Baobab (Adansonia digitata L.) fruit production in communal and conservation land-use types in Southern Africa

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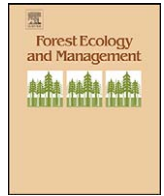
Baobab (*Adansonia digitata* L.) fruit production in communal and conservation land-use types in Southern Africa

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ABSTRACT

Baobab fruit are harvested and used throughout Africa as an important source of food and are sold to generate income. Commercial use is increasing rapidly as derivatives of the fruit such as baobab seed oil and fruit pulp are being exported to Europe and North America. The cash derived from the sale of fruit support thousands of rural people. This study examines baobab fruit yields in an area being harvested for commercial use. It represents baobab populations and harvesting scenarios typically found in Southern Africa and is the first study in Africa to combine demographic and production data in determining baobab fruit yields.

Fruit production was examined across five land-use types (nature reserves, rocky outcrops, plains, fields and villages) and over three consecutive years. Factors assessed included differences in life-stage, tree size, land-use type, inter-annual variation and quantifiable fruit predation.

Results showed that adult trees produced 8 times more fruit than sub-adult trees. Fruit production fluctuated between size-classes and exhibited weak linear and logarithmic trends between fruit production and dbh and crown volume, respectively. There was high variation between trees with 41% of adult trees consistently producing <5 fruit per year, which we classed as 'poor-producers'. Different land uses showed no significant differences in fruit production per tree, but where baboons were present, in nature reserves and rocky outcrops, predation of immature fruit resulted in up to 85% fruit loss. Villages and fields had the highest tree density and yielded the most fruit/ha. Inter-annual variation was significant with a two and a half fold difference between the highest and lowest year.

The results of this study are important for economic planning and management and are key to determining sustainable harvesting levels of baobab fruit in Southern Africa.

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1. Introduction

Baobabs (*Adansonia digitata* L. (Malvaceae)) are valued in Africa for food, fibre and medicine. Where baobab products are sold in informal markets, they form an important source of income for thousands of rural people (Sidibe and Williams, 2002). Recently derivatives of the fruit, such as baobab seed oil and baobab fruit pulp, have been exported to countries outside Africa, mainly Europe, Canada and the USA. As baobab extracts become more popular, it is predicted that the demand for the resource will grow (Sidibe and Williams, 2002). Such commercial use of the fruit provides an income to many thousands of people throughout Africa. In Zimbabwe, for instance, the sale of baobab fruit has increased the income of rural people by 250% (Gruenwald and Galizia, 2005). It is therefore important that the resource is managed sustainably. One of the first steps in achieving this goal is to gain a thorough understanding of the biology and ecology of baobabs, for which there is surprisingly little information.

Sustainable utilization of non-timber forest products (NTFPs) is essential for the conservation of the plants and for the livelihoods of the rural people who depend on them (Ticktin, 2004). For most NTFPs there is too little information to make informed decisions about sustainable harvesting and management (Chamberlain, 2003; Lawes et al., 2004) and this also applies to baobab products. Many baobab studies have focused on food value, socioeconomic importance, ethnobotanical knowledge, taxonomy, morphology and genetic aspects (Dovie, 2003; Wickens and Lowe, 2008; Assogbadjo et al., 2009; De Caluwe et al., 2009; Tsy et al., 2009). However, in order to determine NTFP yields, reliable data is necessary on population demographics and plant production levels associated with plant size, site characteristics, predation and interannual variation (Goldwin, 1992; Peters, 1996; Tilman, 1997; Fenner and Thompson, 2005).

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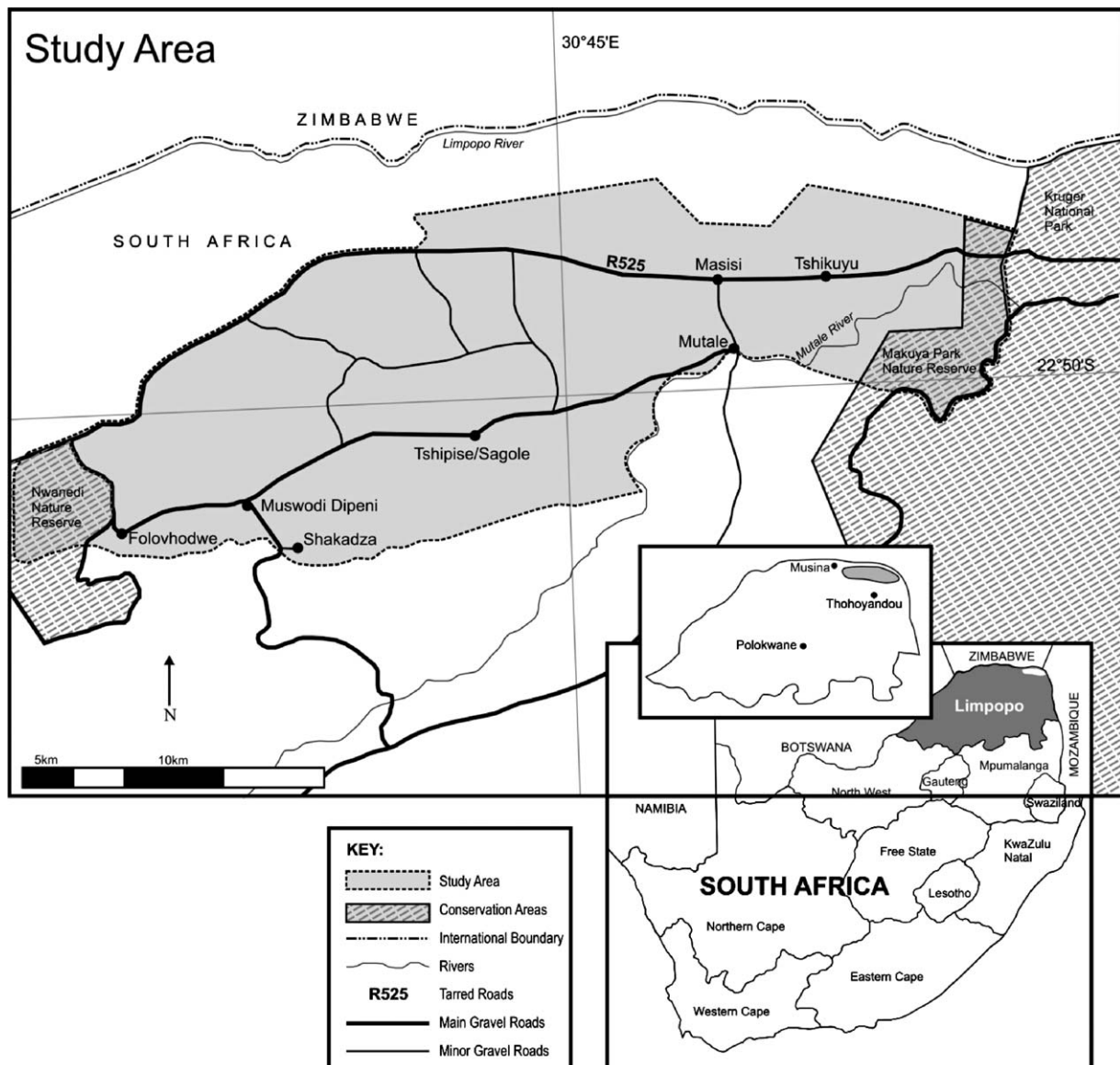Edward.Witkowski@wits.ac.za (E.T.F. Witkowski).

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

Whilst baobab demographic studies have been done in various parts of Africa (Kelly, 2000; Hofmeyer, 2001; Dhillion and Gustad, 2004; Assogbadjo et al., 2006; Chirwa et al., 2006; Edkins et al., 2007; Venter and Witkowski, 2010), few have assessed the amount of fruit produced by trees and the factors that influence fruit production (Dhillion and Gustad, 2004; Assogbadjo et al., 2005; Cuni Sanchez et al., 2009). Hence, the aim of this study was to determine differences in fruit production between land-use types, between tree life-stages, size-classes and between successive years.

Commercial use of baobab fruit began in the northern part of South Africa in 2005. Fruit is collected from trees in fields, villages and surrounding communal land by local people, mainly otherwise unemployed women. They are processed *in situ* and sold to a locally-based company that makes oil from the seeds and packages the fruit pulp. The resulting products are sold to the markets as cosmetic and food ingredients. Similar arrangements occur throughout sub-Saharan Africa (Gruenwald and Galizia, 2005). Income from the sale of baobab fruit in northern South Africa goes to over 1500 people for whom this forms part of their livelihood strategy (Venter, unpublished data). These commercial fruit harvesting activities prompted this study on fruit production in this area.

Baobab fruit production was studied over three seasons and across five land-use types within conservation areas and communal land. It was predicted that there would be high fruit losses in land-use types where baboons were present, such as nature reserves and rocky outcrops. In addition trees in villages and fields would be more productive than trees in other land-use types due to higher soil fertility and sparser ground cover reducing competition for limited ground water. Fruit production was expected to vary with tree size and that there would be high inter-annual variation depending on rainfall with higher fruit production in high than in low rainfall years. The paper also evaluates the methods used to determine baobab fruit yields and recommends further studies to improve the sustainable management of baobab resources.

The findings are discussed in relation to a fascinating study by Assogbadjo et al. (2008, 2009) on 'male' and 'female' characteristics of baobab trees. Baobabs have hermaphroditic flowers (both male and female parts in the same flower) (Baum, 1995a), yet local people throughout Africa distinguish between 'male' and 'female' trees. Assogbadjo et al. (2008) describe 'male' baobabs as producing very few fruit and 'female' baobabs as producing many fruit. In this study these trees are called 'poor-producers' and 'producers'. The

paper provides further information on the extent of this tendency and its impacts on fruit yield predictions.

Given that seed oil is being extracted from many other African tree species, the study provides a template for similar studies in other species.

2. Materials and methods

2.1. Study area

The research was conducted in the northern part of Limpopo Province (around 22°19′S and 30°28′E), South Africa. The area is commonly known as northern Venda and is about 1250 km² in size. Two provincially-managed nature reserves formed part of the study area; Nwanedi Nature Reserve lies in the west, and Makuya Nature Reserve in the east (Fig. 1). This area represents about 10% of the distribution of baobabs in South Africa (Palgrave, 1983).

The study area falls within the Zambezian regional centre of endemism which includes Angola, Namibia, Botswana, Zambia, Zimbabwe, Mozambique and South Africa. Baobabs are common in *Colophospermum mopane* (mopane) woodland within this region (Wickens and Lowe, 2008). Mucina and Rutherford (2006) describe the area broadly as the Savanna Biome with the following specific vegetation types: Musina Mopane Bushveld, Limpopo Ridge Bushveld and Makulele Sandy Bushveld which are dominated by *Colophospermum mopane* (mopane), *Terminalia sericea* (silver terminalia), *Grewia flava* (brandybush) and *Combretum apiculatum* (red bushwillow). Vegetation in general is low sparse woodland with an average tree height of 4–5 m and a tree cover of 20% with emergent baobabs (Butt et al., 1994). Bush fires are not common due to low grass and herb biomass, and elephants are infrequent visitors.

The average altitude of the region is 400 m above mean sea level and has a gently undulating topography underlain by sandstones of the Karoo Supergroup and the Clarens and Letaba Formations (Brandl, 1981; Mucina and Rutherford, 2006). Soils are generally deep sands and shallow sandy lithosols (Mucina and Rutherford, 2006).

Northern Venda is semi-arid with a rainfall averaging between 334 and 423 mm and a high coefficient of variation of 35–40% (Schulze, 1997). Summers (October–March) are characteristically hot and winters (April–September) are mild. Frost seldom occurs (Mucina and Rutherford, 2006).

Poverty and low employment are endemic to Venda so subsistence agriculture is important. The ratio of men to women is 1:4 with a 0.78–2.38% level of formal employment (Statistics-S.A., 2001). Wooded plains, interspersed with sandstone outcrops are used mainly for grazing cattle, goats and donkeys. There is open access to these natural resources with minimal control from traditional institutional structures and government.

2.2. Study species

Adansonia digitata is one of the eight species of baobab in the genus *Adansonia* L. (Malvaceae, subfamily Bombacoideae) and the only one which naturally occurs on mainland Africa. It is present throughout most of Africa south of the Sahara (Baum, 1995b). In South Africa the population is limited to the Limpopo River valley, with the exception of a few isolated trees found further south (Wickens and Lowe, 2008).

Phylogeographic research show that baobabs originated in West Africa and spread by human-assisted dispersal to the rest of Africa. Three distinct groups of baobabs are found, two in West Africa and the third in Southern and Eastern Africa. Baobabs in Southern and Eastern Africa can be regarded as one phylogeographic population due to low genetic variation within this group (Tsy et al., 2009).
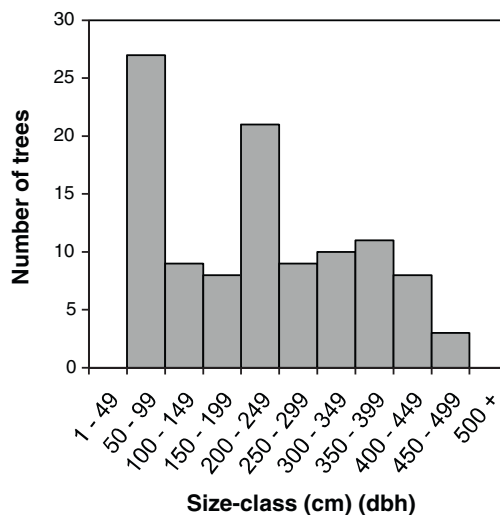

Fig. 2. Number of sampled trees per size-class.

Baobabs are deciduous, bearing leaves and flowers in the wet season (Wickens, 1982; Baum, 1995a). In well watered environments, such as gardens, trees grown from seed can start to flower from 16 to 22 years of age (Pardy, 1953; Wickens, 1982). However in natural semi-arid environments, it is expected that trees may only start flowering at 125 years of age (Swanepoel, 1993). Flowering usually lasts 4–6 weeks with a few flowers opening each night (Baum, 1995a). The period between flowering and fruit ripening is 5–6 months (Sidibe and Williams, 2002). Developing flowers and fruit are a rich source of food, and are eaten and parasitized by a variety of animals including insects, birds and mammals (Wickens, 1982; Hulme, 2001; Pochron, 2005). Baobabs are known to be extremely long-lived trees and despite the softness of their wood can live to at least 1200 years (Von Breitenbach and Von Breitenbach, 1985; Patrut et al., 2007).

2.3. Sampling and measurement

Field work was done over three summer seasons, starting in October 2006 and ending in March 2009. Measurements were taken in five land-use types: (1) nature reserves; (2) plains; (3) rocky outcrops; (4) fields and (5) villages. Except for nature reserves, all of these represent different categories of communally-managed land. Trees were selected to include a wide range of stem diameters in each land-use type (Fig. 2). In total 106 trees were chosen, 34 in nature reserves and 18 in each of the other land-use types. Each tree was considered a sample. Rain gauges were erected at three village homesteads across the study area and local people were employed to record daily rainfall.

For each tree the following five single measurements were taken: geographic position (latitude and longitude); tree girth (measured with a glass-fibre measuring tape at 1.3 m above the ground) and converted into stem diameter at breast height (dbh); tree height (estimated to the closest 2 m, i.e. 2, 4, 6); crown width (measured to the closest meter under the tree as two perpendicular lines, i.e. A1 north–south and A2 east–west orientation); crown height (CH) which was the vertical length of the crown from the lower branches to the top of the tree. Crown volume (CVOL) was calculated using the formula in Snook et al. (2005). First the crown projection area (CPA) was calculated using the equation for an ellipse: $CPA = [(A1/2) \times (A2/2)]\pi$, then crown volume (CVOL) was calculated by $CVOL = CPA \times CH \times 0.5$.

Trees were visited every 1–2 months during the first two summer seasons (October 2006–May 2008). During the third summer

season only one assessment was done, in March 2009. Three categories of fruit were counted at each visit: (1) fruit on the tree, (2) immature wind-blown fruit on the ground (this does not include mature fruit that drop off the tree at the end of the season) and (3) immature predated fruit (eaten by baboons off the tree). Baboons ate newly formed soft fruit which appear on trees a few weeks after first flowering. Baobab fruit take 5–6 months to mature (Sidibe and Williams, 2002), thus these fruit do not have viable seed and predation, this early in the season, does not contribute to seed dispersal. Baboons ate fruit by taking one or two bites and then discarding the remains on the ground below the tree. In order to quantify predated fruit accurately, the stalk of each eaten fruit was counted and discarded so that it would not be counted again at the next visit.

Data analysis used two categories of fruit, total and mature fruit. Total fruit was the sum of mature fruit (counted at the end of the season) plus immature windblown fruit and immature predated fruit lost during the growing season. Total fruit represents the capacity of trees to produce fruit. All sampled trees were used to compare total fruit production between life-stages, tree sizes and land-use types. The second category of fruit was mature fruit, which excluded immature wind-blown and immature eaten fruit. Fruit was regarded as mature once the shell had hardened and the fruit pulp became powdery which happens at the end of the wet season. Thus fruit counted in March/April represented mature fruit. This distinction is important for recruitment and socio-economic studies.

For analysis of fruit size, only trees that had mature fruit were used. Trees in nature reserves, where fruit predation was particularly high, were not used in fruit size analysis. Matured fruit was divided into three size categories, small (± 10 cm $\times$ 5 cm), medium (± 15 cm $\times$ 8 cm) and large (± 20 cm $\times$ 10 cm). Fruit size was based on fruit length (top to bottom) and fruit diameter (measured midway between top and bottom).

2.4. Data analysis

Inter-annual variability in fruit production (2006–2009) was analysed using Friedman ANOVA (Q) and the methods described in Herrera (1998) to determine population level variability (CVp), within plant variability (mean CVi) and among plant synchrony (W; Kendall coefficient of concordance). When population level variability is equal to within plant variability then there is high between plant synchrony (Herrera, 1998). Size-class distributions for fruit production were constructed for each year to allow for visual comparisons and to test for differences using Kolmogorov–Smirnov tests. The Cochran Q-test was used to compare proportion of fruiting and non-fruiting trees between years. Friedman ANOVA (Q) with Kendall coefficient of concordance (W) was used to analyse the differences in the proportion and number of different sized mature fruit per tree produced between and within each year, respectively.

t-Tests were used to assess the contribution of life-stage to differences in total fruit production. Life-stage was arbitrarily categorized as sub-adult (<100 cm dbh) and adult ($\geq$100 cm dbh). The contribution each life-stage made to fruit production was given as a percentage of total production. A Yates corrected χ^2 2 $\times$ 2 contingency table was used to analyse the proportions of fruit-bearing and non-fruit-bearing trees between life-stages.

To determine if sub-adult trees tended to produce smaller fruit than adult trees, three separate t-tests were done to compare the proportions of small, medium and large-sized matured fruit between life-stages.

The proportion of sub-adult and adult trees falling into each total fruit production class (0–4; 5–24, 25–49, 50–99, 100–199, 200–299, 300–399, 400–499, $\geq$500 fruit/tree) was determined. Adult trees that produced an average of <5 total fruit/year over three years were termed 'poor-producers', the rest were called 'producers'. t-Tests

Table 1
Annual variability in fruit production over three years and annual rainfall (July – June).

Annual variability	Rainfall (mm)	Fruit/tree (mean $\pm$ SE)
Year 2006/2007	275	81.7 $\pm$ 18.1[a]
Year 2007/2008	484	29.7 $\pm$ 6.6[b]
Year 2008/2009	334	68.7 $\pm$ 15.3[a]

Different superscript letters indicate significant differences between years ($p < 0.001$).

were done to determine if there were significant differences in total fruit production and stem diameter (dbh) between the two categories. A χ^2 2 $\times$ 5 contingency table was used to determine if there were differences in the number of trees of each category within each land-use type. Friedman ANOVA with Kendall coefficient of concordance (W) tested inter-annual variation in fruit production for 'poor-producers'.

Trees were divided into 50 cm dbh size classes and the mean number of fruit per tree per size-class was displayed graphically. To determine whether a senescent category should be defined, a t-test compared fruit production between the largest and second largest size-class. Regression analyses were performed to test the following: the relationship between tree dbh, crown-volume and crown-area; total fruit production as a function of tree size (dbh); and the influence of tree size (dbh) on size of fruit.

Both total fruit production and mature fruit production were compared between five land-use types using ANOVA followed by Fisher's Least Significant Difference tests (LSD, $p < 0.05$). The proportions of small, medium and large-sized fruit were determined for each communal land-use type. Friedman ANOVA (Q) with Kendall coefficient of concordance (W) tested for inter-annual variation in total fruit production within each land-use type.

The proportion of predated fruit from trees that produced fruit in each land-use type was compared using ANOVA followed by Fisher's LSD ($p < 0.05$). Using a χ^2 2 $\times$ 2 contingency table with Yates correction, the number of trees which did and which did not have predated fruit was compared between land-use types where baboons were common (nature reserves and rocky outcrops) against those where baboons were scarce (plains, fields and villages). Regression analysis compared the proportion of predated fruit against tree size (dbh). The inter-annual differences in the proportion of fruit predated per year was analysed using Friedman ANOVA (Q) with Kendall coefficient of concordance (W). The Cochran Q-test compared the number of trees which did and did not have predated fruit over three years.

A population demographic study was done by Venter and Witkowski (2010) where density of baobabs in different communal land-use types (excluding nature reserves) was determined for the same study area. Using these population data, adult stems/ha were multiplied by adult mature fruit/tree and fruit size figures to determine total fruit yields for the area and for each communal land-use type.

3. Results

3.1. Annual variability in fruit production

The number of fruit produced per year differed significantly between sampling years ($Q_{2,106} = 13.8304$, $p = 0.0009$). Fewer fruit were produced in 2007/2008 than in the preceding (2006/2007) and subsequent year (2008/2009) (Table 1). Inter-annual variability was more strongly determined by within plant variability rather than by between plant synchrony ($CV_p = 44.7$, mean $CV_i = 104.8$, $W = 0.1320$). Fruit production per dbh size class showed high variability between years (Fig. 3b–d) and signifi-

Table 2
Differences between sub-adult and adult life-stages.

Life stages	Proportion of trees producing fruit	Fruit/tree (mean ± SE)	Proportion of fruit per tree (mean ± SE)		
			Small	Medium	Large
Sub adult	0.44[a]	9.9 ± 4.7[a]	0.38 ± 0.01[a]	0.39 ± 0.10[a]	0.23 ± 0.07[a]
Adult	0.81[b]	77.1 ± 13.8[b]	0.32 ± 0.03[a]	0.44 ± 0.03[a]	0.24 ± 0.03[a]

Different superscript letters indicate significant differences between life stages ($p < 0.05$).
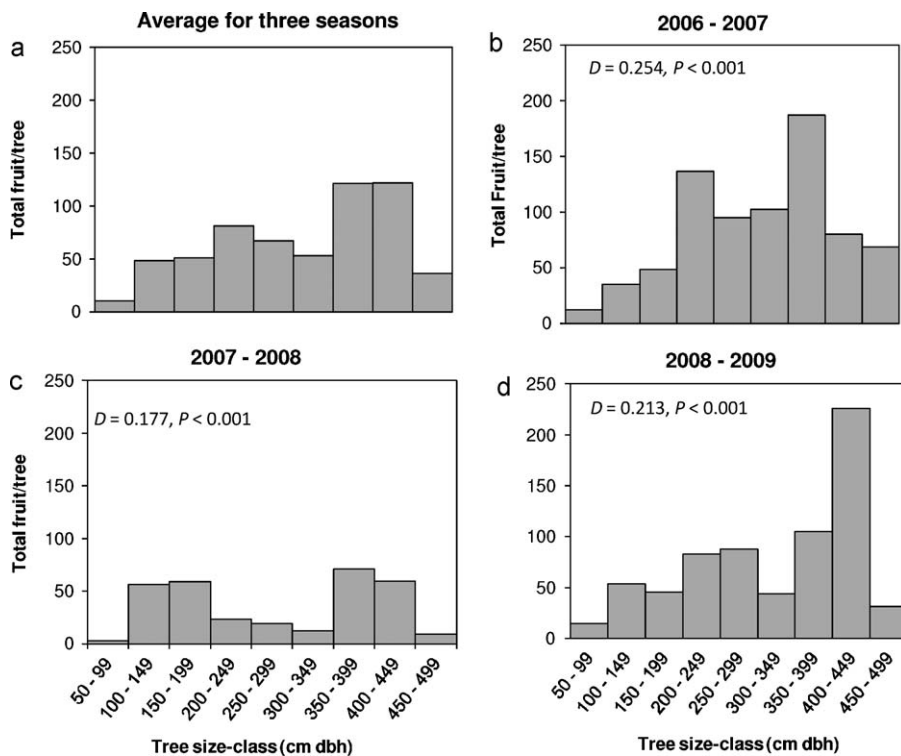

Fig. 3. Mean fruit production per tree size-class ($n = 106$ trees) per year over three seasons (a), and for each season: 2006–2007 (b), 2007–2008 (c), 2008–2009 (d). Kolmogorov Smironov test (D) results for differences in size-class distributions between are also shown.

cant Kolmogorov–Smirnov results. The proportion of trees that produced fruit each year did not differ significantly ($Q = 3.9200$, $p = 0.1409$). Fruit sizes fluctuated significantly between and within years (Fig. 4).

3.2. Comparisons of fruit production between and within life stages

Adult trees produced significantly more fruit per tree than sub-adult trees ($t_{104} = 2.799$, $p = 0.006$) and a significantly greater proportion of adult trees produced fruit than sub-adult trees ($\chi^2_{Yates} = 11.52$, $p < 0.001$) (Table 2). In total, adult trees produced 8 times more fruit than sub-adult trees. In communal land 51% of all trees produced matured fruit. For these the proportion of small, medium and large-sized matured fruit did not differ between life-stages ($t_{35} = -0.9281$, $p = 0.3597$; $t_{35} = 0.4841$, $p = 0.6313$; $t_{35} = 0.5522$, $p = 0.5843$) (Table 2).

The majority (74%) of sub-adults produced less than 5 fruit per year in contrast with 41% of adult trees (Fig. 5). These trees, in the adult life-stage are categorized as poor producers in the next section. The majority of adult trees (59%) produced less than 25 fruit per tree per year and 36% of adult trees produced between 50 and 299 fruit and only 5% produced ≥300 fruit per year (Fig. 5).

Fruit production in adult trees was significantly higher in 'producers' than 'poor-producers' ($t_{77} = -5.2740$, $p < 0.001$), with 'producers' contributing to over 99% of fruit production (Table 3).

There was no significant difference in stem diameters ($t_{77} = 1.4961$, $p = 0.1387$) between 'producers' and 'poor-producers' (Table 3). There was also no significant difference in the numbers of 'producers' and 'poor-producers' in each land-use type ($\chi^2_4 = 3.868$, $p = 0.5758$). Fig. 6a shows that 'poor-producing' trees were present in all tree size-classes. 'Poor producing' trees do not produce fruit every year and 47% of these do not produce fruit at all (Fig. 6b). No significant inter-annual variation in fruit production was found
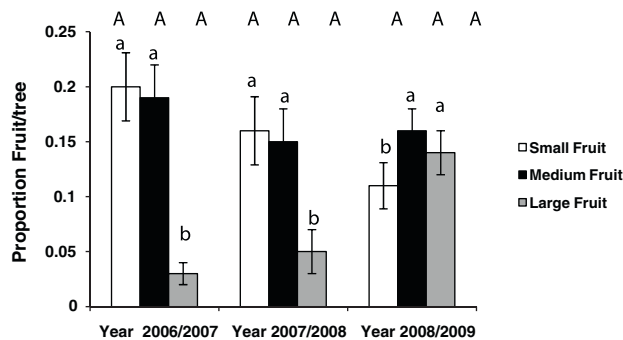

Fig. 4. Proportions of different sized fruit per tree between and within seasons. Capital letters (A,B) show significant differences between seasons and lower case letters (a,b) within seasons ($p < 0.05$). These fruit numbers exclude eaten and wind-fallen fruit which did not reach final mature fruit size.
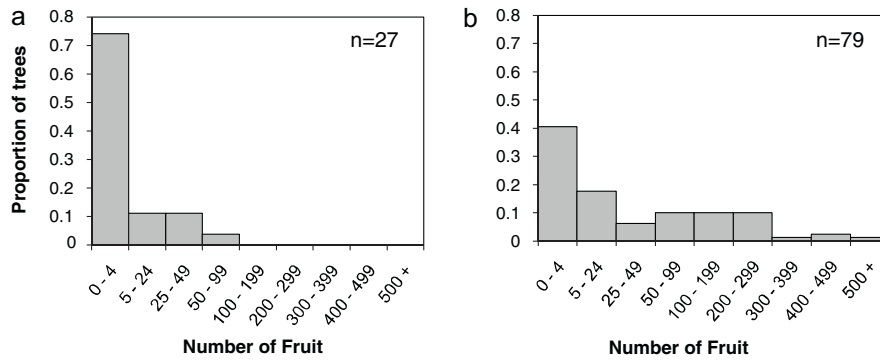
Fig. 5. Proportions of sub-adult (a) and adult (b) trees per fruit number class.

Table 3
Differences between adult 'producer' and 'poor-producer' baobab trees ($n = 79$).

Producer & poor producer	Trees in population (%)	Fruit produced (%)	Stem diameter (cm) (dbh)
Poor producers	41%	0.3%	255 ± 18[a]
Producers	59%	99.7%	293 ± 14[a]

The same superscript letter indicates no significant differences ($p < 0.05$).

in poor-producers ($Q_{(2,32)} = 4.5657$, $p = 0.1035$, $W = 0.0708$) which means that these trees consistently produce few fruit.

3.3. Size-class trends

There were weak logarithmic trends between crown volume and fruit production ($p < 0.001$, $R^2 = 0.1213$) and crown area and fruit production ($p < 0.001$, $R^2 = 0.1020$) and strong linear trends between crown volume and dbh ($p < 0.001$, $R^2 = 0.5373$) and crown area and dbh ($p < 0.001$, $R^2 = 0.5904$). Total fruit production fluctuated between size-classes (Fig. 3a), with a weak positive linear trend between fruit production and dbh ($p = 0.0043$, $R^2 = 0.0756$). In the largest size-class (450–500 cm dbh) fruit production dropped off, but not enough to define a senescent category ($t_9 = 0.7210$, $p = 0.4892$).

Regression analyses of the proportion of different sized fruit showed a weak negative trend between small-sized fruit and dbh ($p = 0.0153$, $R^2 = 0.1566$). Weak positive trends but no significant relationships were found for medium or large-sized fruit and dbh ($p = 0.2490$, $R^2 = 0.0378$; $p = 0.1336$, $R^2 = 0.0631$).

3.4. Comparisons of fruit production between land-uses

There was no significant difference in total fruit production between land-use types ($F_{4,101} = 1.2078$, $p = 0.3122$) (Fig. 7a). How-

ever due to fruit predation (see next section) significant differences were found in final mature fruit numbers between land-use types ($F_{4,101} = 8.6286$, $p < 0.0001$) (Fig. 7b). A greater proportion of medium-sized fruit was produced in all land-use types except villages, where an equal proportion of small-sized and medium-sized fruit were produced (Fig. 7c). Fruit production also differed significantly between the three years within all land-use types except for rocky outcrops (rocky outcrops: $Q_{2,18} = 1.3778$, $p = 0.5021$, $W = 0.0382$; plains: $Q_{2,18} = 13.4737$, $p = 0.0012$, $W = 0.3742$; fields: $Q_{2,18} = 10.8000$, $p = 0.0045$, $W = 0.3000$; villages: $Q_{2,18} = 10.3044$, $p = 0.0057$, $W = 0.2862$; nature reserves: $Q_{2,34} = 14.1123$, $p = 0.0009$, $W = 0.2075$).

3.5. Predation

The proportion of fruit predated from trees that produced fruit in rocky outcrops and nature reserves was much higher than from those found in plains, fields and villages ($F_{4,48} = 86.951$, $p < 0.001$). In the latter three land-use types, predation was negligible (Fig. 8a). Fewer trees with predated fruit where found in areas where baboons were seldom found (plains, fields and villages) ($\chi^2_{Yates} = 11.52$, $p < 0.001$) (Fig. 8b). Regression analysis showed no relationship between tree size and proportion of fruit predated ($R^2 = 0.0133$, $p = 0.4060$). There was also no significant difference in the proportion of fruit predated between years ($Q_{2,40} = 4.0274$, $p = 0.1335$, $W = 0.0503$) nor in the number of trees that had predated fruit ($Q = 2.666$, $p = 0.2636$).

3.6. Estimated fruit yields

Venter and Witkowski (2010) determined that there were 0.90 ± 0.18 stems/ha of adult baobab trees in the population as a whole, with 0.47 ± 0.31 occurring in plains, 0.56 ± 0.31 in rocky
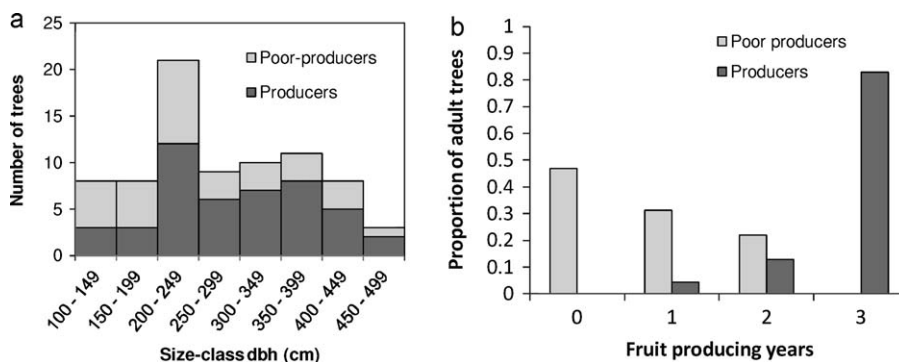

Fig. 6. Number of 'producing' and 'poor-producing' trees in adult size-classes (a) and the proportion of 'producer' and 'poor-producer' trees producing fruit by number of years over the 3 year study period (b).
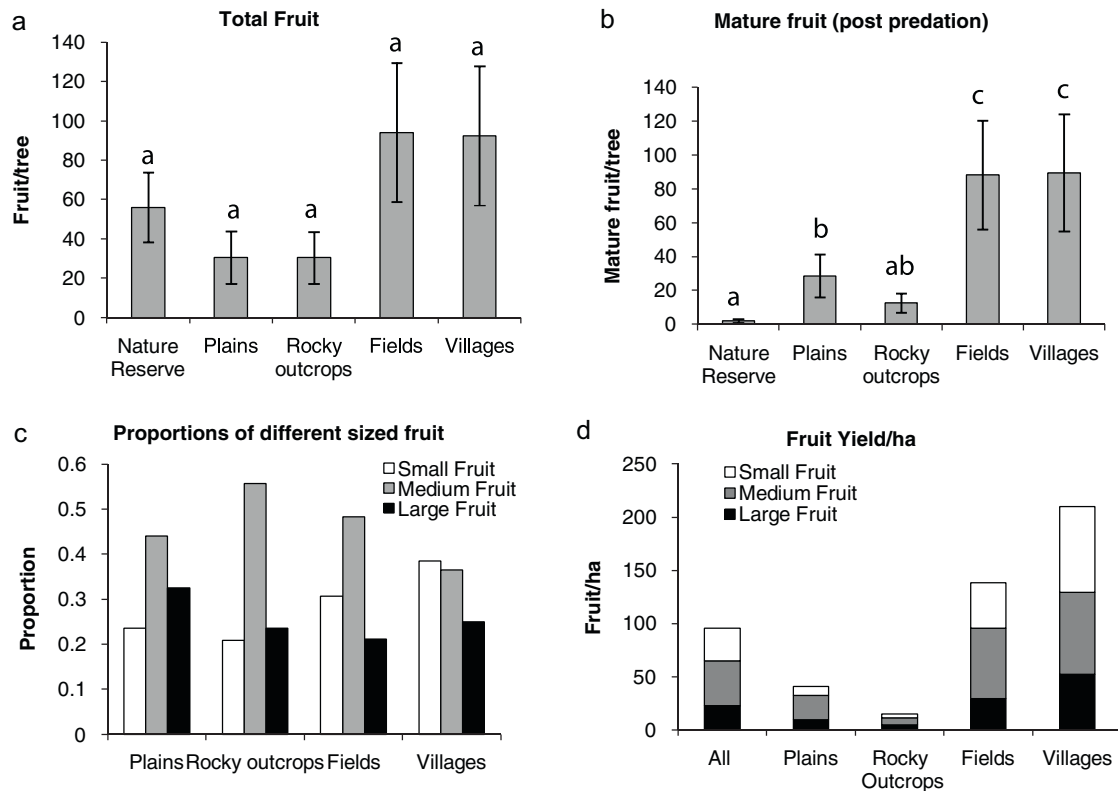
Fig. 7. Land-use type differences in mean total fruit (a), mean mature (post-predation) fruit (b), proportions of small, medium and large-sized fruit in different communal land-use types (c) and mature fruit yields per hectare for all communal land-use types (d). Fruit yields were calculated using stem density data from Venter and Witkowski (2010). Lower-case letters (a–c) indicate significant differences ($p < 0.05$).

outcrops, 0.87 ± 0.3 in fields and 1.7 ± 0.31 in villages. The combination of high tree densities and high fruit yields showed villages and fields to have produced the highest number of fruit per hectare and plains and rocky outcrops the least (Fig. 7d). The population as a whole produced 96 fruit/ha on communal land-use types with similar proportions of small, medium and large sized fruit.

4. Discussion

The estimation of fruit yield is important for economic planning and management and is key to determining sustainable levels of resource extraction, particularly for fruit which have a high socio-economic value such as baobabs (Chamberlain, 2003; Cunningham and Shackleton, 2004; Ticktin, 2004; Shackleton et al., 2005). Fruit inventories can be time consuming and costly therefore knowing what factors have an influence on fruit production can help make them more efficient and accurate.

Stem diameter and crown volume are often used as predictors of fruit production. However these are generally only accurate for species with small fruit and not for species with large fruit, such as baobabs (Chapman et al., 1992; Botelle et al., 2002; Shackleton et al., 2002; Killmann et al., 2003). Killmann et al. (2003) tested methods for assessing baobab fruit production in Kenya and suggested that stem diameter and crown size cannot be used as indicators of fruit production because fruit production was extremely variable. They suggested that visual counts of fruit on primary or randomly selected branches would be the most accurate and efficient method.

Similarly our study showed that stem diameter (dbh), crown volume and crown area were too poorly related to fruit production (low R^2 values) to allow the use of these variables as predictors of fruit production. However, stem diameters can reliably be used to distinguish between sub-adult and adult trees. Our study showed that sub-adults produced very few fruit, thus excluding
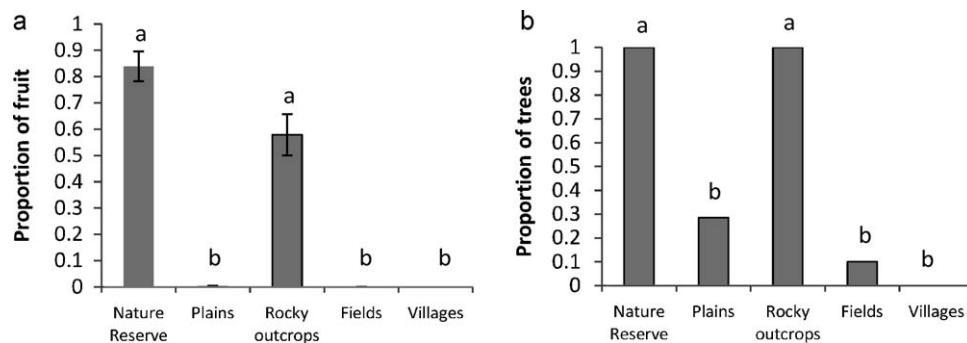

Fig. 8. Proportion of fruit predated per land-use type (a) and proportion of trees which had fruit predated per land-use type (b). Lower-case letters (a,b) indicate significant differences ($p < 0.001$).

trees <100 cm dbh (sub-adults) would make fruit inventories more efficient.

Fruit production figures from other parts of Africa are limited or not widely published. Ibiyemi et al. (1988) quoted an unsubstantiated figure of 250 fruit per mature plant. In contrast, Swanepoel (1993) reported that, over a four year period, baobabs in the Mana Pools area of the Zambezi River valley did not produce any mature fruit. He attributed this to the trees not having enough reserves to produce fruit after leaf flush and flowering, and that bark stripping by elephants may also have reduced the capacity of trees to produce fruit. No mention was made of baboon predation which could have been the main reason for poor fruit production. Assogbadjo et al. (2005) reported that mean fruit production in Benin varied between 57.1 and 157.4 fruit per tree in different climatic zones. Fruit production in communal land in South Africa of 77.1 ± 13.9 (SE) thus falls within the levels found in Benin.

Site characteristics can influence fruit production (Peters, 1996). Assogbadjo et al. (2005) found that variability in site conditions across three climatic zones in Benin significantly influenced baobab fruit productivity. Our study found that total fruit production (when including predated fruit) did not differ between land-use types, but tended to be higher in human-modified landscapes (fields and villages) and lower in natural landscapes (nature reserves, plains and rocky outcrops). Sparse ground cover resulting in reduced inter-plant competition, dripping taps (pers. obs.) which increases moisture availability–a limited resource in this arid environment, may have been responsible for the slight increase in fruit production in villages and fields.

Predation of immature baobab fruit by baboons, although not quantified, has been observed elsewhere in Africa (Wickens, 1982; Pochron, 2005; Kunz and Linsenmair, 2007; Watson, 2007). In our study fruit production was reduced by between 58% and 85% in areas where baboons were found, in contrast to 0% and 1% in areas where baboons were scarce. As baboons eat fruit that do not contain mature seed they contribute to seed destruction rather than dispersal. This shows the dramatic effect baboon predation can have on final mature fruit yield and therefore the presence of baboons needs to be taken into account when assessing areas for fruit harvesting and recruitment. Furthermore baobab populations are threatened by elephant populations (Edkins et al., 2007) in nature reserves and together with the prevalence of baboons, populations are likely to decline further in the long-term and in the end will predominate in refugia where elephant densities are low.

Baobab trees produce a wide variety of different fruit sizes (Gebauer et al., 2002; Sidibe and Williams, 2002; Assogbadjo et al., 2005). In Benin, differences in fruit size and shape are so pronounced that people use these, in addition to other morphological characteristics, to distinguish between types of baobab (Assogbadjo et al., 2008). Studies on genetic variation could not find a genetic explanation for the production of different sized fruit (length) (Assogbadjo et al., 2009).

We found that adult trees tended to produce more medium-sized (44%) than small (32%) and large-sized fruit (24%). The larger the fruit the more seed and fruit-pulp they have (Venter, unpublished data), thus by including fruit-size differences in fruit inventories, more accurate predictions of total seed, seed oil and fruit-pulp can be made.

High inter-annual variability makes predicting fruit production and assessing the economic and ecological sustainability of commercial fruit harvesting very difficult (Botelle et al., 2002; Shackleton, 2002). Our study indeed showed high inter-annual variation. Fruit production varied from as much as 81.7 ± 18.1 fruit per tree in 2006/2007 to as little as 29.7 ± 6.6 fruit per tree in 2007/2008, a two-and-a-half-fold difference between the highest and lowest year. Smaller trees showed less variation than larger

trees, as has been found for other species (Snook et al., 2005). The overall number of fruit-bearing trees did not differ between the years yet trees exhibited high within tree variability and weak between tree synchrony. Rainfall figures did not correspond to in-season fruit production. The year (2007/2008) that produced the fewest fruit had the highest rainfall. Similarly Shackleton (2002) found that fruit production in marula (*Sclerocarya birrea*), another highly valued fruit species, could not be explained by rainfall during the current growing season. He suggested that the rainfall in the preceding season might have had a greater influence on fruit production. To understand the factors that influence fruit production between years would require a much longer and more expansive study.

We categorized adult trees that produced <5 fruit a year as 'poor-producers', the rest of the adult trees we called 'producers'. Assogbadjo et al. (2008, 2009) described 'male' trees as those that produce few fruit and 'female' trees as those that produce many fruit. This could be equated to what local people in the Venda study area refer to as male (poor-producers) and female trees (producers) and they say that poor-producers are consistently so over many years (Venter, unpublished data). Tree size did not have an influence on whether trees were 'producers' or 'poor-producers' and neither did land-use type. Although we do not know what is driving this pattern, it appears that environmental conditions do not play a role because 'poor-producers' and 'producers' were often observed next to each other, presumably sharing the same soil and water conditions. Assogbadjo et al. (2009) did not find genetic difference between trees with these traits and suggested that the poor fruit production in 'male' trees may be due to self-incompatibility. Physical characteristics that could distinguish between 'poor-producers' and 'producers' where not observed by us and until these trees can be easily identified, large sample sizes would be required to get accurate predictions of population level fruit production. Further data is required to assess flowering and fruit-set patterns and to describe the extent and causes of this phenomenon.

The purpose of fruit inventories is to determine population level fruit yield. For this we need to multiply tree density with mean tree productivity. Quantifying and describing variability in both production and demographic data helps to enhance the accuracy and meaning of results. In our study high tree density in fields and villages coupled with fruit production figures meant that these land-use types delivered the highest yields. Plains and rocky outcrops had similar tree densities, but high fruit predation in rocky outcrops meant much lower mature fruit yields.

Peters (1996) suggests that enhancing recruitment of trees can have a much greater effect on future yield than trying to increase the productivity though silvicultural treatments. Baobabs are long lived trees and in arid environments may only start to produce fruit after 125 years (Swanepoel, 1993), so boosting recruitment now will only improve production in over 100 years. Needless to say removal of large quantities of seed may have negative consequences to the population in future. Thus to quantify the effects of fruit harvesting on recruitment we need to improve our understanding of what affects current recruitment rates such as seed viability, germination and seedling survival.

5. Conclusion

The capacity of trees to produce fruit did not differ significantly between land-use types. Trees in villages and fields tended to produce slightly more fruit than trees in plains, rocky outcrops and nature reserves. A greater proportion of medium-sized fruit were produced in all land-use types, except in villages where similar proportions of small and medium-sized fruit were found.

As predicted, baboons have a major impact, with up to 85% reduction in mature fruit production in nature reserves and rocky outcrops. This may have severe implications for recruitment and for the availability of fruit for human use.

It was predicted that larger trees would produce larger-sized fruit and a greater quantity of fruit than smaller trees, but the findings showed that fruit production fluctuated widely between size-classes with weak relationships between tree size (dbh and crown volume) and fruit production.

Fruit production differed significantly between sub-adult trees (<100 cm dbh), and adult trees ($\geq$100 cm dbh) with fewer sub-adult trees producing fruit than adults. It is suggested that, in order to save time and cost, only trees $\geq$100 cm dbh should be enumerated in fruit inventories.

We found high inter-annual variability in fruit production with a two and a half fold difference between the highest and lowest year. We predicted that this would be linked to in-season rainfall, but we found that this was not so and suggest that rainfall in the preceding year might have a greater impact than the current year.

A high proportion of adult trees (41%) produced less than 5 fruit per year. These were called 'poor-producers' and were equated to 'male' trees as described in West Africa (Assogbadjo et al., 2008). Poor-producers were found in all size-classes and land-use types. The extent of this tendency in Africa should be investigated as it may reveal interesting patterns in the reproductive biology of baobabs.

Baobab fruit are harvested and sold commercially throughout Africa. The use of the resource is increasing rapidly as derivatives of the fruit become sought after in international markets. This study aimed to improve the understanding of baobab fruit production in Southern Africa and to permit easier management by users, managers and conservationists and greater sustainability of this important resource.

Acknowledgements

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