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Baobab (*Adansonia digitata* L.) density, size-class distribution and population trends between four land-use types in northern Venda, South Africa

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ABSTRACT

Baobabs are important to people's livelihoods as a source of food, fibre and medicine. Baobab products are increasingly being commercialised and exported around the world, and pressure on the resource is growing (Sidibe and Williams, 2002). This paper examines baobab population structure and trends in northern Venda, South Africa.

We compare the density and life stage data of baobabs in four land-use types (plains, rocky outcrops, fields and villages). Villages and fields had higher densities of trees (2.16 ± 0.44 and 1.13 ± 0.52 plants/ha) than plains and rock outcrops (0.96 ± 0.25 and 0.83 ± 0.24 plants/ha). All land-use types had positively skewed size-class distribution (SCD) curves and negative to flat SCD slopes indicating low recruitment relative to adult density. Villages and fields had the highest juvenile densities, but exhibited flat SCD slopes indicating lowest recruitment relative to mature plant densities. High human numbers, minimal use of baobab fruit and no protection afforded to seedlings, explains low recruitment in villages and fields. Recruitment relative to adult density was most successful in the plains, which exhibited the most positively skewed SCD curves, steepest SCD slopes and the highest percentage of juvenile plants.

Overall, the population is stable with healthy numbers of mature trees. Mortality is very low, and is attributed to the lack of elephants. Quotients and the permutation index suggest that recruitment and mortality is episodic. It is concluded that current levels of recruitment are enough to maintain this population of long-lived trees. Comparisons are made with communal land elsewhere in Africa and neighbouring conservation areas, which exhibit different demographic patterns. This paper serves as a benchmark in the light of demographic changes that may arise from increased commercial use of fruit and a predicted reduction in rainfall due to climate change.

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1. Introduction

The baobab (*Adansonia digitata* L. (Malvaceae)) is an iconic tree. Throughout its range the baobab makes an important contribution to people's livelihoods for food, fiber and medicine. Baobab products are bartered and sold in urban and informal markets across Africa. They form an important source of income, especially in the dry season or at times of drought (Sidibe and Williams, 2002). Most recently, general baobab products and, in particular, derivatives of the fruit, such as baobab seed oil and baobab fruit pulp, have been exported to countries outside Africa, mainly Europe, Canada and USA. As baobab extracts become more popular, it is predicted that the demand for these resources will grow (Sidibe and Williams, 2002). To manage these resources sustainably, a

thorough understanding of the biology and ecology of the tree is required, along with an understanding of the prevailing socio-economic drivers.

In the Vhembe Municipal District, South Africa, commonly known as northern Venda, commercial use of baobab fruit began in 2005. Fruit is collected from the trees in the communal lands, fields and villages by people (mainly unemployed women). The fruit is 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 cosmetic and food ingredients markets. Similar arrangements occur throughout sub-Saharan Africa.

The study of plant population dynamics assesses changes in population size and age distribution. Abundant juveniles relative to adults resulting in an inverse J-shaped size-class distribution curve may be interpreted as a healthy and potentially growing population, but the absence of juveniles indicates a declining population (Condit et al., 1998; Miller, 1998). However, this may not hold for larger, longer-lived species – such as the baobab – where trees can sustain population levels with low or episodic

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recruitment (Condit et al., 1998). In long-lived multi-cohort populations, demographic trends are better described by life-stages than in terms of size-classes. Werner and Caswell (1977) found that stage-related models were better predictors of changes in seed and vegetative reproduction than age-related models.

Baobab populations tend to form bell-shaped or positively skewed size-class distribution curves, with many trees in the middle (100–300 cm dbh) size-classes (Assogbadjo et al., 2005; Chirwa et al., 2006; Dhillon and Gustad, 2004; Edkins et al., 2007; Hofmeyer, 2001). This general lack of recruits in baobabs has led to concern that these populations are vulnerable to severe disturbances such as wild fires, livestock browsing and clearing of fields, which have the potential to cause population collapse (Assogbadjo et al., 2005; Chirwa et al., 2006; Sidibe and Williams, 2002). In parts of Africa where baobab fruit is used in large quantities for domestic purposes and where people protect baobab seedlings, recruitment is better in villages and in fields than in untended areas such as parklands and fallows (Dhillon and Gustad, 2004; Duvall, 2007). Rocky outcrops also provide good areas for baobab recruitment because of seed dispersal by baboons which roost in rocky areas, as well as the protection inaccessible rocky areas afford baobabs from elephants (Duvall, 2007; Edkins et al., 2007; Hofmeyer, 2001; Watson, 2007; Wickens and Lowe, 2008).

This study describes population trends and compares populations in four land-use types (plains, rocky outcrops, fields and villages). We examine the proposition that because baobabs are long-lived trees, with low and episodic mortality (Kelly, 2000; S.M.

Venter, unpublished data; Whyte et al., 1996) apparent poor recruitment does not necessarily mean the population is in decline.

2. Materials and methods

2.1. Study site

This research was conducted in northern Vhembe district (northern Venda; 22°19'S and 30°28'E), Limpopo Province, South Africa (Fig. 1). The region has an average altitude of 400 m above mean sea level with gently undulating topography underlain by Karoo Supergroup rocks of 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 experiences semi-arid summer rainfall, characterised by hot summers (October–March) and mild winters (April–September) with mean annual rainfall of between 334 and 423 mm (Mucina and Rutherford, 2006). Annual precipitation is highly variable with a 35–40% coefficient of variation (Schulze, 1997). Frost seldom occurs (Mucina and Rutherford, 2006).

The study area is within the Savanna Biome and comprises Musina Mopane Bushveld, Limpopo Ridge Bushveld and Makulele Sandy Bushveld broad vegetation types (Mucina and Rutherford, 2006). This bioregion unit is dominated by *Colophospermum mopane* (mopane), *Terminalia sericea* (silver terminalia), *Grewia flava* (brandybush) and *Combretum apiculatum* (red bushwillow). The vegetation in general is low sparse woodland with an average tree height of 4–5 m, and a tree cover of 20% (Butt et al., 1994) with emergent baobabs.

Subsistence agriculture and animal husbandry are the main land-use activities between densely inhabited villages. Wooded plains, interspersed with sandstone outcrops are used mainly for grazing cattle, goats and donkeys. Subsistence crops are grown in the wet season (dryland cropping). There is open access to these natural resources with minimal control from traditional institutional structures and government. Bush fires are not common due to low grass and herb biomass, and elephants are infrequent visitors. The 2001 population census estimated a density of approximately 200 people/km². The ratio of men to women is 1:4 with a 0.78–2.38% level of formal employment (Statistics-S.A., 2001).

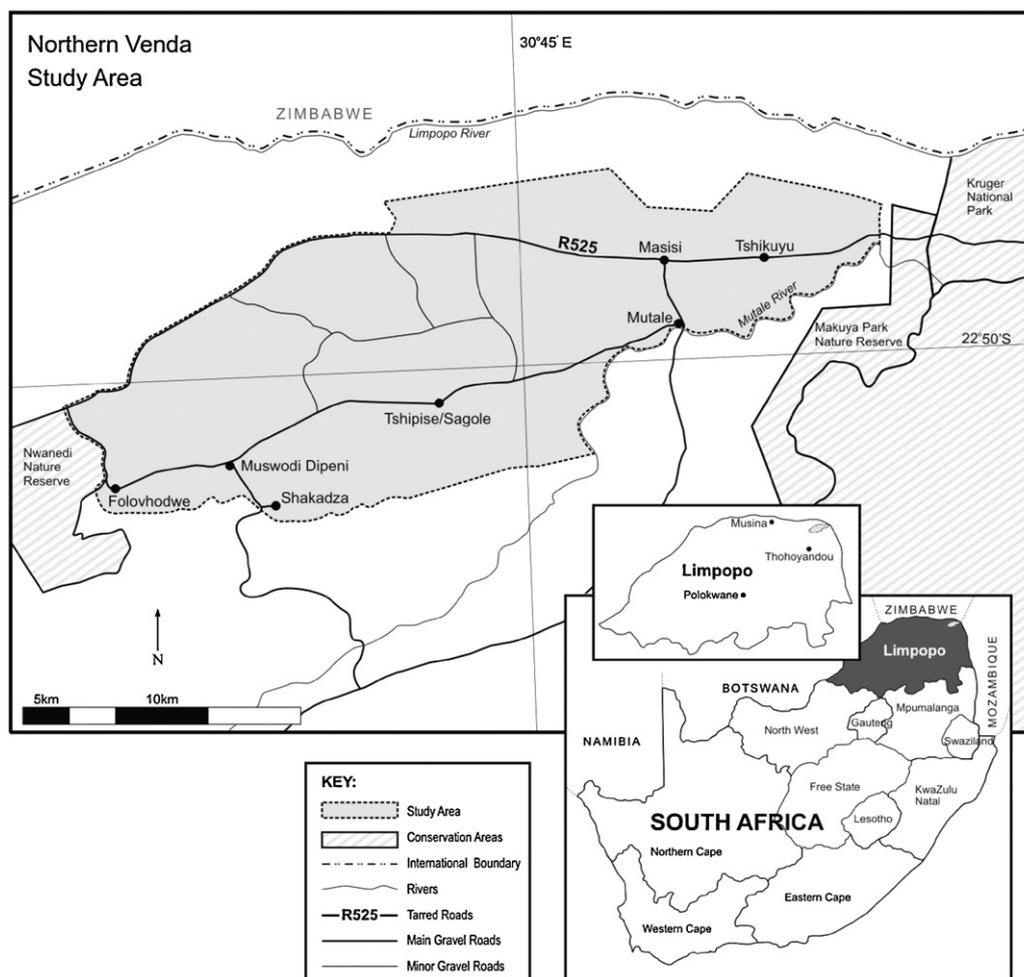


Fig. 1. Map indicating location of Northern Venda study area in Limpopo Province, South Africa.

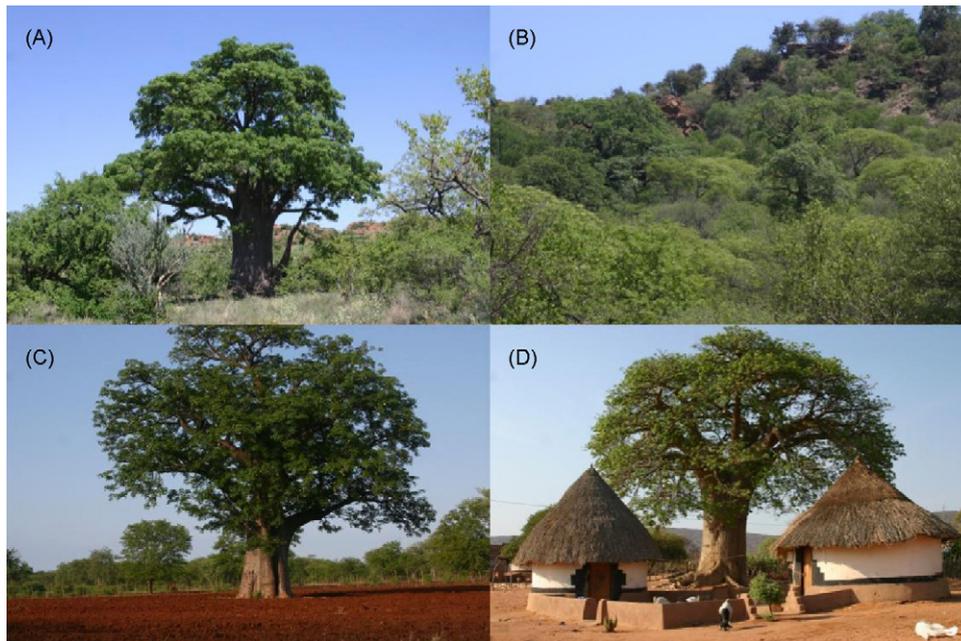


Fig. 2. Photographs of the four land-use types which were compared during the study. (A) plains, (B) rocky outcrops, (C) fields, (D) villages.

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 that occurs on mainland Africa (Baum, 1995). It is present throughout most of Africa, south of the Sahara. 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).

Baobabs generally inhabit a wide range of well-drained soils (clays to sands) in the drier plant communities of the Sudanian and Zambebian lowlands where rainfall is 200–800 mm annually (Wickens, 1982; Wickens and Lowe, 2008). They are often found along seepage lines and on the crests of rock outcrops (Wickens and Lowe, 2008). In southern Africa baobabs are emergents, associated with *Colophospermum* (mopane), *Cordyla* (wild mango) and *Kigelia* (sausage tree) woodlands in low-lying, dry, hot and generally frost-free areas (Wickens, 1982; Wickens and Lowe, 2008). Baobabs are deciduous in the dry season. Flowering lasts for two to three months during the wet season and coinciding with early leaf production (Baum, 1995; Wickens, 1982).

Baobab fruits are large, +12 cm in length (Palgrave, 1983). The pericarp is woody and indehiscent. Seeds are distributed by humans and animals, like baboons, chimpanzees and elephants (Wickens and Lowe, 2008). Baobabs are known to be extremely long-lived trees, despite the softness of their wood. Age estimates vary between 1000 and 2000 years (Wickens, 1982).

2.3. Sampling and measurement

Trees were sampled in October and November 2006. Four land-use types were sampled: (1) plains; (2) rocky outcrops; (3) fields and (4) villages (Fig. 2). Six sample sites were randomly selected from maps for each of the four land-use types. Sites were sampled using strip transects 1 km long \times 50 m wide (i.e. 5 ha). Village plots were the exception with 0.5 km long transects. This was done to accommodate small villages. The number of transects done in each land-use type was determined by their relative sizes: plains had 48 transects (48 ha \times 5 ha = 240 ha); rocky outcrops had 24 transects (24 ha \times 5 ha = 120 ha); Fields had 12 transects (12 ha \times 5 ha = 60 ha) and villages had 12 transects (12 ha \times 2.5 ha = 30 ha).

All baobab trees in the transects were measured. Diameter at breast height (DBH) was measured. Height for each tree was estimated to the closest 2 m (i.e. 2, 4, 6, ...m). Baobab saplings (DBH < 1 cm) were counted. Dead and decomposing trees were recorded.

2.4. Data and statistical analysis

Diameter at breast height (DBH) was used and is reported here. However, we also analysed mean girth so that comparisons could be made with a similar analysis by Edkins et al. (2007) in the Kruger National Park.

2.4.1. Population density per land-use type

Tree numbers were converted into densities (plants/ha), and girth to diameter. Statistica 7 was used for univariate analyses. Analysis of Variance (ANOVA)

followed by Fisher's Least Significant Difference (LSD, $p < 0.05$) test was used to compare baobab densities across the land-use types.

2.4.2. Size-class distributions

ANOVA was used to compare girth at breast height (gbh) between land-use types (following Edkins et al., 2007). To allow for visual comparisons, size-class distributions (SCDs) were constructed and displayed graphically. Size-classes were determined as 50 cm increments in diameter at breast height (dbh), i.e. 0–49 cm, 50–99 cm, 100–149 cm, ..., ≥ 500 cm dbh. Kolmogorov–Smirnov tests were used to compare size-class distributions and to test the prediction that all size-classes occurred in similar proportions among land-use types.

2.4.3. Population trends

Trees were divided into juveniles (≤ 99 cm dbh generally not yet producing fruit) and mature (≥ 100 cm dbh-producing fruit), based on fruit production per tree size-class (SM Venter, unpublished data). A senescent category was not defined because there is no significant reduction of fruit production in large trees (SM Venter, unpublished data). Percentages and densities of mature and juvenile plants are reported for each land-use type. ANOVA followed by Fisher's LSD was used to compare the density of juvenile and mature populations between land-use types. Paired *t*-tests were used to compare juvenile and mature tree densities within each land-use type and across the whole population. Using a chi-square contingency table, mature and juvenile population sizes within the four land-use types were compared.

Size-class distribution (SCD) slopes for each land-use type were calculated using the method described in Condit et al. (1998) and Lykke (1998). SCD slopes were used as indicators of population structure (Mwavu and Witkowski, 2009; Obiri et al., 2002). A least-squares linear regression was performed on the SCD data, with size-class midpoint (ln transformed) as the independent variable and the average number of individuals per size-class ($\ln(N_i+1)$) as the dependent variable. The interpretation of the SCD slopes is based on those described by Obiri et al. (2002): negative slopes indicate good recruitment, with more individuals in smaller size-classes than in larger size-classes; flat slopes indicate equal numbers of individuals in small and large size-classes; and positive slopes indicate poor recruitment with more trees found in larger than in smaller size-classes. Steepness of the slope was used to further describe recruitment trends. Steep negative slopes indicate better recruitment than shallow slopes (Lykke, 1998; Mwavu and Witkowski, 2009; Obiri et al., 2002).

Population stability was examined by calculating quotients between successive size-classes and displaying the results graphically. Constant quotients between successive size-classes indicate a stable population, while fluctuating quotient values are an unstable population (Botha et al., 2004; Shackleton, 1993).

The Permutation Index (P) was developed by Wiegand et al. (2000) to measure the degree of deviation from the monotonic decline expected in an undisturbed population. Size-classes are ranked from smallest (most frequent) to largest (least frequent). A monotonically declining population will have a Permutation Index = 0 and a population with a discontinuous SCD will have a permutation index > 0.

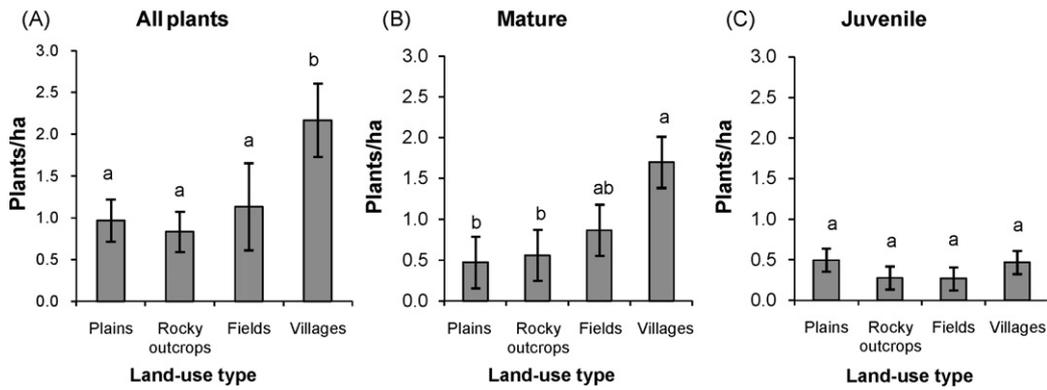


Fig. 3. Density (mean \pm SE) of all plants (A), mature (B) and juvenile (C) baobab populations in different land-use types. Bars marked with different letters (a and b) are significantly different (Fisher's LSD, $p < 0.05$).

3. Results

3.1. Population density per land-use type

The density of the baobab population across all land-use types was 1.03 ± 0.21 (S.E.) plants/ha. Villages had slightly higher densities of trees than all other land-use types ($F_{3,20} = 2.5309$, $p = 0.0860$), followed by fields, plains and rocky outcrops (Fig. 3).

3.2. Size-class distributions

The SCD for the whole population and the populations of baobab trees in each land-use type had positively skewed distribution curves, with most trees in the 50–200 cm dbh size-classes (Fig. 4). Plains have the most positively skewed SCD curve and Kolmogorov–Smirnov comparisons confirmed that it was significantly ($p < 0.05$) different to the SCD curves in other land-use types. The mean girth

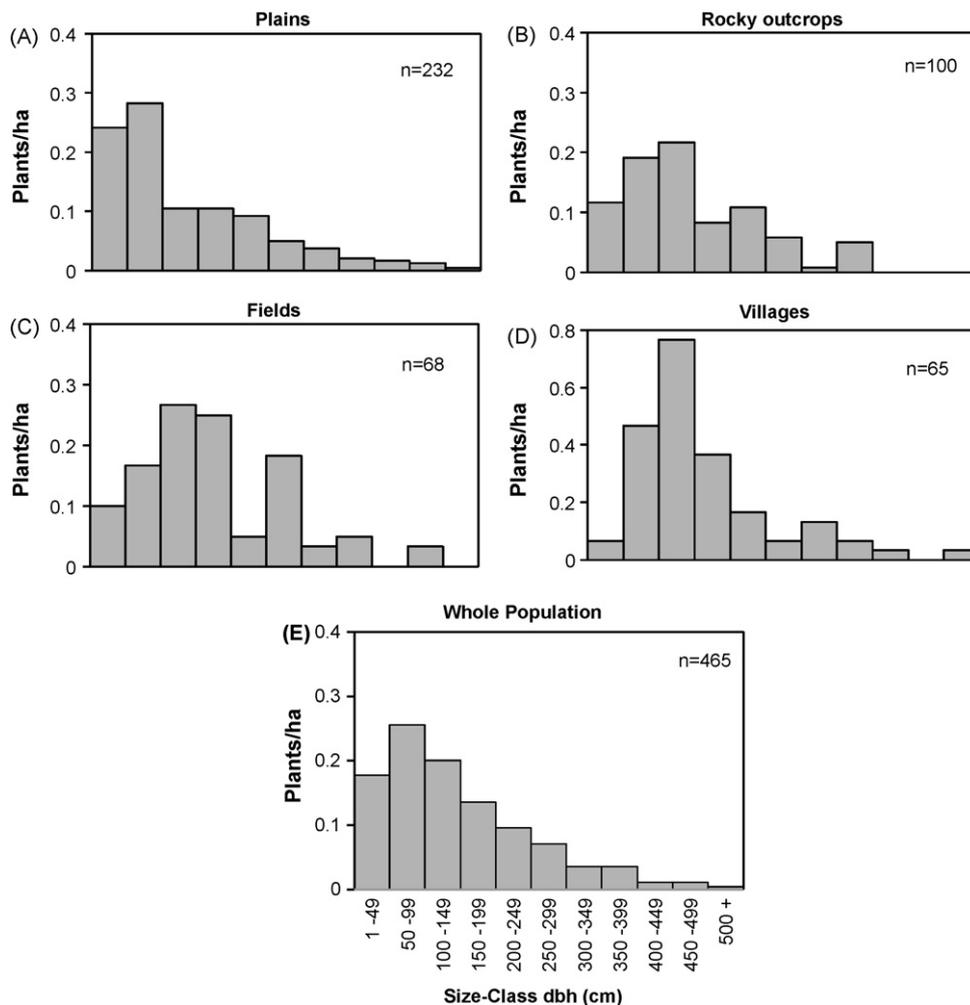


Fig. 4. Size-class distributions (dbh in 50 cm intervals) for each land-use type: plains (A), rocky outcrops (B), fields (C), villages (D) and for the whole population (E). Note Y-axis of villages (D) double the length of other figures.

Table 1
Percentage juveniles, slope of regression (dbh versus number of individuals), and Permutation Index (P) for the whole population and for different land-use types.

Land-use type	%	SCD slope				Permutation Index P
		Juveniles	Slope (°)	r ²	t	
Whole population	39%	-0.38	0.75	-5.13	<0.001	6
Plains	51%	-0.28	0.88	-7.96	<0.001	3
Rocky outcrops	33%	-0.12	0.55	-3.33	<0.01	11
Fields	24%	-0.06 [*]	0.26	-1.78	>0.05	21
Villages	22%	-0.05 [*]	0.18	-1.42	>0.05	16

^{*} Flat slope.

at breast height (gbh) of the land-use types were not significantly different.

3.3. Population trends

Plains have the highest percentage of juveniles followed by Rocky outcrops, fields and villages (51%, 33%, 24%, and 22% Table 1). The population as a whole had 39% juveniles (Table 1). The density of juveniles was similar between land-use types with plains and villages having slightly higher densities than rocky outcrops and fields (Fig. 3). The density of mature plants was significantly higher in villages, ($F_{3,20} = 3.1772, p = 0.0464$) followed by fields, rocky outcrops and plains (Fig. 3).

Paired *t*-tests comparing the densities of mature and juvenile plants within each land-use type found significant differences in rocky outcrops and villages ($p < 0.05$), but not in plains and fields (Fig. 5). Chi-squared contingency table confirmed significantly different abundances of mature and juvenile trees among the four land-use types ($X^2_3 = 31.38, p < 0.0001$). Regional density of juveniles (0.38 ± 0.07 plants/ha) was significantly lower ($p < 0.05$) than the regional density of mature plants (0.90 ± 0.18 plants/ha; Fig. 5).

SCD slopes were negative for plains and rocky outcrops, indicating that there were more individuals in smaller size-classes

than in larger size-classes (Table 1). Plains had the steepest slope, i.e. the best recruitment-followed by rocky outcrops. Fields and villages had the flattest slopes with close to equal numbers of plants in small and large size-classes, indicating lowest recruitment.

Quotients calculated between successive size-classes indicated that the populations of baobab trees in all land-use types were not evenly distributed (Fig. 6). Quotients calculated for the population as a whole masked much of this variation, showing a more even distribution in the smaller size-classes and an uneven distribution in the larger size-classes.

The Permutation Index for the regional population as well as for populations in different land-use types was greater than zero (Table 1) suggesting that recruitment and mortality are episodic events.

No dead or decomposing baobab trees were found.

4. Discussion

4.1. Trends at land-use level

Our study has revealed a number of important patterns and contrasts at the land-use level. Differences in the demographic patterns exhibited by plains and villages are particularly noteworthy. Villages had a significantly higher density of trees than plains (Fig. 3) and yet they had similar densities of juveniles (Fig. 3). Paired *t*-tests confirmed significantly lower densities of juveniles to mature trees in villages, and not in plains (Fig. 5). This shows that adult trees in villages did not recruit as successfully as those in plains. Further statistical analyses confirmed that recruitment success, relative to adult populations, in plains was better than in villages. The SCD curve in plains was more positively skewed than in villages (Fig. 4), which was confirmed by Kolmogorov–Smirnov tests, and SCD slopes were steeper in plains indicating better relative recruitment (Table 1). Quotients showed a more stable population (Fig. 6) and the permutation index was lower in plains (Table 1).

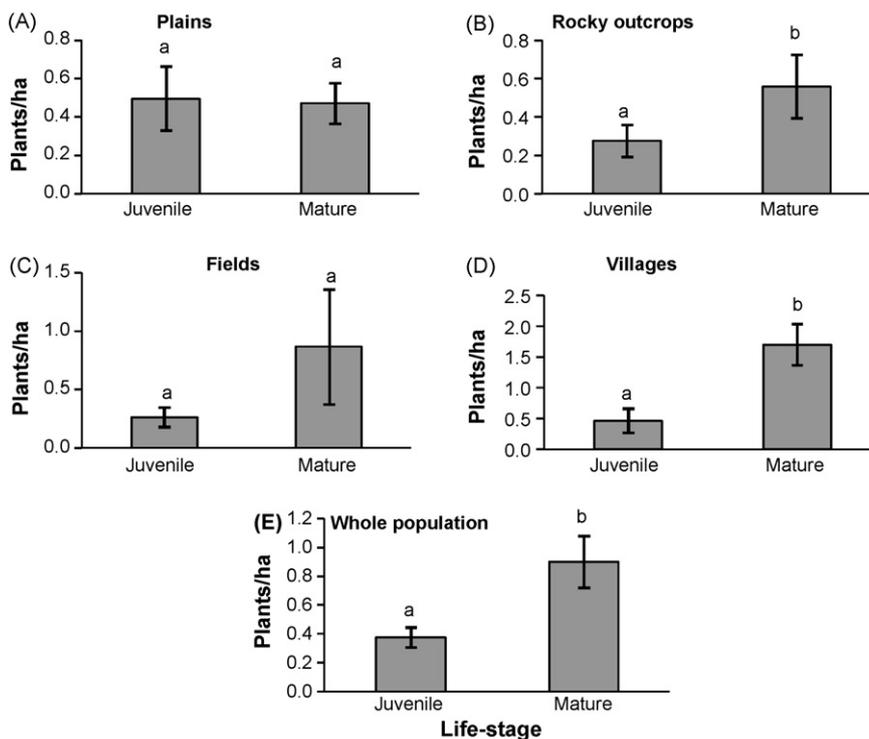


Fig. 5. Density of juvenile versus mature baobabs (mean ± SE) in plains (A), rocky outcrops (B), fields (C), villages (D) and whole population (E). Bars marked with different letters (a and b) are significantly different (Fisher's LSD, $p < 0.05$). Note different Y-axis scales.

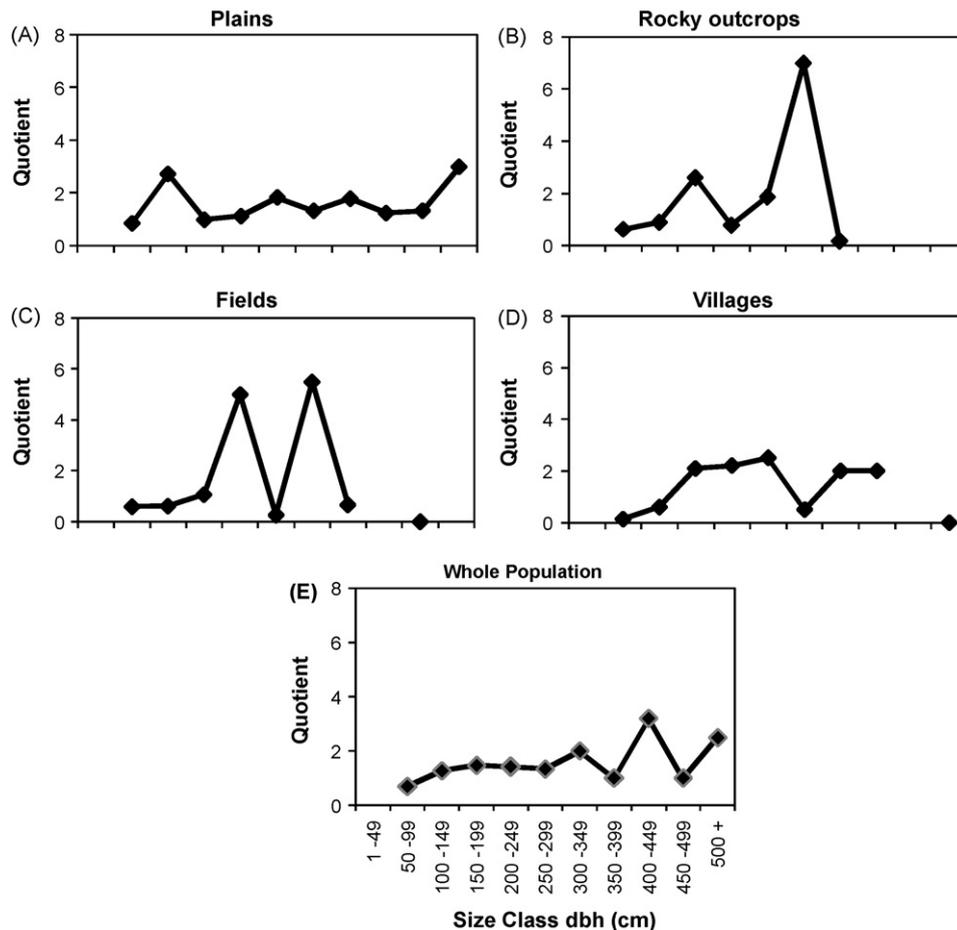


Fig. 6. Quotients between density of baobabs in successive size-classes (dbh in 50 cm intervals) for plains (A), rocky outcrops (B), fields (C), villages (D) and whole population (E).

In contrast, studies in West Africa have found that high baobab density and good recruitment is often associated with human settlement and activity (Assogbadjo et al., 2005; Dhillion and Gustad, 2004; Duvall, 2007). Duvall (2007) reports that the Manika-speaking people of West Africa effectively disperse baobab seed by collecting and using large quantities of fruit, the seeds of which are discarded around villages, where they germinate. There is also a culture of actively protecting seedlings from livestock thus increasing recruitment success of baobabs near human habitation (Assogbadjo et al., 2005; Dhillion and Gustad, 2004; Duvall, 2007). In West Africa, low recruitment rates in plains (fallows), are attributed to livestock browsing and trampling, clearing new fields, digging up seedlings to eat tap-roots, fire and overharvesting of fruit and leaves (Assogbadjo et al., 2005; Chirwa et al., 2006; Dhillion and Gustad, 2004). Our data shows that plains have a more stable population than villages with better recruitment relative to adult populations. In Northern Venda the population of trees in plains is widely spread with less exposure to disturbances caused by human activity. High human densities, infrequent domestic use of baobab fruit and lack of seedling protection may have a negative effect on recruitment in villages. The people in West Africa appear to have a stronger 'baobab culture' than the people in northern Venda which may be the reason for the difference between the two areas.

In the neighbouring Kruger National Park, density and recruitment of baobabs in plains is lower than on rocky outcrops (Edkins et al., 2007; Hofmeyer, 2001; Kelly, 2000). In contrast our data showed higher densities of baobabs and better recruitment on

plains than on rocky outcrops. In the Kruger National Park elephants have a major impact on baobabs, rocky outcrops are often inaccessible to elephants and thus act as refuge sites (Edkins et al., 2007). Both the present lack of elephants in northern Venda and the impact of baboons on seed production in rocky outcrops (SM Venter, unpublished data) may explain why the baobab population is distributed differently in northern Venda compared to the Kruger National Park.

4.2. Trends in baobabs at a population level

The classic inverse J-shaped SCD is generally used by biologists as an indication of a healthy, regenerating population, deviation from this would normally be a cause of concern (Wilson and Witkowski, 2003). Therefore, low recruitment rates and bell-shaped or positively skewed size-class distributions, which are typical of baobab populations across Africa (Assogbadjo et al., 2005; Chirwa et al., 2006; Wilson, 1988) has led many authors to express concern about the maintenance of baobab populations (Assogbadjo et al., 2005; Chirwa et al., 2006; Wickens and Lowe, 2008). However, due to the long-lived nature of baobabs and extremely low adult mortality rate, low recruitment rates may not be a cause for concern.

A number of authors have pointed out that baobab recruitment is often underestimated because of the false predictions made about baobab growth rates. Dhillion and Gustad (2004) argued that the direct conversion of girth to age underestimates baobab recruitment, as young baobabs grow faster relative to older trees,

suggesting that recruitment is not as poor as it appears. Breitenbach and Breitenbach (1985) analyzed the growth of 40 planted baobab trees of known age, and found that baobab tree growth tapers off within the first quarter of the lifespan of the tree (after 200 years of an 800-year old tree); thus three quarters of its life (± 600 years) is spent at almost the same diameter. They too warned that the extremely slow growth of adult trees could lead to false predictions of baobab ages. This was supported by Patrut et al. (2007), who did radiocarbon dating of the 'Grootboom' (meaning big tree) baobab in Namibia.

Condit et al. (1998) confirm that trees which grow rapidly in small size-classes and trees that have a high overall rate of survival will exhibit flat SCD slopes, and also that large, long-lived trees are able to sustain population levels with low or episodic recruitment. Wickens and Lowe (2008) also pointed out that, because of the longevity of baobabs, only a few recruits are necessary to maintain the current population of trees. Hofmeyer (2001), came to the same conclusion in the Kruger National Park, 20 km east of our study site. She has suggested that there are sufficient trees in reproductive size-classes, and that the low number of small trees simply indicate a poor recruitment phase for baobabs.

During our surveys we did not come across any dead or decomposing baobabs. Interviews with villages confirmed that mortality has been very low for many years and that baobabs only die in bad droughts (SM Venter, unpublished data). Kelly (2000) and Wilson (1988) calculated baobab annual mortality rates from populations across Africa and obtained mortality rates of between 0.69 and 3.7%. Whyte et al. (1996) found that baobab mortality was strongly linked to elephant numbers and that drought caused episodic baobab mortality.

Despite the acceptability of low recruitment rates for baobabs, Wickens and Lowe (2008) were of the opinion that baobabs may currently be threatened by climate change because regeneration appears to be confined to areas with higher rainfall. This concern was also expressed by Maranz (2009) who found that ecosystems in the African Sahel are losing large trees due to changing climate patterns.

Our conclusion is that the baobab population in northern Venda is currently stable. Our data indicates a population that has a healthy proportion of mature trees in all land-use types. The lack of elephants in the area explains low mortality rates. Although SCD curves are not typically inverse J-shaped (normally associated with good recruitment), baobabs are very long-lived trees so that even with low recruitment, current population levels can be maintained. Our data indicates that recruitment (specifically seedling establishment) and mortality are very likely to be episodic events. More information is required on factors that trigger these events.

However, recent expansion of baobab fruit harvesting and the predicted drop in rainfall attributed to climate change may negatively affect future recruitment and may increase tree mortality. Thus knowledge of current recruitment and mortality rates will guide resource management decisions and serve as a valuable reference point in future population studies. In villages, where baobab populations have relatively low recruitment rates, resource managers should encourage a 'culture' that will enhance regeneration.

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References

- Assogbadjo, A.E., Sinsin, B., Codjia, J.T.C., Van Damme, P., 2005. Ecological diversity and pulp, seed and kernel production of the baobab (*Adansonia digitata*) in Benin. *Belg. J. Bot.* 138, 47–56.
- Baum, H.G., 1995. The comparative pollination and floral biology of baobabs (*Adansonia-Bombacaceae*). *Ann. Mo. Bot. Gard.* 82, 322–348.
- Botha, J., Witkowski, E.T.F., Shackleton, C.M., 2004. Impact of communal harvesting on *Warburgia salutaris* ('pepper-bark tree') in Mpumalanga, South Africa. *Biodivers. Conserv.* 13, 1675–1698.
- Brandl, G., 1981. The Geology of the Mesina Area. Geological Survey. Dept of Mineral and Energy Affairs, South Africa, Pretoria.
- Breitenbach, v.F., Breitenbach, v.J., 1985. Aantekeninge oor die groeitempo van aangeplante kremetartbome (*Adansonia digitata*) en opmerkinge ten opsigte van lewenstyd, groeifases en genetiese variasie van die spesie. *Dendrologiese Tydskrif* 5, 1–21.
- Butt, M.J., Everard, D.A., Geldenhuys, C.J., 1994. The Distribution and Composition of Vegetation Types in the Soutpansberg-Blouberg Mountain Complex. CSIR.
- Chirwa, M., Chithila, V., Kayambazinthu, D., Dohse, C., 2006. Distribution and Population Structures of *Adansonia digitata* in Some Parts of Ntcheu, Dedza and Mangochi Districts, Malawi. FRIM, Zomba, Malawi.
- Condit, R., Sukumar, R., Hubbell, S.P., Foster, R.B., 1998. Prediction population trends from size distributions: a direct test in a tropical tree community. *Am. Nat.* 152, 495–509.
- Dhillon, S.S., Gustad, G., 2004. Local management practices influence the viability of the baobab (*Adansonia digitata* Linn.) in different land use types, Cinzana, Mali. *Agric. Ecosyst. Environ.* 101, 85–103.
- Duvall, C.S., 2007. Human settlement and baobab distribution in south-western Mali. *J. Biogeogr.* 34, 1947–1961.
- Edkins, M.T., Kruger, L.M., Harris, K., Midgley, J.J., 2007. Baobabs and elephants in the Kruger National Park: nowhere to hide. *Afr. J. Ecol.* 46, 119–129.
- Hofmeyer, M.V., 2001. Spatial demography of selected tree species in the Kruger National Park in relation to elephant impacts. In: Progress report for research committee meeting, University of Witwatersrand, South Africa.
- Kelly, H.L.P., 2000. The Effect of Elephant Utilization on the *Sterculia rogersii* and *Adansonia digitata* Populations of the Kruger National Park. Faculty of Natural and Agricultural Sciences, University of Pretoria, Pretoria.
- Lykke, A.M., 1998. Assessment of species composition change in savanna vegetation by means of woody plants' size class distributions and local information. *Biodivers. Conserv.* 7, 1261–1275.
- Maranz, S., 2009. Tree mortality in the African Sahel indicates an anthropogenic ecosystem displaced by climate change. *J. Biogeogr.* 36, 1181–1193.
- Miller, G.T., 1998. *Living in the Environment: Principles, Connections and Solutions*. Wadsworth Publishing Company, USA.
- Mucina, L., Rutherford, M.C. (Eds.), 2006. *The Vegetation of South Africa, Lesotho and Swaziland*. South African Botanical Institute, Pretoria.
- Mwavu, E.N., Witkowski, E.T.F., 2009. Population structure and regeneration of multiple-use tree species in a semi-deciduous African tropical rainforest: implications for primate conservation. *Forest Ecol. Manage.* 258, 840–849.
- Obiri, J., Lawes, M., Mukolwe, M., 2002. The dynamics and sustainable use of high-value tree species of the coastal Pondoland forests of the Eastern Cape Province, South Africa. *Forest Ecol. Manage.* 166, 131–148.
- Palgrave, K.C., 1983. *Trees of Southern Africa*. Struik Publishers, South Africa.
- Patrut, A., Von Reden, K.F., Lowy, D.A., Alberts, A.H., Pohlman, J.W., Wittmann, R., Gerlach, D., Xu, L., Mitchell, C.S., 2007. Radiocarbon dating of a very large African baobab. *Tree Physiol.* 27, 1569–1574.
- Schulze, R.E., 1997. *South African Atlas of Agrohydrology and Climatology*. Water Research Commission, Pretoria.
- Shackleton, C.M., 1993. Demography and dynamics of the dominant woody species in a communal and protected area of the eastern Transvaal Lowveld. *S. Afr. J. Bot.* 59, 569–574.
- Sidibe, M., Williams, J.T., 2002. Baobab *Adansonia digitata*. International Centre for Underutilized Crops, Southampton, UK.
- Statistics-S.A., 2001. In: <http://www.statssa.gov.za/census>.
- Watson, R., 2007. *The African Baobab*. Struik Publishers, Cape Town, South Africa.
- Werner, A., Caswell, H., 1977. Population growth rates and age versus stage-distribution models for Teasel (*Dipsacus sylvestris* Huds.). *Ecology* 58, 1103–1111.
- Whyte, I.J., Nel, P.J., Steyn, T.M., Whyte, N.G., 1996. Baobabs and Elephants in the Kruger National Park: Preliminary Report. Scientific Report Number 5/96. Scientific Services Section, Kruger National Park, South Africa.
- Wickens, G.E., 1982. The Baobab-Africa's upside-down tree. *Kew Bull.* 37, 173–209.
- Wickens, G.E., Lowe, P., 2008. *The Baobabs: Pachycauls of Africa, Madagascar and Australia*. Springer.
- Wiegand, K., Ward, D., Thulke, H., Jeltsch, F., 2000. From snapshot information to long-term population dynamics of *Acacia* by a simulation model. *Plant Ecol.* 150, 97–114.
- Wilson, R.T., 1988. Vital statistics of baobab (*Adansonia digitata*). *Afr. J. Ecol.* 26, 197–206.
- Wilson, B.G., Witkowski, E.T.F., 2003. Seed banks, bark thickness and change in age and size structure (1978–1999) of the African savannah tree, *Burkea africana*. *Plant Ecol.* 167, 151–162.