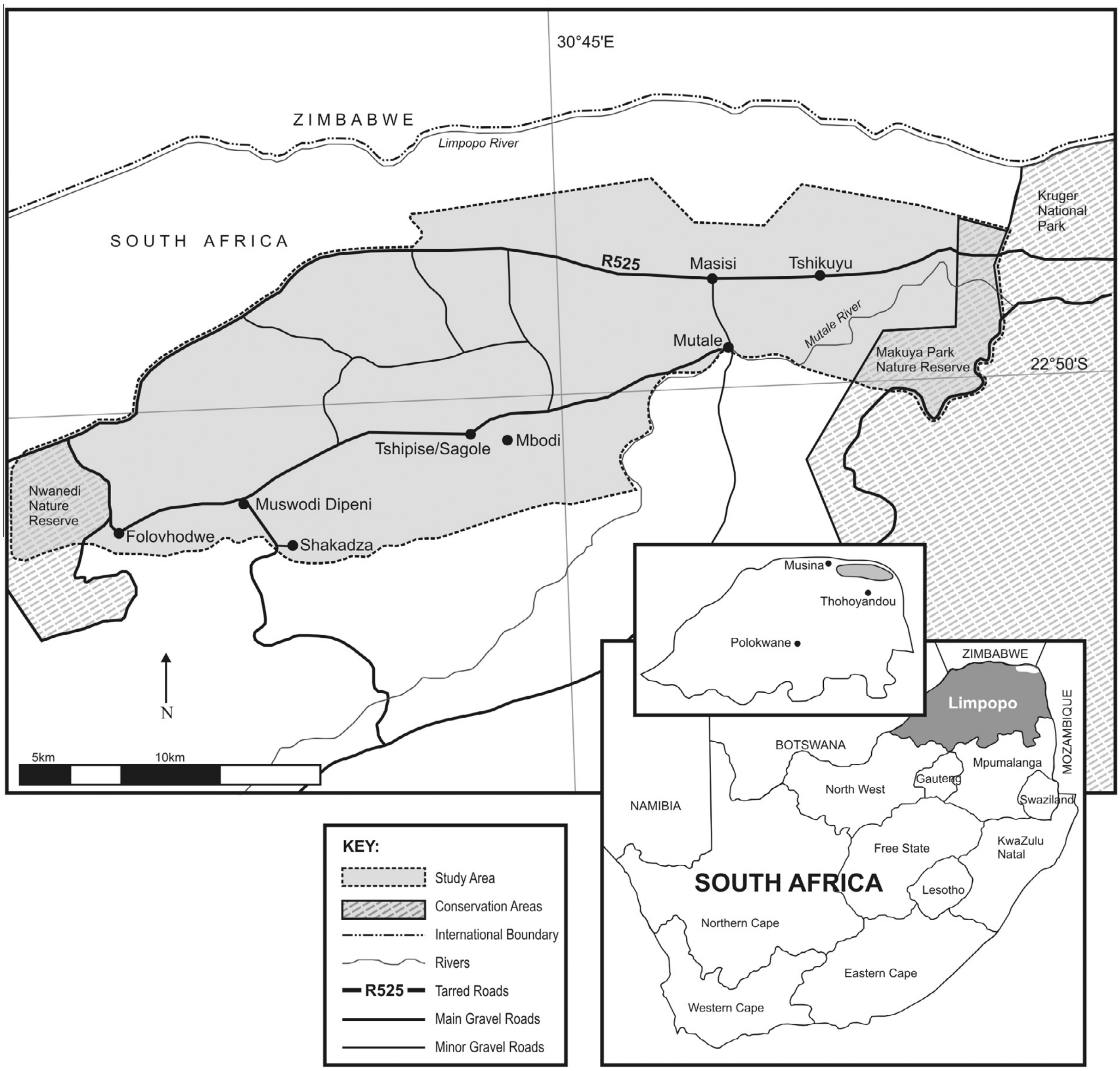

Fig. 1. Map indicating location of study area in Limpopo Province, South Africa.

impacts (Venter and Witkowski, 2010, 2011, in press; Venter, 2012; Venter and Witkowski, 2013a,b). This paper draws on the ecological knowledge gained from these and other long-term studies. Numerous studies have shown that the majority of households within communal lands in South Africa keep livestock for the multiple benefits they provide (Dovie et al., 2006). A deterministic stage-based population projection matrix model is used to determine population trends in five land-use types and under different levels of livestock numbers and fruit harvest levels.

It was predicted that livestock would reduce the stability of baobab populations through trampling and browsing of seedlings and saplings and as a result reduce tolerance to fruit harvesting in the long-term due to lack of recruitment. It was also predicted that in areas where baboons are common, such as in nature reserves and rocky outcrops, predation of immature fruit would result in unstable populations with very low tolerance to harvesting.

2. Materials and methods

2.1. Study area

Northern Venda is situated in the north eastern section of Mutale District Municipality, Limpopo Province, South Africa (around 22°50′S and 30°45′E) (Fig. 1). It forms part of the former Venda homeland where ownership and management of natural resources is the responsibility of traditional structures, civic organizations and government. The local population is mostly of the BaVenda ethnic group (Stayt, 1931), numbering just over 100,000 people with low levels of employment and education (Statistics-S.A., 2001).

The area is made up of five land-use types, namely; nature reserves, rocky outcrops, plains, fields, and villages. Nature reserves are under the control of provincial authorities and here the conservation of plants and animals is the main management objective and no domestic animals are allowed. Plains and rocky outcrops are used as communal grazing lands; fields are used for dry-land cropping, and villages are densely populated, consisting of closely-spaced houses with electricity and communal water taps. In Venda, livestock densities are generally high in villages where they are kept at night and allowed to browse in fallow fields adjacent to villages. In these areas livestock numbers are typically higher than the accepted carrying capacity of three small livestock units per hectare (Tobie Fourie pers. comm.). In plains and rocky outcrops, livestock densities are moderate to low respectively. Fruit harvesting takes place in all communal land-use types, except nature reserves, however this may change in future.

Venda has a semi-arid summer rainfall regime with a mean annual precipitation of between 334 and 423 mm (Mucina and Rutherford, 2006). Summers (i.e. October–March) are hot, winters (April–September) are mild, and frost seldom occurs. The soils are mainly derived from sandstone, basalt and aeolian deposits (Brandl, 1981) in a gently undulating topography averaging about 400 m above sea level. This study area falls in the Mopane and Lowveld Ecoregions of the Savanna Biome (Mucina and Rutherford, 2006). Wild fires seldom occur, due to a prevalent low fuel load. Wildlife is scarce outside of the nature reserves, and elephants are now infrequent visitors.

2.2. Study species

Baobabs (*Adansonia digitata* L., family Malvaceae, subfamily Bombacoideae) are distributed widely across Africa south of the Sahara, where they are associated with the drier plant communities of the Sudanian and Zambezian lowlands (Wickens and Lowe, 2008). The northern part of South Africa forms the southern limit of their distribution. Here baobabs are closely associated with vegetation dominated by *Commiphora*, *Grewia* and *Colophospermum mopane* (Venter and Witkowski, in press) and have the highest densities in villages, followed by fields, plains and rocky outcrops. Baobabs are known to be extremely long lived, reaching up to 1800 years of age. Analysis of size-class distributions suggests that baobab populations in all land-use types are stable due to the persistence of the adult trees, despite recruitment being largely episodic (Venter and Witkowski, 2010; Patrut et al., 2013).

Fruits start to form in December and they drop 6 months later, in May/June, which is when they are ready for harvest (Venter, 2012). Fruit production varies significantly between years and land-use types (Venter and Witkowski, 2011) and is strongly determined by variations in flower numbers (Venter, 2012). This fruit is a hard indehiscent capsule consisting, in the study area, of 24–194 seeds embedded in a dry powdery pulp (Venter and Witkowski, 2013b). A high proportion (>89%) of seed is viable and forms persistent seed banks (Venter and Witkowski, 2013b), yet natural regeneration is poor and severely hampered by infrequent rainfall and livestock browsing (Venter and Witkowski, 2013b).

2.3. Methods and analysis

Following Caswell (2001), Desmet et al. (1996) and Emanuel et al. (2005), a deterministic stage-based population projection matrix model, was constructed. This is a Lefkovitch model based on life-history stages. Four baobab life stages were used: (1) seedling, (2) sapling, (3) juvenile and (4) adult. The following parameters were required to construct the model: P_i, the probability that an individual in life stage i will survive and remain in that life stage; G_i, the probability that an individual in life stage i will survive and grow into the next life stage and F_i, the probability of an individual's fecundity in life stage i. G_i, and P_i are determined by average duration (d_i) and survival probability (s_i) of an individual in life stage i. These transitions are represented graphically in a life stage graph (Fig. 2).

The duration of each life stage was determined. Seedlings were regarded as newly germinated plants <1 year old, and saplings as plants 1–3 years old (Table 1). Saplings are identified in the field by having second year growth and thus taller and more sturdy than first year seedlings. Venter and Witkowski (2011) found that trees <100 cm diameter breast height (dbh) (termed sub-adults) could be considered juvenile because fruit production was insignificant compared to that of trees ⩾100 cm dbh, which were then regarded as adults. The growth rates of trees within the juvenile and adult life stages from two data sets were used to calculate the duration of these two: (1) accelerated mass spectrometry (AMS) radiocarbon

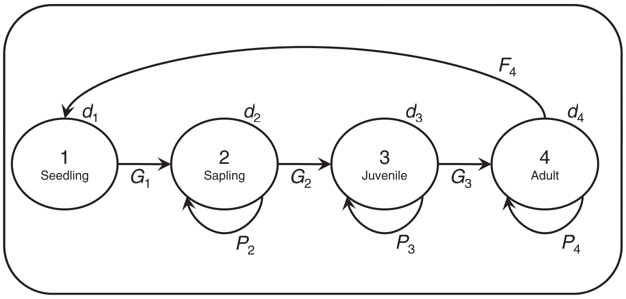

Fig. 2. A 4-stage life diagram for baobab. Nodes represent each life stage: seedling (N_1), sapling (N_2), juvenile (N_3) and adult (N_4). d_i is the number of years an individual spends in a life stage; F_i is fecundity; G_i is the probability of an individual surviving through the life stage and moving on to the next stage; P_i is the probability of an individual surviving and staying in the stage.

Table 1
Time in life stage, survival and transition probabilities and fecundity for the four baobab life stages. Survival probabilities for the sapling life stage represent survival under three levels of livestock: no livestock, moderate livestock and high livestock. Livestock damage results from goat browsing and cattle trampling (Venter and Witkowski, 2013a,b).

Life stage	Time in stage (years) d_i	Survival probabilities s_i	Probability of moving to next stage G_i	Probability of staying in this stage P_i	Fruit production Fruit/tree	Fecundity F_i
Seedling	1	0.05[a]	0.05000	0.00000	0	0
Sapling (no livestock)	2	0.87[a]	0.40476	0.46524	0	0
Sapling (moderate livestock)	2	0.50	0.16670	0.33333	0	0
Sapling (high livestock)	2	0.13[a]	0.01496	0.11504	0	0
Juvenile	246[d]	0.89[b]	0.00026	0.98118	0	0
Adult – nature reserve	1114[d]	0.99[b]	0.00004	0.99630	2[c]	6.926547
Adult – rocky outcrops	1114[d]	0.99[b]	0.00004	0.99630	13[c]	45.02255
Adult – plains	1114[d]	0.99[b]	0.00004	0.99630	29[c]	100.4349
Adult – fields	1114[d]	0.99[b]	0.00004	0.99630	88[c]	304.7681
Adult – villages	1114[d]	0.99[b]	0.00004	0.99630	90[c]	311.6946

[a] From Venter and Witkowski (2013a,b).

[b] From Musina 20 year data, unpublished.

[c] From Venter and Witkowski (2011).

[d] Derived from radiocarbon dating results and Skelmwater girth increment measurements (Patrut et al., 2010).

dating results of three local trees; one juvenile and two adults and their corresponding tree sizes, were used to calculate growth rates (Patrut et al., 2010), Venter et al., unpublished data); and (2) growth rates of a further six juvenile and four adult trees were determined from the 80-year increment measurements (unpublished data) collected at Skelmwater Nature Reserve, near Musina, South Africa, which has essentially the same climatic conditions as the Venda sites. The average growth rate was thus calculated as 0.4 and 0.26 cm dbh/year for juvenile and adult trees respectively. The duration of each life stage (di) was determined by multiplying these growth rates by the following tree sizes: 99 cm dbh was chosen for juvenile trees because this is the size at which juvenile trees become adults (Venter and Witkowski, 2011); and 350 cm dbh was chosen for adult trees, because this is the largest size-class that still represents a notable number of adults in the population (Venter and Witkowski, 2010). Results are given in Table 1.

Survival rates (s_i) for each life stage were determined from two sets of data. First, juvenile and adult survival rates came from 20-year monitoring data carried out in Musina Nature Reserve (unpublished data) and second, seedling and sapling survival rates came from Venter and Witkowski (2013b). Sapling survival rates were calculated for plants that were protected from livestock and for plants that were exposed to high (but typical) livestock numbers. Thus it was decided to solve the matrix model for both these scenarios and to add a third level, half-way between, indicating moderate livestock numbers (Table 1).

F_i, fecundity, is a function of seed production, germination and seedling survival. Using data from Venter and Witkowski (2011, 2013b), the following values were used for the different variables: percentage viable seed, 89%; number of seed per fruit, 97 (medium-sized fruit); fruit-producing adults, 59%; seedling survival, 5% and seedling emergence percentage from sown seeds, 7%. Venter and Witkowski (2011) determined the mean number of fruit per tree for each of the five land-use types in the study area (Table 1). Low (mature) fruit production figures in nature reserves and rocky outcrops are due largely to the presence of baboons which reduce fruit production up to 85% and 58% in each land-use type respectively. Using these figures the matrix model was solved for each of the five land-use types.

Matrix parameters were determined using the following equations:

$$G_i = \left(s_i^{d_i}(1 - s_i)\right) / \left(1 - s_i^{d_i}\right)$$

$$P_i = \left(\left(1 - s_i^{d_{i-1}}\right) / \left(1 - s_i^{d_i}\right)\right) \times s_i$$

$$F_i = (\text{Seed/tree}) \times (\%\ \text{fruit producing trees}) \times (\text{germination or emergence}\ \%) \times (\text{seedling mortality})$$

Using Microsoft Excel, these parameters were entered into the projection matrix (Fig. 3), and the dominant eigenvalues (λ) calculated using poptools (Hood, 2010). This λ represents the relative stability of the population; if $\lambda = 1$, the population is stable, if $\lambda \geqslant 1$ the population is increasing and if $\lambda < 1$ then the population is declining (Caswell, 2001).

Eigenvalues (λ) were calculated for unharvested baobab populations in each land-use type and under the three levels of livestock browsing described above ($5 \times 3 = 15$). To assess the impact of seed (through fruit) harvesting on the population, a sensitivity analysis was conducted by reducing seed availability in incremental reductions by 10% from 100%. The maximum allowable reduction of seed was reached when $\lambda = 1$.

3. Results

Parameters, P_i, G_i and F_i are given in Table 1. As livestock levels increase, the probability of sapling survival (s_i) decreases with a resultant influence on G_i and P_i, the probabilities of staying in that life stage and moving on through the life stage, respectively. The survival of adult trees is high due to low adult mortality rates, however fecundity (F_i) of adult trees differs between land-use types due to differences in fruit production levels. In nature reserves and rocky outcrops baboon predation is high resulting in low adult fecundity in these land-use types.

Fig. 4 shows the decrease in λ under a range of simulated seed harvesting intensities for each land-use type and three levels of livestock scenarios. Maximum harvest levels are indicated for each

$$\begin{pmatrix} P_1 & F_2 & F_3 & F_4 \\ G_1 & P_2 & 0 & 0 \\ 0 & G_2 & P_3 & 0 \\ 0 & 0 & G_3 & P_4 \end{pmatrix}$$

Fig. 3. A standard deterministic population projection matrix model based on a 4-stage life diagram for baobab.

scenario where $\lambda = 1$. Harvest level 0% indicates the pre-harvest population state for each scenario.

Fig. 4 shows that the rate of population increase (λ) in nature reserves was <1 under all three livestock scenarios. In the absence of livestock and 0% harvest, $\lambda = 0.999$, which is close to stable; thus any improvement in environmental conditions could improve the baobab population trend. The population in rocky outcrops is shown to be stable/increasing with no ($\lambda = 1.008$) or moderate ($\lambda = 1.001$) livestock numbers, and can tolerate 78% and 33% fruit harvest rates respectively (Fig. 4). Under high livestock numbers, the population shows a decline ($\lambda = 0.999$) with no tolerance to fruit harvesting. The population in the plains is stable/increasing, with no ($\lambda = 1.016$) and moderate livestock ($\lambda = 1.006$) numbers and can tolerate up to 90% and 70% fruit harvest rates respectively. Under high livestock numbers, the population is in decline ($\lambda = 0.997$) with no tolerance to harvesting (Fig. 4). Baobab populations in fields and villages, which produce the highest quantity of fruit (88 and 90 fruit/tree respectively) show similar results, with populations being stable/increasing with no ($\lambda = 1.034$) and moderate ($\lambda = 1.016$) livestock numbers, and able to tolerate 96% and 90% fruit harvesting. Even with such high fecundity, however, field and village populations cannot increase under the current high livestock numbers ($\lambda = 0.999$) (Fig. 4), although they are close to stable.

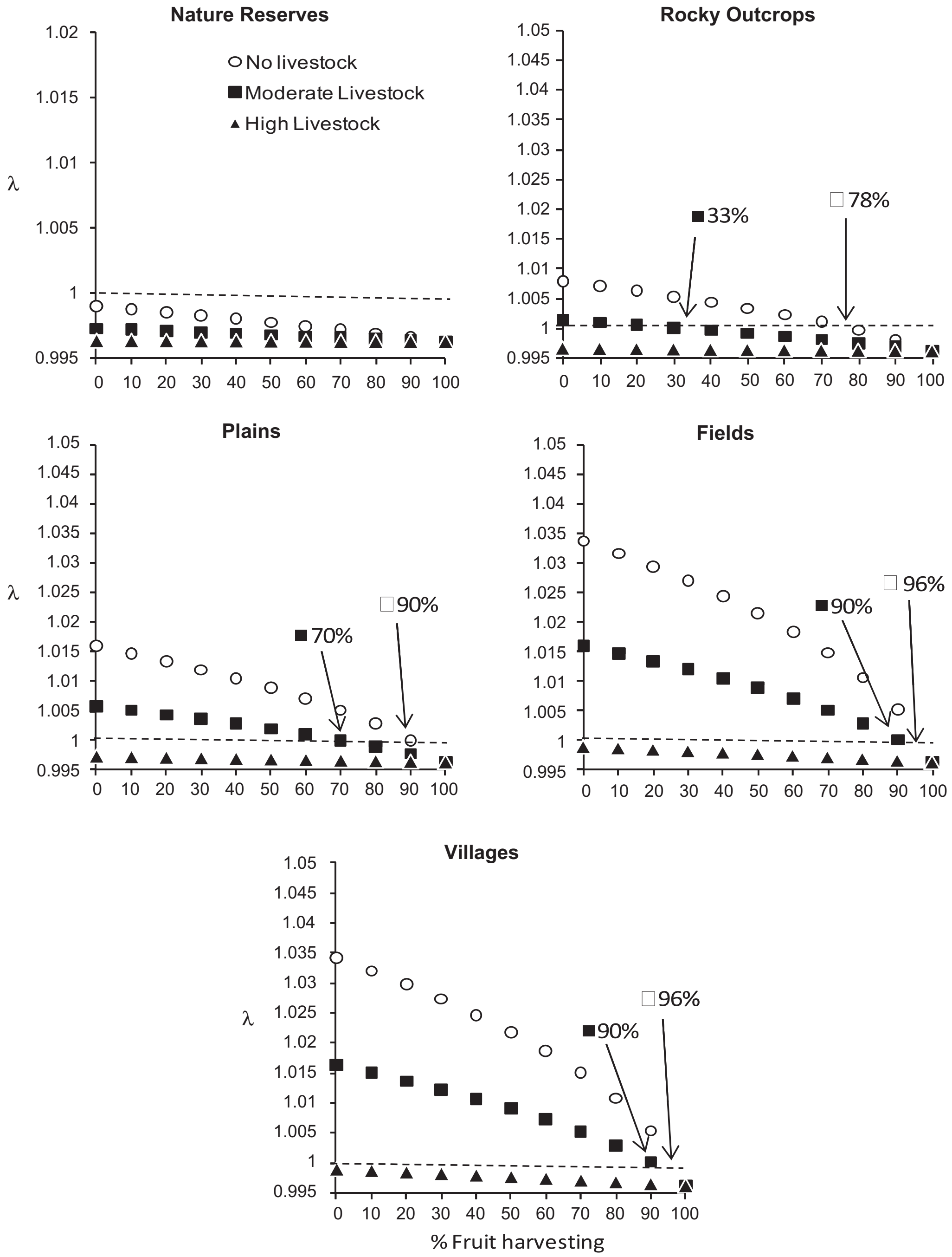

Fig. 4. Change in projected population growth (λ; *Y*-axis) for each 10% increase in fruit harvesting (*X*-axis) at three levels of livestock (none, moderate and high) within five land-use types, nature reserves, rocky outcrops, plains, fields and villages. Maximum harvest levels ($\lambda = 1$) indicated for moderate levels of livestock (filled square) and no livestock (open circles). At high livestock levels (filled triangles), all populations are in decline ($\lambda < 1$). Nature reserve population is in decline at all levels of livestock. Note different *Y*-axis scale for nature reserve. Percentage numerals in the figures represent estimates of allowable fruit harvest at population equilibrium.

High livestock numbers thus have a negative effect on population growth in all land-use types. If livestock numbers are kept at moderate levels, all baobab populations, except those in nature reserves (which have higher densities of indigenous mammalian herbivores to contend with), can tolerate fruit harvesting at levels between 33% and 90%. However the typical situation in communal lands is that livestock numbers are generally much higher than the commercial carrying capacity and it is highly unlikely that numbers will be voluntarily reduced by livestock owners.

4. Discussion

Dendro-demographic studies, using size-class distributions, show that baobab populations in the study area are stable (Venter and Witkowski, 2010) and that, because of the long-lived nature of baobab trees, episodic recruitment could maintain population levels. However, the output of the matrix model shows a different picture, with populations in most land-use types threatened by the current high livestock numbers. Size-class distributions reflect population trends in the past, whereas projection models use current circumstances to determine the future rate of population increase or decrease (Desmet et al., 1996). Furthermore, unlike stochastic models, deterministic models do not account for environmental variability and, in particular, episodic recruitment events that may take place in exceptional years, such as a number of consecutive years with above-average rainfall. If an episodic recruitment event is able to make a substantial contribution to recruitment, then the population can be maintained under this life-history strategy, but in the face of climate change, land-transformation and growing human populations, successful recruitment events may not have a chance to occur again. The main factors found to drive predicted population declines are (1) high livestock numbers, (2) baboon predation of immature fruit and (3) low and potentially increasingly erratic rainfall.

It was predicted that livestock would reduce the stability of baobab populations and as a result reduce tolerance to fruit harvesting. The results of this study have indeed shown that high livestock numbers are a major cause of population decline. Results show that, even where fruit production is good, e.g. in villages and fields, populations would be unable to tolerate the current high livestock numbers. High numbers of goats and cattle are found around villages, where animals drink water and are kraaled (corralled) at night (pers. obs). On plains and rocky outcrops, livestock tend to spread out in search of forage with their browsing intensity becoming progressively less the further they are away from villages (Grossman et al., 1999). Fields exclude livestock except when fallow, but hoeing before the planting season also results in high sapling mortality (Dhillion and Gustad, 2004). This explains why, despite high baobab population densities and good fruit production, recruitment is poor in human-modified landscapes (villages and fields) in comparison to natural landscapes (plains and rocky outcrops) (Venter and Witkowski, in press).

It was also predicted that in areas where baboons are common, such as in nature reserves and rocky outcrops, predation of immature fruit would result in unstable populations with very low tolerance to fruit harvesting. The low fruit numbers in nature reserves are due to baboon predation of immature fruit early in the season when there is little other food available (Venter and Witkowski, 2011). Even though fruit harvesting and livestock are not allowed in nature reserves, this land-use type was included in the study so that we could model what the combined effect of baboons, harvesting and livestock would be on population stability as livestock levels could be used to reflect herbivore levels in the reserves. Our results show that this is a major contributor to population decline, as $\lambda < 1$ even when there is no effect of livestock herbivory or fruit harvesting. However, there may be years when high or early rainfall provides alternative food sources for baboons (and other fruit predators), thus reducing pressure on immature baobab fruit (pers. obs). This would allow baobab fruit to mature and potentially result in episodic recruitment that this model does not consider. Furthermore, baobabs have persistent seed banks and exhibit delayed germination (Venter and Witkowski, 2013b), this in addition to tree longevity means that populations are buffered by the 'storage effect', allowing them to persist through bad periods and increase in numbers again during better times (Lamont and Witkowski, 1995; Higgins et al., 2000). Yet, it would still be prudent to have a conservative prediction concerning population growth when testing for sustainable harvesting, so as to provide for a margin of error.

Growth, germination and seedling survival are marginal in the study area, which is semi-arid with highly erratic seasonal rainfall (Schulze, 1997). Trees that are consistently watered (in gardens) grow exceptionally fast compared to those in the wild and are known to produce flowers within 23 years (Pardy, 1953), compared to the predicted average of 246 years in the study region. In nursery conditions, unscarified seed have germination percentages of between 20% and 50% in contrast to 0–7% found in the wild (De Villiers, 1951; Venter and Witkowski, 2013b). Seedling mortality due to infrequent rainfall is 95%, but negligible in nursery conditions due to regular watering (pers. obs). Thus baobab populations found in areas of higher rainfall, such as parts of Malawi, Tanzania and northern Mozambique may be more stable than in more arid regions such as represented by the Limpopo Valley.

Adult tree mortality is another potential threat to baobab populations. Excessive bark harvesting for weaving can kill adult baobab trees (Romero et al., 2001). In areas where elephants strip bark off baobabs, this too has lead to large-scale loss of adult trees (Barnes, 1980; Edkins et al., 2007). Adult trees are also known to die when weakened by severe drought, excessive use of ground water, and disease (Piearce et al., 1994; Caplan, 1995). Species with very long-lived adults have been shown to sustain populations for very long periods, as long as adults are not removed by land clearing (e.g. Drechsler et al., 1999) or are impacted upon by harvesting methods (or harvesting of critical tissues) or diseases that eventually result in mortality.

Mitigation can be attempted at three levels: direct harvesting interventions, additional management practices and landscape level management (Ticktin, 2004). Harvest-level mitigation entails control over the frequency and quantity of fruit collection. Fruit collection, staggered over time and between areas, allows trees to have rest years and release seed back into the environment. Limited allowable harvest per year would also allow a certain percentage of fruit to remain each year. However, it would be naive, in an open-access situation, to expect harvesters to leave fruit on trees when there is cash to be earned. Furthermore, seedlings germinating from naturally dispersed seed may have a much lower chance of survival than hand-planted seeds and saplings (Witkowski and Lamont, 1997).

Sowing seed and planting saplings are additional management interventions that can boost recruitment. Saplings have a higher survival rate than seedlings (Venter and Witkowski, 2013b), but seed sowing does not need a nursery, which is expensive to run. Young plants would need to be protected until they escape the browse trap, e.g. by forming a 'cage with thorny branches' (using for example *Dichrostachys cinerea*) around them and thus should be planted in areas where they can easily be monitored, such as near fields and villages. At the same time, efforts should be made to include plantings in areas away from villages to reduce artificial clumping and to spread the risk of losing trees due to urban expansion and local catastrophes, such as fires or flooding. Care should be taken to use locally-sourced seed so as not to introduce unwanted genes. However, equally important is the use of seed from a wide variety of trees to avoid loss of genetic diversity. The use of truncheons and grafted trees also limits genetic diversity, and such trees have an artificial look, raising aesthetic concerns. Although grafted material has been shown to produce fruit much sooner than trees grown from seed (Sidibe and Williams, 2002), this requires additional water, a scarce commodity in these arid areas. In West Africa, local people have a culture of planting and protecting seedlings, presumably driven by the relatively quick return on leaf production, an important food source (Schumann et al., 2010). In southern Africa, benefits are not immediate and population decline is treated as an externality; thus investing in nurseries and planting programmes may be necessary, even if costly.

At the landscape level, enhancing recruitment and controlling the activities that would affect fecundity and survival of adult trees, need to be considered. Lowering livestock numbers would have a direct positive effect on sapling survival, but livestock are important for many rural people and a reduction of numbers in order to enhance baobab recruitment is unlikely to be widely supported. The harvesting of other plant parts, such as leaves and bark, is known to reduce fruit production and increase tree mortality respectively (Romero et al., 2001; Schumann et al., 2010). The commercial harvesting of these plant parts should be strongly discouraged.

Finally, the impact of harvesting on ecosystems is a complex issue and not much is known about its secondary effects (Hall and Bawa, 1993). The removal of fruit may have an impact on fruit-eating animal species (Moegenburg and Levey, 2003). When mature fruit are available, baboons rely on these as a food source late in the season (Kunz and Linsenmair, 2007). In this area, elephants are infrequent visitors, but they do occur in other areas with baobabs; if harvesting took place there, this would reduce the fruit available to them. Frequent human visits to the trees during the harvest season may disrupt the wildlife, such as birds and mammals, that roost or nest in the baobabs (Wickens and Lowe, 2008). Studies aimed at better understanding these impacts will be important in guiding wider mitigation strategies.

5. Conclusion

The study found that baobab populations cannot tolerate high livestock numbers, which result in unstable and declining populations. Moderate livestock numbers do not cause population decline, but do reduce tolerance to harvesting by up to 20%. In the absence of livestock, tolerance to harvesting is high (90–96%). Baboon predation of immature fruit causes population decline especially where baboons are common and predation is high, such as in nature reserves. Where baboon predation is moderate there is some tolerance to fruit harvesting, but only if there is no or moderate livestock numbers.

The results of this paper clearly show that baobabs are sensitive to environmental change, and thus concerns over the future survival of the species should be taken seriously. Baobabs are an important species, and their fruit will continue to be harvested for subsistence and commercial use. Fortunately, fruit harvesting *per se* has a relatively small impact on population stability, therefore mitigation of population decline should not only focus on reducing the impacts of fruit harvesting, but more importantly address the effect of predation, livestock numbers and climate change.

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