Phenology, flowering and fruit-set patterns of baobabs, *Adansonia digitata*, in southern Africa

Sarah M. Venter*, Ed T.F. Witkowski

School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg, South Africa

ABSTRACT

Baobabs (*Adansonia digitata*) are iconic and highly valued trees that characterise many semi-arid environments across Africa. The aim of this study was to describe leaf, flowering and fruit phenology, flower production and fruit-set patterns of southern African baobabs. This was done on a sample of 106 trees across five land-use types at monthly intervals over two-years. Rainfall in the first year (2006/7, Year 1) was only 275 mm, but doubled in the second year (516 mm; 2007/8, Year 2), being below and above the long term mean of 461 mm, respectively. Leaf flush preceded the onset of rains (October) in 88% of trees in Year 1, but after the onset of rains (August) in all trees in Year 2. Leaves flushed in November and were retained until April and in October and retained until March, respectively. Leaf fall occurred one month later in Year 1 (May) than in Year 2 (April). Flowering followed a steady-state pattern, lasting for 1–5 months with peak flowering in November in both years. For adult trees, flower number/tree (Year 1: 711 ± 72 (S.E.) and Year 2: 287 ± 33), but not fruit-set (mean of 20 ± 4%) varied significantly between years. Flower number showed a logarithmic relationship with tree size (stem diameter) ($R^2 = 0.3830$, $P < 0.0001$), while fruit-set was unrelated to tree size ($R^2 = 0.0045$, $P = 0.5081$). Flower number and fruit-set did not vary between five land-use types, but length of flowering did, with village trees flowering for the longest period. Baobabs are hermaphrodite plants with both male and female reproductive structures in the same flower. Yet, across Africa many people refer to individual trees as being 'male' (fruiting is absent or minimal) or 'female' (substantial fruiting). Producer 'female' and poor-producer 'male' trees, did not differ in flowering phenology (number, timing and length of flowering), but fruit-set over two sequential years differed greatly between producer (33.5 ± 5.2%) and poor producer (0.2 ± 0.1%) trees. Leaf flush was responsive to early rains and hence baobabs appear to be facultative early greeners. However flowering and fruit-set patterns were not significantly different between these two years, despite the large rainfall difference. Although flower production was not different between producer and poor-producer trees in either year, fruit set was three orders of magnitude higher in producer than poor-producer trees. These quantitative results suggest that baobabs may be functionally dioecious and thus a complete characterization of the reproductive biology is required. Mechanisms underlying this pattern are discussed in terms of tree age, environment, pollination, genetics and evolutionary biology.

1. Introduction

Knowledge of plant phenology at the individual and population levels improves our understanding of community and ecosystem dynamics and aids in management (Childes, 1989; Chidumayo, 2001, 2015; Whitecross et al., 2016, 2017a,b; Adole et al., 2018). Observed changes in plant phenology, both in leaf and flowering/fruiting, of crops and indigenous plants, are likely to be long-term responses to global change (e.g., Cuni Sanchez et al., 2011; Craparo et al., 2015). Flowering phenology of the African baobab (*Adansonia digitata* L.) (Cron et al. (2016)) has been described for a number of sites around

Africa, however very little quantitative work has been published. Dhillion and Gustad (2004) and Assogbadjo et al. (2005) included phenological diagrams in their work in West Africa and Fenner (1980), Wickens (1982) and Swanepoel (1993) contributed personal observations from other parts of Africa. Von Breitenbach and Von Breitenbach (1974) spent a season enumerating the nocturnal opening of flowers on one tree in northern South Africa. These accounts indicate that baobab phenology varies across Africa with latitude and rainfall, but none offer information on between tree, environmental and inter-annual variation in flowering phenology.

A thorough and informative contribution on floral morphology

comes from Baum (1995a). However, studies on other aspects of the reproductive biology are scarce with limited observations of bat pollination in West and East Africa (Baum, 1995a). To date, breeding system studies have not been done.

Baobabs are hermaphrodite plants with cosexual flowers (Baum, 1995a). Female and male reproductive organs are large and conspicuous in the flowers and yet right across Africa, there is a pervasive belief that individual adult trees are either male or female (Assogbadjo et al., 2008; Venter and Witkowski, 2013b; Venter et al., 2017; Diana Mayne, Colin Bristow and Kemi NKaelang, pers. comm.). Trees that consistently produce a substantial number of fruit from year to year are referred to as 'female' and those that consistently produce very few or none, as 'male'.

In West Africa, local people associate female baobabs with desirable traits such as delicious leaves, easy-to-harvest bark, sweet acidic non-slimy pulp and large good tasting kernels, whereas male trees are associated with slimy fruit pulp, tasteless kernels, bitter leaves and difficult-to-harvest bark (Assogbadjo et al., 2008). In southern Africa, local people also distinguish between male and female trees. Interviews conducted with baobab fruit harvesters revealed that 90% believed that there were male and female baobab trees (Venter and Witkowski, 2013b). Local African people and park rangers in both southern and East Africa regularly mention this phenomenon (Diana Mayne, Colin Bristow and Kemi NKaelang pers. comm.). The results of a baobab fruit production study by Venter and Witkowski (2011) found that 41% of adult trees consistently hardly produced any fruit despite apparent normal flowering year after year. These trees were termed 'poor-producers' and it was suggested that they might be likened to 'male' trees, while those trees producing many fruits were terms producers, equivalent to the 'female' trees. The high prevalence of male trees in the population is intriguing.

Many savanna trees flush leaves prior to the first significant rains at the start of the rainy season (Chapotin et al., 2006; Chidumayo, 2015, Ryan et al., 2017; Whitecross et al., 2017a). Savanna trees flush new leaves prior to the start of the summer rains, usually in late winter (August) which may provide an advantage over the grasses, which only produce new leaves when the rains start (Whitecross et al., 2017b). Baobabs in general occur in some of the driest savannas, therefore quantifying their leaf phenology between land-use types and between years or growing seasons would be valuable. Climate assessments indicate that Africa will probably experience significant changes in climate in the 21st century, with drying and warming in most subtropical regions (Cuni Sanchez et al., 2011). Baobab leaves are commonly eaten as a "spinach" in west African countries, to the point that the trees can be defoliated to the extent that flowering and fruiting is prevented (Schumann et al., 2010; Agundez et al., 2018), but it has not been quantified as to how leaf harvesting effects leaf phenology in subsequent years.

The aim of this study was to describe baobab leaf and reproductive phenology and to quantify flowering and fruit-set in relation to intrinsic (tree size and life-stage) and extrinsic (environmental) factors. It was predicted that flowering and fruit-set would increase with tree size, that there would be differences between land-use types and that high inter-annual variation would be linked to rainfall patterns. We looked at the difference in flowering and fruit-set between "producer" and "poor-producer" trees, predicting that "poor-producers" would have more flowers and flower for longer as a functional allocation to male fitness (pollen donation).

The specific objectives of the study were:

1) Describe baobab phenology in southern Africa.
2) Describe and quantify inter-annual variation in flowering and fruit-set for two sequential years.
3) Test the prediction that flowering and fruit-set increases with tree size (dbh).
4) Investigate how flowering and fruit-set differs between adult and sub-adult (< 100 cm dbh) life stages.
5) Compare fruit-set and flowering between land-use types.
6) Test whether 'producers' and 'poor-producers' differed in flowering and fruit-set.

2. Materials and methods

2.1. Study site

Research was conducted in northern South Africa (around 22°19′S and 30° 28′E), an area commonly known as Northern Venda. It is a semi-arid savanna with annual rainfall between 334 and 423 mm with a high 35–40% interannual coefficient of variation (Schulze, 1997). Summers (October-March) are commonly hot and winters (April–September) are mild. Frost seldom occurs (Mucina and Rutherford, 2006). The average altitude of the region is 400 m a.s.l. and is underlain by sandstones of the Karoo Supergroup and the Clarens and Letaba Formations (Mucina and Rutherford, 2006). Soils are generally deep sands and shallow sandy lithosols (Mucina and Rutherford, 2006). It is part of the Zambezian Regional Centre of endemism where baobabs are associated with *Colophospermum mopane* (mopane) woodland (Wickens and Lowe, 2008). Bush fires are not common, due to low grass and herbaceous plant biomass. Elephants are infrequent visitors. The area comprises communally managed land consisting of rangelands, fields and villages with two provincially managed nature reserves, Makhuya and Nwanedi, flanking the study area to the east and west respectively (Fig. 1).

2.2. Study species

Adansonia digitata is one of eight species of baobab in the genus *Adansonia* L. (Malvaceae, subfamily Bombacoideae) and the only one which naturally occurs on mainland Africa (Baum, 1995b; Cron et al., 2016). In South Africa baobabs are limited to the Limpopo River valley, with the exception of a few isolated trees further south (Wickens and Lowe, 2008).

Phylogeographic research shows that the African baobab is tetraploid and may have evolved from a diploid ancestor originating in West Africa. Three distinct groups 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).

Baobabs are deciduous, bearing leaves and flowers in the wet season (Wickens, 1982; Baum, 1995a). Flowers are large (8–12 cm), white and pendulous with stigma, anthers and nectar spatially separated in the same flower. Anthesis usually occurs in the evening, with 10–15 flowers/tree opening synchronously each night. This takes place rapidly when the calyx, which completely encloses the flower bud, splits open and flexes back. Flowers abscise within 24 h (Baum, 1995a). Stigma receptivity commences at the time of anthesis and remains receptive until morning. Controlled hand pollination experiments on baobab flowers showed that *A. digitata* are self-incompatible (Venter et al., 2017). In well-watered environments such as gardens, trees grown from seed can start to flower from 22 years of age (Pardy, 1953). However, in their natural semi-arid environment, trees may only start flowering at 125–189 years of age (Swanepoel, 1993; A. Patrut, D. Mayne and S.M.Venter, unpublished data). The period between flowering and fruit ripening is usually 5–6 months (Sidibe and Williams, 2002). Seed production is substantial and seed viability is consistently very high (> 89%), but recruitment is limited by poor rainfall and herbivory (Venter and Witkowski, 2013a,b).

2.3. Sampling and measurement

Field work was done over two years, starting in July 2006 and ending in June 2008 covering two rainfall seasons in Year 1 (October
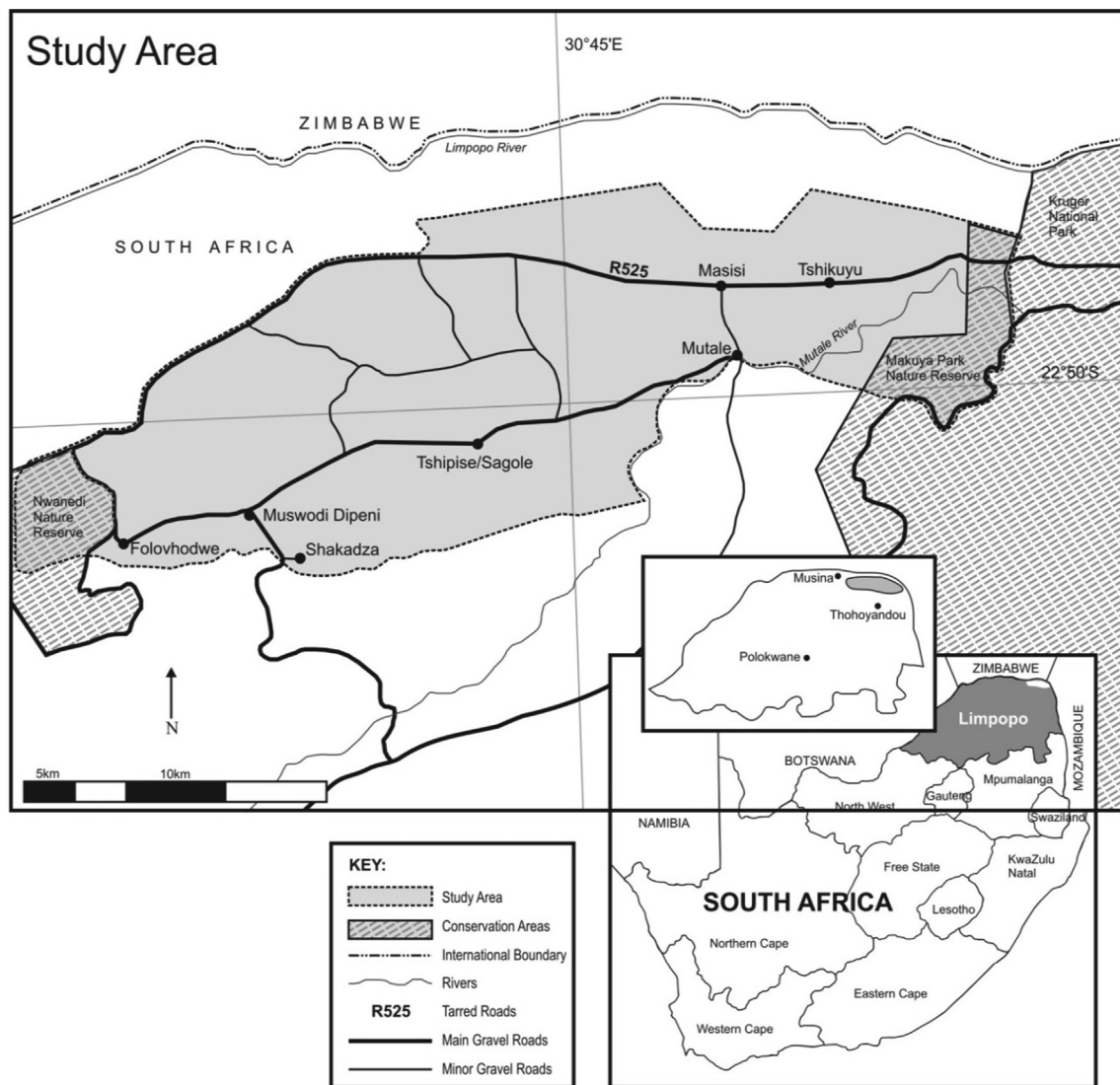
Fig. 1. Map indicating location of study area in Limpopo Province, South Africa.

2006 to April 2007) and Year 2 (October 2007 to April 2008). 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 (Venter and Witkowski, 2010). In total, 106 trees were sampled, 34 in nature reserves and 18 in each of the other land-use types, and include a wide range of stem diameters.

Geographic position (degrees latitude and longitude) and diameter at breast height (dbh, at 1.3 m above the ground) was recorded for each tree. Each tree was assessed repeatedly for leaves, flowers and fruit at 1 month intervals. For each assessment, the presence and absence of leaves were recorded. Flowers and fruit on all the trees were counted. Fallen fruit were counted and discarded, to prevent double counting. Fruit-set was determined as the percentage of fruit to flowers per tree. Rainfall and temperature records were sourced from the adjacent Kruger National Park and the Musina Weather Station.

2.4. Data analysis

Phenological diagrams were constructed for each year, using the proportion of adult trees that were in leaf, flower and fruit each month. These were visually compared with rainfall and temperature variations to discern possible environmental cues.

The onset of flowering and leaf flush for each year was compared to each other and to the onset of rainfall by using the percentages of trees in flower and in leaf. To test if there were significant differences in the number of trees that flowered in November and December of each year, Cochran Q tests were used.

The total number of flowers (log transformed), length of flowering (months), percentage fruit-set (arcsine transformed) and proportion of flowering trees were compared between years using the Wilcoxon matched pairs test and the Cochran Q test. Data were combined for both years and ANOVA followed by Fishers Least Significant Difference (LSD) ($p < 0.05$) was used to test length of flowering against number of flowers (log transformed), number of fruit (log transformed), fruit-set (arcsine transformed) and tree size (dbh). For this analysis only 2, 3 and 4 month data were used because the few trees that flowered for 1 month (3 trees) and for 5 months (5 trees) exhibited high variability.

Population peak flowering was defined as > 50% of adult trees in flower in a calendar month. For individual trees, a peak flowering month was defined as the month in which the tree produced the largest number of flowers compared to other months. These were depicted graphically against rainfall. Differences in flower number (log transformed), fruit number (log transformed) and fruit-set (arcsine transformed) of trees that had peaked in different calendar months within each year were analysed using t-tests and ANOVA. November was

considered a peak flowering month, so, to test if this was consistent between years, the Cochran Q test was used.

The proportion of adult trees falling into each flower production class (0–4, 5–49, 50–199, 200–399, 400–599, 600–799, 800–999, 1000–1499, ≥1500 flowers/tree) and fruit-set class (0%, 0.1–0.9%, 1–19%, 20–39%, 40–59%, 60–79%, 80–100% fruit set/tree) was illustrated. Further figures show average fruit-set and fruit number per flower class. Regression analysis tested the relationship between flower number and fruit-set. Diameter at breast height (dbh) was chosen as an indicator of tree size because it is well related to crown size ($R^2 = 0.5904$) (Venter and Witkowski, 2011). Regression analysis determined if flowering and fruit-set increased with dbh. Frequency distributions of flowers/tree were constructed for each year and for both years combined. This allowed for visual comparisons and to test for differences between years using Kolmogorov-Smirnov tests. Trees were divided into sub-adult (< 100 cm dbh) and adult (≥ 100 cm dbh) life-stages, (Venter and Witkowski, 2011) and the difference in numbers of flowers (log transformed) and fruit-set (arcsine transformed) between life-stages within each year was tested using t-tests. Differences between years in flowering, fruit-set and number of flowering trees was tested using the Wilcoxon matched pairs test and the Cochran Q test.

Differences between land-use types in number of flowers (log transformed), length of flowering and fruit-set (arcsine transformed) were compared over both years using ANOVA followed by Fisher's LSD ($p < 0.05$).

Using t-tests, adult trees that were classed as 'poor-producers', based on consistently producing < 5 fruit per year (Venter and Witkowski, 2011), were compared to adult 'producers', for flower number (log transformed), length of flowering and fruit-set (arcsine transformed). Regression analysis tested the relationship between flowering and fruit-set for 'producers' and 'poor-producers' separately.

3. Results

3.1. Phenological patterns

Rainfall in Year 1 was below average (275 mm), starting in October and stopping in May, while in Year 2 the rains were above average (516 mm) and with exceptionally high early rains, but stopping in April, a month earlier than the previous season. (Fig. 2). Temperature did not differ much between years, with both years following typical heating up and cooling patterns.

Leaf flush responded more quickly to early rain than did flowering (Fig. 2). In Year 1, trees flowered and flushed leaves at the same time, whereas in Year 2 trees flushed leaves one month earlier than flowering, apparently in response to the exceptionally early and above-average rainfall in Year 2 (Table 1). Leaf fall occurred one month later in Year 1 than in Year 2 presumably in response to the rainfall ending later in Year 1 than in Year 2 rather than in response to temperature, which stayed similar, month to month for both years. Overall the trees were in leaf for 6 months in both years, despite the large differences in rainfall, but started a month later in Year 1 compared to Year 2 (Fig. 2).

Baobabs followed a steady-state flowering pattern (Gentry, 1974) with flowering starting in November (Year 1) and October (Year 2) and continuing until April in both years (Fig. 2). Flowering between years was compared for October, November and December. In October of Year 1 no trees flowered, whereas in October of Year 2, 75% had started flowering. There was no significant difference in the number of trees that flowered in November of each year (Q = 2.0000, $P = 0.1573$). However, significantly more trees flowered in December of Year 1 than December of Year 2 (Q = 16.1333, $P < 0.0001$) (Fig. 3(a and b)). Adult trees flowered for significantly longer in Year 1 than Year 2 (Z = 2.8996, $P = 0.0037$) (Fig. 3c). In both years, flowering decreased in January and stopped in April, but in Year 1 10% more trees continued to flower during the late summer season (January – April), possibly in response to in season rainfall events (Fig. 3(a and b)). Trees

that flowered for 4 months produced significantly more flowers than trees that flowered for only 2 and 3 months ($F_{2,144} = 4.7959$, $P = 0.0096$) (Fig. 4a). Population peak flowering differed between years, although the majority of trees peak-flowered in November in both years (Q = 0.0265, $P = 0.8728$) (Fig. 3). Trees that peak-flowered in different months of the same year did not differ in number of flowers produced (Table 2). The proportion of adult trees (> 100 cm dbh) per flower production class (Fig. 5a) had a positively skewed distribution, the majority of adult trees (53%) produced between 200 and 599 flowers. Nine percent produced > 1000 flowers per year, and 4% produced < 49 flowers per year (Fig. 5a).

3.2. Fruit-set and fruit production patterns

Trees that peak-flowered in different months of the flowering season did not differ in fruit-set or fruit production (Table 2).

Adult trees that produced between 50 and 400 flowers had the highest average fruit-set of 30%. After this, fruit-set declined with flower number (Fig. 5c). Trees that produced > 1500 flowers had a fruit-set of $< 1\%$. This explains why trees that ranged from 200 to 1500 flowers produced similar amount of fruit (Fig. 5b), with the exception of trees that produced > 1500 flowers; these trees, by contrast, produced very few fruit. However adult trees that produced < 50 flowers did not produce any fruit and may have been compromised by the environment. Regression analysis (excluding trees with < 50 flowers) shows a weak negative trend between flower number and fruit-set ($R^2 = 0.0973$, $P = 0.0065$) confirming the negative trend in Fig. 5c. Fig. 5d shows that the proportion of trees per fruit-set class had an inverse J-shaped distribution. 23% of adult trees did not set fruit at all, and 31% had fruit set of $< 1\%$. Fruit-set decreased with an increase in flowering time ($F_{2,144} = 3.6770$, $P = 0.0277$) (Fig. 4b). However, fruit production did not differ significantly between flowering periods ($F_{2,144} = 1378$, $P = 0.2562$). Declining fruit-set may have counteracted the increase in flower number, thus evening out fruit production against length of flowering (Fig. 4).

3.3. Tree size in relation to flowering and fruit-set

Regression analysis showed that there were weak logarithmic trends between dbh and flowering ($R^2 = 0.3830$, $P < 0.0001$), and no trend between dbh and fruit-set ($R^2 = 0.0045$, $P = 0.5081$). Neither length of flowering (Fig. 4d) nor timing of peak flowering differed with tree size ($F_{2,146} = 0.0814$, $P = 0.9218$; $F_{2,152} = 0.4636$, $P = 0.9541$).

3.4. Inter-annual variation

There was a significant difference between years in the number of flowers produced by adult trees (Z = 5.4613, $P < 0.0001$) (Table 3). The shape of the size-class distribution for flower production did not differ between years, which means that all trees, regardless of size, produced fewer flowers in Year 2 (D = 0.09, $P > 0.05$), despite the higher rainfall (Fig. 6). There was no significant difference in fruit-set between the years (Z = 0.6141, $P = 0.5391$) (Table 3). Furthermore, the number of adult flowering trees did not differ between years (Q = 1, $P = 0.3173$) (Table 3).

3.5. Life-stage

Trees < 100 cm dbh produced significantly fewer flowers, but did not have significantly lower fruit-set than trees ≥ 100 cm dbh (Table 3). Sub-adults produced significantly more flowers in Year 1 than in Year 2 (Z = 3.8826, $P < 0.0001$) (Table 3). Fruit-set did not differ significantly between years (Z = 1.2602, $P = 0.2067$) (Table 3). A significantly different number of sub-adult trees flowered each year (Q = 8, $P = 0.0047$) (Table 3).
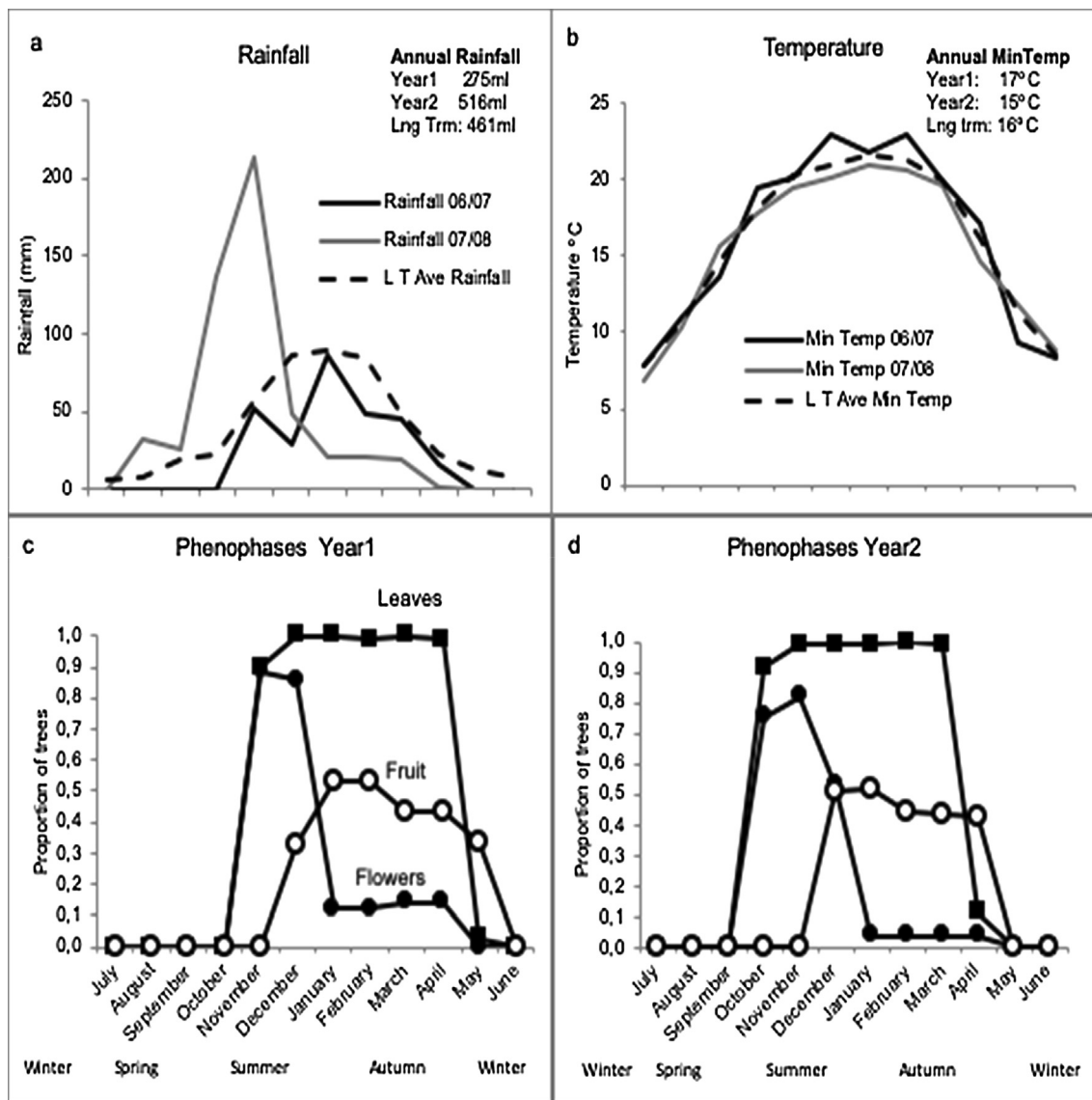
Fig. 2. Relationship between monthly weather conditions and phenological states: (a) Monthly rainfall for Year 1 and Year 2 and the long-term (80 yr) average; (b) Monthly minimum temperature for Year 1 and Year 2 and the long-term (19 yr) average minimum temperature; (c) & (d) Proportion of *Adansonia digitata* trees in Year 1 (c) and Year 2 (d) that were in leaf (filled squares) and which had flowers (filled circles) and fruit (open circles) each month (n = 106).

3.6. Land-use type

There were no differences in flower number ($F_{4,150} = 1.5133$, $P = 0.2011$) or in fruit-set ($F_{4,150} = 0.8419$, $P = 0.5006$) between land-use types over both years. However, trees in villages tended to produce more flowers and flowered for significantly longer ($F_{4,150} = 6.4694$, $P < 0.0001$) than in other land-use types.

3.7. Producers versus poor producers

Individual trees classified as 'poor-producers' in the Year 1

remained the same in Year 2. There was no significant difference in the number of flowers produced by 'poor-producers' versus 'producers' (Table 4). The same number of 'producer' trees flowered each year and for 'poor-producers' only one more tree flowered in the second year compared to the first (Table 4). Similarly, length of flowering period did not vary between 'producers' and 'poor-producers' for either of the two years (Year 1: $t = -0.6837$, $P = 0.4962$; Year 2: $t = 0.1359$, $P = 0.8923$). Fruit-set, however, differed significantly between 'poor-producer' and 'producer' categories (Table 4). 'Poor-producers' had an average fruit-set of 0.17% and 'producers' an average fruit-set of 33.48%. Regression analysis showed that for 'producers' fruit-set

Table 1
Percentage of trees that are in leaf and in flower in relation to the onset of rainfall and leaf flush each year (n = 106).

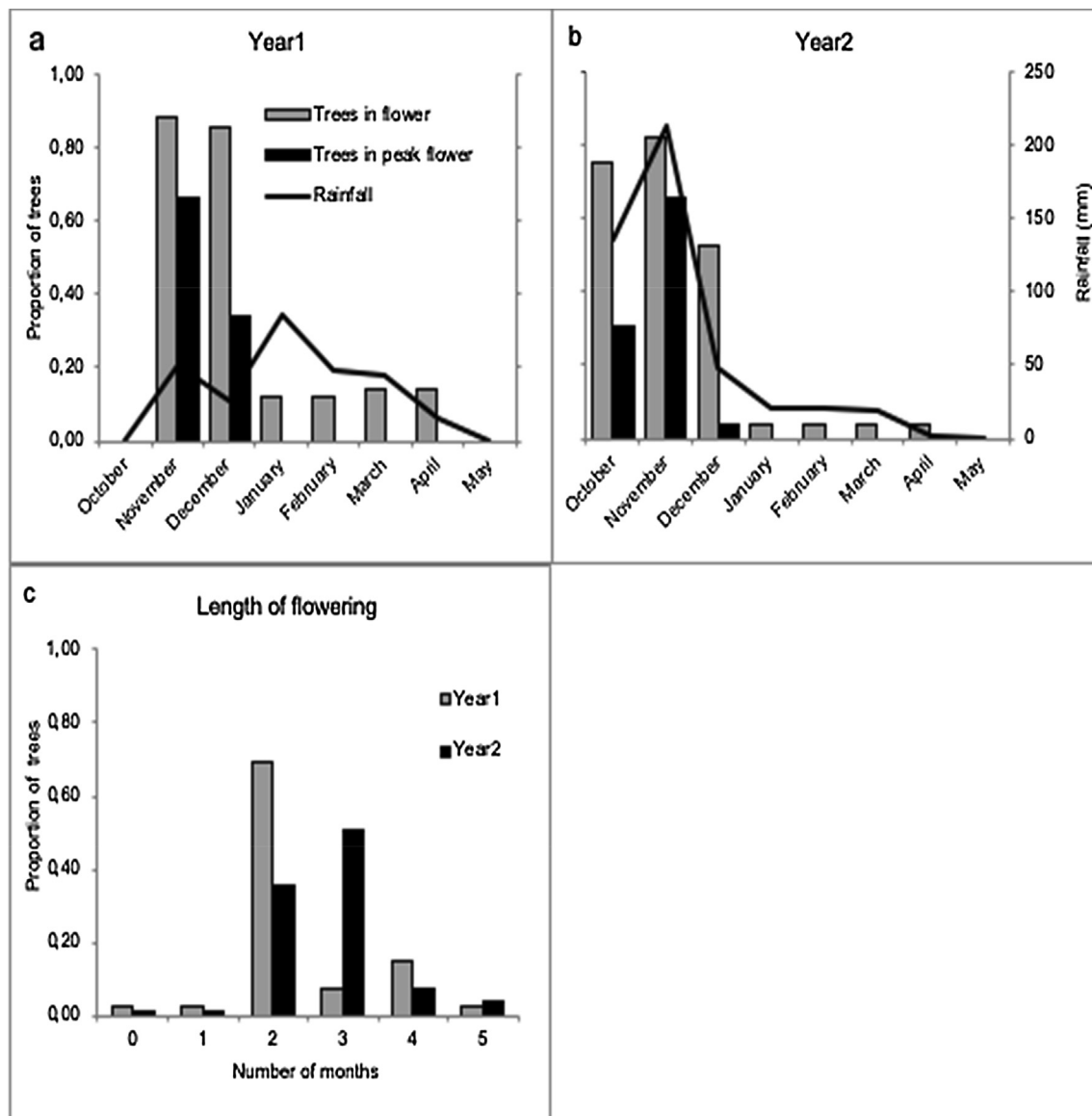| Year (July - June)	Leaf flush preceeds rain	Flowering preceeds rain	Flowering preceeds leaf flush	Flowering and leaf flush at the same time	Leaf flush preceeds flowering
	(% of trees)	(% of trees)	(% of trees)	(% of trees)	(% of trees)
Year 1	88%	84%	5%	54%	42%
Year 2	0%	0%	3%	39%	59%

Fig. 3. Proportion of adult trees (n = 79) in flower and exhibiting peak flowering, as well as rainfall each month in Year 1 (a) and Year 2 (b). Proportion of trees flowering for different lengths of time in Year 1 and Year 2 (c).

declined with an increase in flower number ($R^2 = 0.2486$, $P = 0.0004$) and for 'poor-producers' fruit-set did not change with flower number ($R^2 = 0.0039$, $P = 0.7395$).

4. Discussion

4.1. Phenology

4.1.1. Leaf phenology

We found that interannual variation in leaf flush and leaf fall was influenced by rainfall rather than temperature and day-length. Leaf flush was later when seasonal rains were late and earlier when seasonal rain came early. Temperature rise and drop was similar in both years, but rainfall in the first year went on one month longer than in the second year, with leaf fall following a similar pattern, with the net affect of the trees being in leaf for 6 months each year, despite the large differences in annual rainfall. This suggests that the availability of water plays a bigger role in determining leaf fall than temperature in baobab trees. Furthermore the distribution of rainfall within a season is also important for leaf phenology. Baobab trees that grow in fields that

are watered in the dry season often stay in leaf much longer than surrounding trees (SM Venter, pers. obs.). It has also been observed that one half of a tree may stay in leaf for longer than another half, when a root on the leafing side of the tree has access to water such as a leaking pipe or river (SM Venter, pers. obs.).

It is well known that rainfall, temperature and day-length are important variables in determining leaf flush and leaf fall in arid savanna ecosystems (Chidumayo, 2001; Archibald and Scholes, 2007; Ryan et al., 2017). For trees that flush leaves before the onset of rains, day length and temperature determine the initiation of leaf flush (Borchert and Rivera, 2001; Archibald and Scholes, 2007). This suggests that trees which flush leaves before rains are more deterministic in their behaviour, accepting the risk of poor growing seasons in order to take advantage of a number of factors, such as the pulse of nutrients which are released with the onset of first rain, minimal insect activity and high irradiance in order to be ready to photosynthesize (Wright and van Schaik, 1994; Archibald and Scholes, 2007, February and Higgins, 2016).

These large trees are likely immune to the occasional frost events that impacts mopane in this region (Whitecross et al., 2012) as the vast
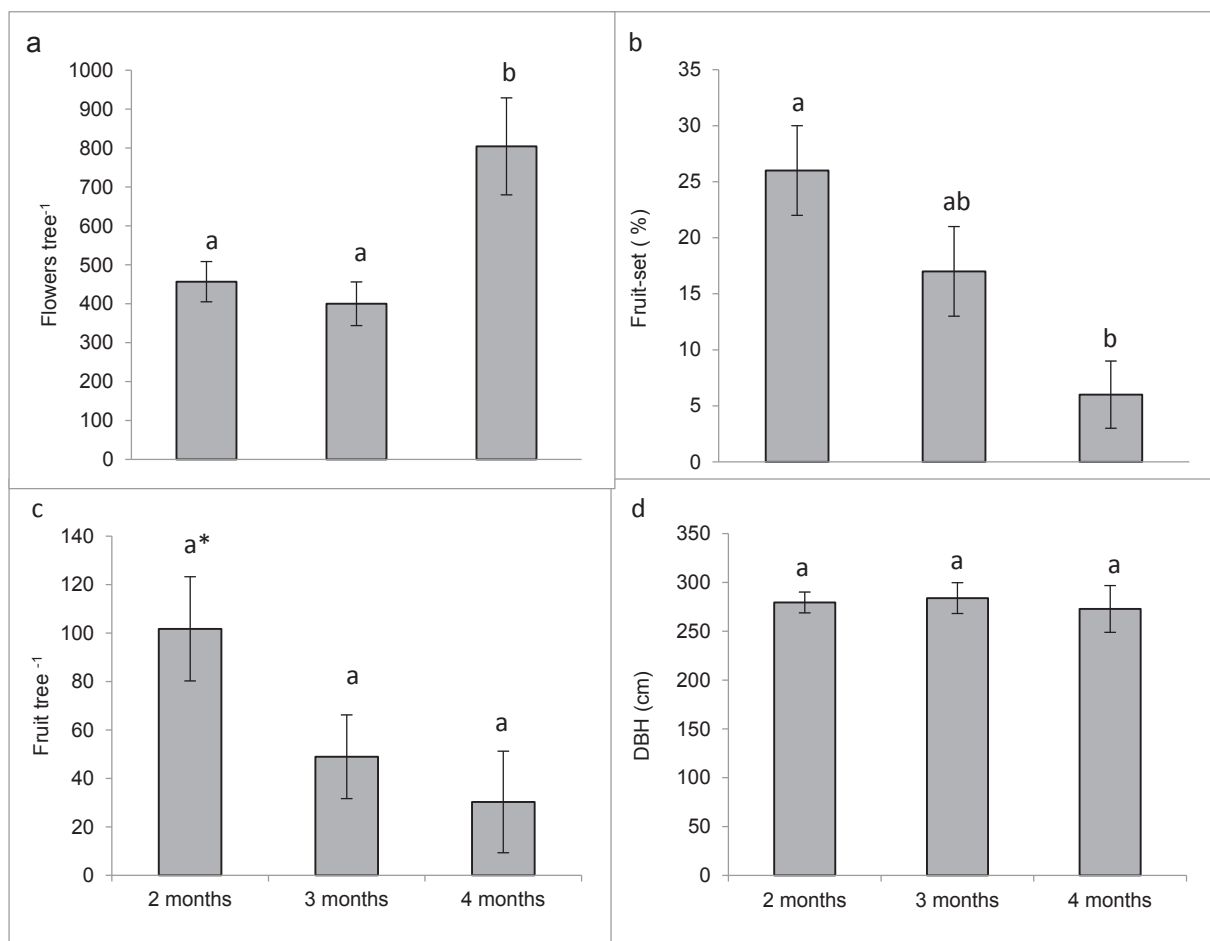
Fig. 4. Length of flowering time per tree versus number of flowers per tree (a), fruit-set per tree (b), number of fruit per tree (c) and tree size (cm dbh) (d) (mean ± SE). Trees were sampled over two consecutive years and results combined. 1 and 5 month categories excluded due to small sample sizes. Lower-case letters (a and b) indicate significant differences. a* indicates that *t*-test shows significant difference ($p < 0.05$).

Table 2
Results from tests on differences in flowering, fruit-set and fruit production of adult trees that peak flowered in different months of each year. Peak flowering month for individual trees is the month in which the tree produces the largest number of flowers. For analysis flower and fruit data was log transformed and fruit-set data arcsine transformed (n = 79).

Peak Flowering months	Flowers	Fruit-set	Fruit
Year 1	$t_{75} = 0.7335$	$t_{75} = -0.7264$	$t_{75} = -0.4459$
November & December	$P = 0.4656$	$P = 0.4689$	$P = 0.6569$
Year 2	$F_{(2,75)} = 1.1102$	$F_{(2,75)} = 1.6885$	$F_{(2,75)} = 1.7541$
October, November & December	$P = 0.3348$	$P = 0.1918$	$P = 0.1801$

majority of the population are > 4 m in height. *Colophospermum mopane* shrubs and trees < 4 m in height are heavily impacted by these frost events, and hence baobab seedlings and saplings may also be vulnerable, particularly as they may have a higher level of stored water. This could be an additional reason for the lack of "young" baobabs (Venter and Witkowski, 2013a). In terms of the timing of germination/seedling emergence, seedlings from newly collected seeds only emerged after about a year in the soil, with the majority germinating in the warmest month, January in the middle of the rainy season (Venter and Witkowski, 2013a). Leaf phenology of arid savanna species such as mopane and baobab may be different to trees in mesic savannas.

4.1.2. Flower phenology
The start of flowering differed between years with trees starting to

flower slightly earlier with early rains and slightly later with later rains. When late rains fell, flowering started before the onset of rains and is probably supported by stem-water reserves. In both years, trees peak flowered at the same time in November of each year. This supports the notion of a deterministic mechanism, such as day-length or temperature (Gentry, 1974; Rathcke and Lacey, 1985) has a bigger influence on cueing baobab flowering than rainfall. In both years flowering decreased after December and stopped altogether in April. We found that flowering did increase with tree size, but that landuse type did not have a significant effect on number of flowers produced. However, it must be noted that trees in villages tended to have more flowers and flower for longer than trees in other landuse types, presumably due to the availability of higher nutrients and water found in villages.

Baobab flowering exhibits sufficient variation in length of flowering and peak flowering period for it to be under relaxed selection pressure. This allows the population more flexibility in its responses to changes in the environment, and to respond to possible stronger selection pressures in future (Ollerton and Lack, 1992). Fruit-set is not affected by the timing of individual flowering peaks, nor by land-use. Therefore, flexible flowering phenology may allow baobabs to be more resilient to environmental fluctuations.

Good stem water and stored energy or limiting nutrient reserves from a previous favourable growing season may allow trees to produce more flowers and thus produce more fruit (Witkowski, 1990). This may explain why in 2007–2008 (Year 2), despite having almost double the rainfall, trees produced far fewer flowers and fruit than in 2006–2007 (Year 1), when rainfall had been poor. Fruit production increased again
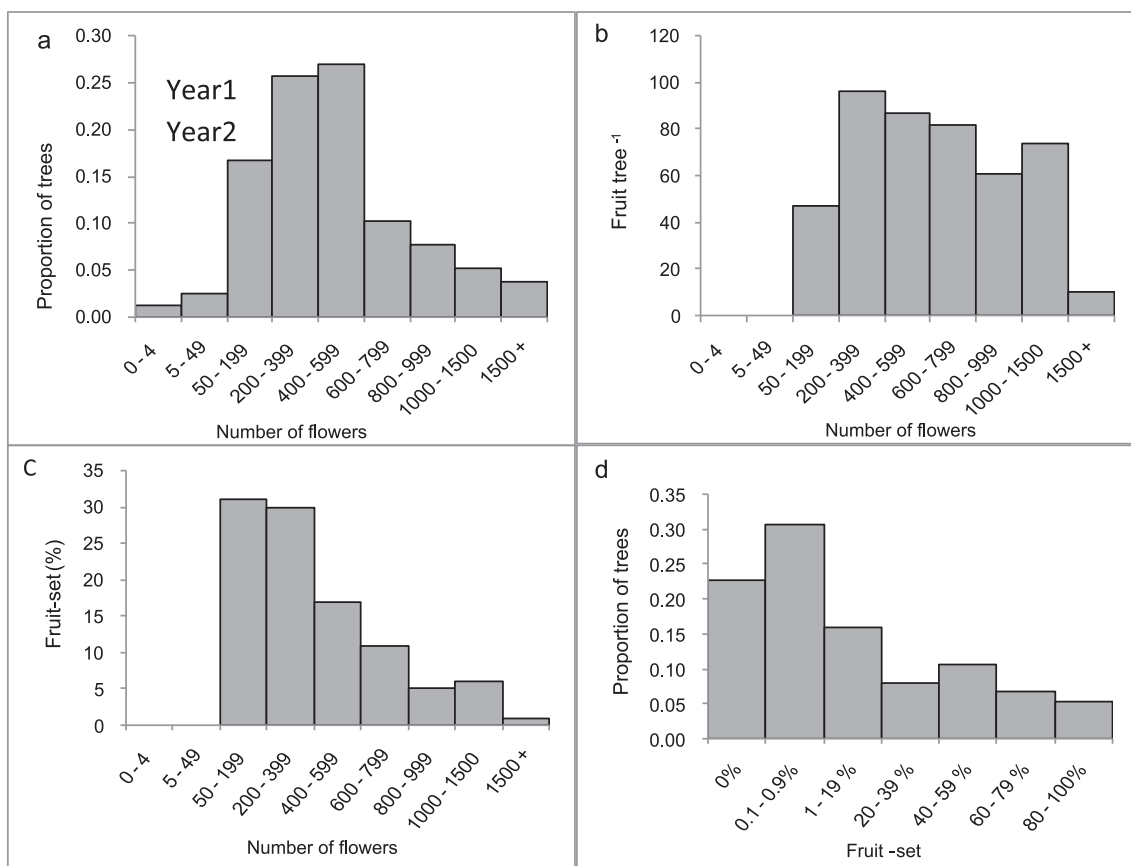
Fig. 5. Proportion of adult trees (a), number of fruit (b) and fruit set (c) per number of flowers-class, as well as the proportion of trees per fruit-set-class (d) (n = 79).

in the following year, 2008–2009 (Venter and Witkowski, 2011), either due to the previous season's above average rains or because of poor production in the previous year allowing the trees to build up reserves.

4.2. Reproductive strategy

4.2.1. Excess flower production

We found that baobabs exhibited a steady-state flowering pattern which lasted for one to five months. Fruit-set and fruit production did not differ between trees that peak-flowered in different months, suggesting that baobabs are well adapted to cope with unpredictable flowering seasons without a loss in fecundity. This allows trees to invest in a form of bet-hedging. The advantage of such a strategy is to spread over a longer time, the risk of poor environmental conditions and unpredictable pollinators (Zimmerman, 1988).

A further advantage of a steady-state flowering pattern is that it achieves higher out-crossing. Plants with few flowers produced over a longer time have a better chance of outcrossing than plants that produce all their flowers together, adopting a 'big bang' strategy (Richards, 1986). Furthermore, plants that flower late in the season achieve higher out-crossing than plants that flower in peak season (Zimmerman, 1988). This is because there are fewer available pollinators, and pollinators have to travel greater distances to reach flowers and thus move pollen further (Zimmerman, 1988). Thus a steady-state flower strategy could enhance out-crossing in baobabs.

The production of excess flowers is common in hermaphrodite plants (Sutherland and Delph, 1984). It is hypothesized that this has a number of advantages, including bet-hedging, allocation to male fitness (pollen donation) and allocation to female fitness (selective abortion) (Sutherland and Delph, 1984; Ayre and Whelan, 1989).

Table 3
Flowers and fruit-set per tree in sub-adult and adult life stages in Year 1 and Year 2 and the average over both years, as well as number of trees in flower between years within each life stage. Flower numbers were Log transformed and fruit-set arcsine transformed for analysis. Fruit-set was determined only from trees that produced flowers, hence the differences in df. Lower case letters (a and b) indicate differences between life stages in rows and capital letters (A and B) indicate differences within each life stage between years.

|	Year	Sub Adult	Adult	t	P
		mean ± SE	mean ± SE	Between Life stages (a,b)	Between Life stages (a,b)
Flowers/tree	Year 1	75.52 ± 21.30[aA]	710.86 ± 72.73[bA]	$t_{104} = -8.3134$	$P < 0.001$
	Year 2	12.41 ± 5.15[aB]	287.27 ± 32.91[bB]	$t_{104} = -12.3097$	$P < 0.001$
	Ave both Years	43.96 ± 12.59[a]	499.06 ± 45.11[b]	$t_{104} = -10.3675$	$P < 0.001$
Fruit-set /tree	Year 1	14.22 ± 7.92[aA]	19.91 ± 3.54[aA]	$t_{95} = -0.5915$	$P = 0.5555$
	Year 2	21.26 ± 9.16[aA]	20.23 ± 3.67[aA]	$t_{88} = 0.1848$	$P = 0.8538$
	Ave both Years	17.76 ± 8.31 %[a]	20.07 ± 3.61 %[a]	$t_{96} = -0.4177$	$P = 0.6771$
Number of flowering trees	Year 1	20[A]	77[A]		
	Year 2	12[B]	78[A]		
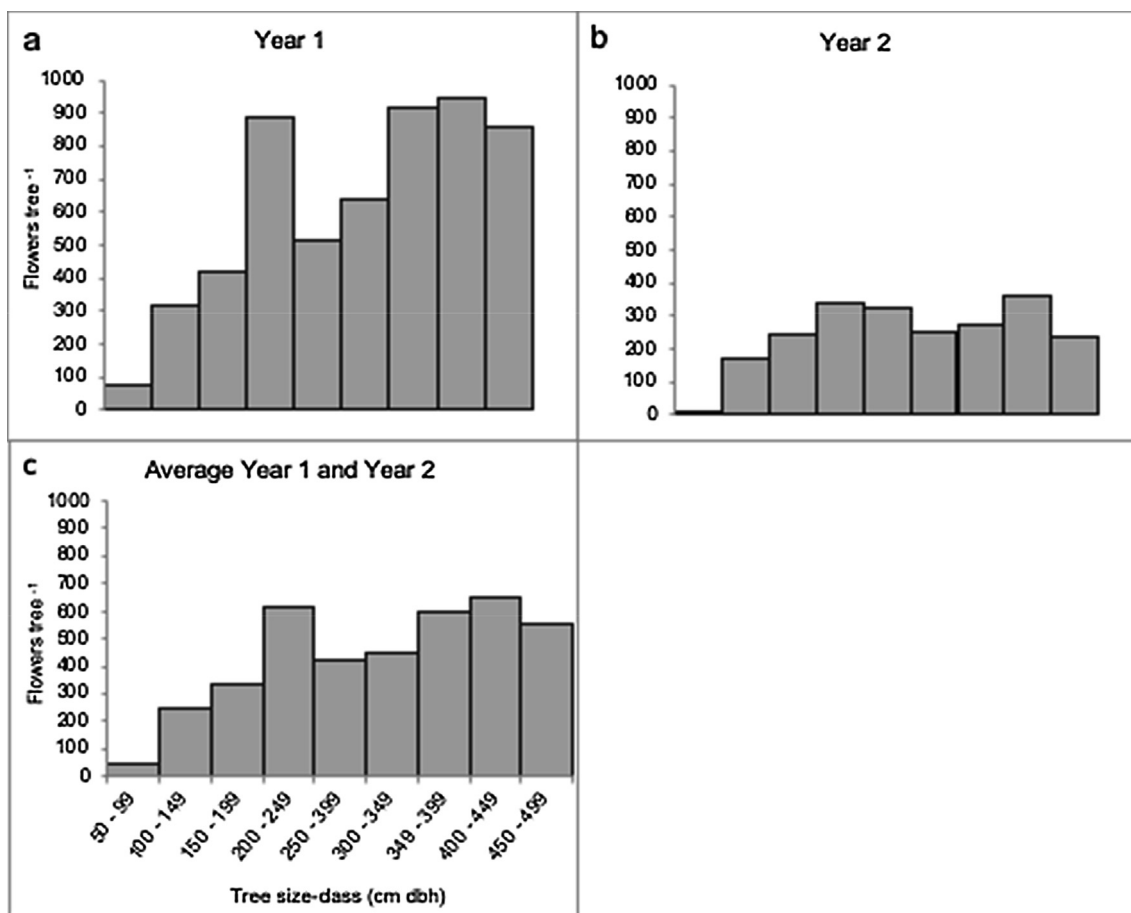
Fig. 6. Mean flower production per tree size-class for each season: Year 1 (a), Year 2 (b) and the average over both seasons (c) (n = 106).

Table 4
Flowers and fruit-set per tree for poor-producer and producer categories in Year 1 and Year 2 and the average over both years, as well as the number of trees in flower between years within each category. Flower numbers were Log transformed and fruit-set arcsine transformed for analysis. Fruit-set was determined only from trees that produced flowers, hence the differences in df. Lower case letters (a and b) indicate differences between columns.

	Year	Poor-producer	Producer	t	P
		mean ± SE	mean ± SE		
Flowers/tree	Year 1	592.37 ± 98.72[a]	791.53 ± 101.28[a]	t_{77} = 1.8020	P = 0.2834
	Year 2	310.56 ± 60.73[a]	271.40 ± 37.18[a]	t_{77} = 0.1497	P = 0.8814
	Ave both Years	451.47 ± 65.74[a]	531.47 ± 61.32[a]	t_{77} = 1.0658	P = 0.2898
Fruit-set /tree	Year 1	0.20 ± 0.07 %[a]	33.20 ± 5.07 %[b]	t_{75} = −5.6783	P < 0.001
	Year 2	0.14 ± 0.09 %[a]	33.77 ± 5.28 %[b]	t_{75} = −5.5991	P < 0.001
	Ave both Years	0.17 ± 0.08 %[a]	33.48 ± 5.16 %[b]	t_{75} = −6.1924	P < 0.001
Number of flowering trees	Year 1	31	46		
	Year 2	32	46		

Sutherland and Delph (1984) argue that an excess in flower production increases male fitness, because plants produce flowers that function solely as pollen donors. Fruit and seed production (female functions) are more costly than pollen production (male function), therefore, in order to balance the investment in male and female functions, plants should produce more flowers than fruit. Charnov (1979) argued that sex allocation is an evolutionary stable strategy (ESS) that depends on the shape of the fitness-gain curves relating to female and male fertility functions. The production of excess flowers in baobabs may therefore be an investment in male function, as argued for other species (Sutherland, 1987; Ayre and Whelan, 1989).

Burd (1998) hypothesized that 'excess' flower production may also increase female fitness by allowing selective maturation of fruit of superior quality. In resource limited environments, maternal plants are known to allocate a disproportionate amount of nitrogen and phosphorus to seeds in order to ensure successful seedling establishment (Witkowski and Lamont, 1996). Baobab recruitment is highly episodic (Venter and Witkowski, 2010; 2013a), so investment in good quality seed may be very important for this species. The study area is also resource poor – low rainfall and generally poor sandy soils.

Excess flower production also increases female fitness by allowing the plant to rapidly adjust fruit-set when conditions improve (Witkowski, 1990; De Jong and Klinkhamer, 2005). However, in baobabs, annual variation in fruit production was linked to a reduction in the number of flowers rather than to a reduction in fruit-set. This means that female fitness was not a post-fertilization decision, as suggested above, but a pre-fertilization decision. The decision to produce fewer flowers, presumably influenced by a lack of resources, would affect

both male and female fitness.

4.2.2. Poor producers or 'male' trees

The almost complete lack of fruit production in 'poor-producers' remains interesting. We found no difference in flowering phenology (flower production, length of flowering, peak flowering), but a substantial difference in fruit-set between these categories, with 'poor-producers' (0.17%) having significantly lower fruit-set than 'producers' (33%).

Low fruit-set can occur for a number of reasons and these include (1) plant age (2) environment, (3) inadequate pollination, (4) genetic aberrations and (5) sexual dimorphism. Bet-hedging and allocation to male and female fitness through pollen donation and ovule abortion may be the reason for excess flower production in 'producers', but these alone do not explain poor fruit-set in 'poor-producers'.

Size-dependent and environment-dependent sex allocation can occur in the form of diphasy, where small adult trees and adult trees in poor environments could be said to be like 'males', which switch to being 'female' once they are bigger, and trees in nutrient rich environments are 'female' (Schlessmann, 1988; De Jong and Klinkhamer, 2005). Our results showed that there was no difference in fruit-set between size-classes (age) or land-use type (environment). An increase in fruit production with tree size was a result of an increase in flowers production and not fruit-set. Furthermore, although trees in villages flowered for longer and tended to produce more flowers than trees in other land-use types, fruit-set did not differ from other land-use types. In addition, field observations indicate that soil and climate conditions did not influence fruit-set as 'poor-producer' and 'producer' trees were often found only a few meters apart within very uniform environments. Thus poor fruit-set, in this case, does not appear to be a function of age or environment.

Pollen limitation, both in terms of quantity and quality, has an influence on fruit-set (Aizen and Harder, 2007). Inadequate quantities of pollen are known to severely limit fruit-set especially when pollinators are scarce (Johnson et al., 2004). Poor pollen quality, particularly in late acting self-incompatible species, such as baobab, disables ovules resulting in poor fruit-set (Aizen and Harder, 2007). Baobab flowers are known to be fruit-bat pollinated, but this has not been observed in southern Africa. Field observations (S.M. Venter, unpublished data) suggest that insects (hymenoptera spp.) may be playing an important role as pollinators in this area. However, flowers may not be adapted to insect pollination and many trees may be receiving a large amount of self pollen or pollen from closely related trees which could result in inbreeding depression. However, this does not explain poor fruit-set in the same individual trees over multiple years, especially where they occur among trees that are good producers.

Low fruit-set may also be controlled on a genetic level. In polyploid species, infertility may be caused by meiotic aberrations, which is the most common cause of sterility in polyploids, and is known to result in semi-sterile adults (Ramsey and Schemske, 2002).

Low fruit-set may also reflect a form of sexual dimorphism (Wilson, 1994). A gradual increase in gender specialization may be seen as a pathway to dioecy (Barrett, 2002). Barrett (2002) suggests that plant gender should be seen more from a functional rather than a morphological perspective and it is suggested that evolution of sex chromosomes may follow once dioecy is established (Charlesworth and Guttman, 1999). Hormonal controls on certain loci are able to modify sex expression that shift the balance between male and female expression (Charlesworth and Guttman, 1999). Such loci would increase sterility effects and development 'decisions' between male and female functions (Meagher, 1988). Baobabs have relatively low diversity across large geographic areas (Baum et al., 1998; Tsy et al., 2009), but high diversity within populations (Assogbadjo et al., 2010) with high levels of polymorphism and polysomic inheritance (Assogbadjo et al., 2006; Assogbadjo et al., 2009; Larsen et al., 2009). This makes identifying genetic markers for morphological variation and sexual behaviour

complex but it also allows for evolutionary change to take place (Wilson, 1994). However, Pannell (2002) argues that plant populations that are 'functionally dioecious' still need to make equal contributions to male and female function, therefore if 'poor-producers' are 'functionally male' then 'producer' should be 'functionally female' and not hermaphrodite. To assess if baobabs are 'functionally dioecious' the paternal and maternal contribution of both categories of trees would need to be established.

The quantitative results of this study suggest that further work is required to investigate how and why baobab trees are either 'male' or female'. Mechanisms to do this would include self-incompatibility tests, pollen limitation and determining rates of floral visits in 'producer' and 'poor-producer' individuals. Cross-fertilizing individuals, considered to be males and females, should be done using a common pollen pool which would help determine if there are differences in levels of fruit and seed set between the 'male' and 'female' trees. A comparison of the levels of fruit set obtained from this experiment with levels observed under natural pollination conditions would test for pollen limitation due to deficiency in pollination service.

5. Conclusion

Leaf flush responded more quickly to early rain than did flowering. In the first year, trees flowered and flushed leaves at the same time, whereas in the second year trees flushed leaves one month earlier than flowering, probably in response to the exceptionally early and above-average rainfall. Leaf fall coincided with the end of rainfall rather than drop in temperature.

Baobab flowering exhibits a steady-state pattern. Peak flowering occurs at the same time each year, suggesting that flowering is more strongly determined by day-length or temperature than by rainfall. Flowering and fruit production are highly variable between years, and may be influenced by the previous season's conditions. There was a significant difference between the number of flowers produced between years, but no significant difference in fruit-set. Thus it would seem that variation in fruit production between years is a consequence of reduced flower production and not the capacity of the trees to set fruit. Likewise, flowering, not fruit-set, increased with tree size and life-stage, thus fruit production is influenced by increases in flowers and not fruit-set. Neither did fruit-set differ between land-use types although trees in villages flowered for longer and tended to produce more flowers than trees in other land-use types. Lastly, 'producers' and 'poor-producers' did not differ in flowering phenology but did differ significantly in fruit-set.

The results of this study show that the pervasive belief that there are distinct 'male' and 'female' baobabs may not be as far-fetched as previously thought. Investigations into the mechanisms that determine these patterns are required. Genetic, pollination and breeding system studies would help establish if low fruit production in 'male trees' is a result of poor pollination, self-incompatibility or female sterility.

References

Adole, T., Dash, J., Atkinson, P. Mp., 2018. Large-scale prerain vegetation green-up across Africa. Glob. Change Biol. 24 (9), 4054–4068.

Agundez, D., Lawali, S., Mahamane, A., Alia, R., Solino, M., 2018. Consumer preferences for baobab products and implications for conservation and improvement policies of foreset food resources in Niger (West Africa). Econ. Bot. 72 (4), 396–410.

Aizen, M.A., Harder, L.D., 2007. Expanding the limits of the pollen-limitation concept: effects of pollen quantity and quality. Ecology 88, 271–281.

Archibald, S., Scholes, R.J., 2007. Leaf green-up in a semi-arid African savanna - separating tree and grass responses to environmental cues. J. Veg. Sci. 18, 583–594.

Assogbadjo, A.E., Glelekakai, R., Kyndt, T., Sinsin, B., 2010. Conservation genetics of baobab (*Adansonia digitata* L.) in the parklands agroforestry systems of Benin (West Africa). Notulae Botanicae Horti Agrobotanici Cluj-Napoca 38, 136–140.

Assogbadjo, A.E., Kakai, R.G., Chadare, F.J., Thomson, L., Kyndt, T., Sinsin, B., Van Damme, P., 2008. Folk classification, perception, and preferences of babobab products in West Africa: consequences for species conservation and improvement. Econ. Bot. 62, 74–84.

Assogbadjo, A.E., Kyndt, T., Chadare, F.J., Sinsin, B., Gheysen, G.O.E.-M., Van Damme, P., 2009. Genetic fingerprinting using AFLP cannot distinguish traditionally classified baobab morphotypes. Agrofor. Syst. 75, 157–165.

Assogbadjo, A.E., Kyndt, T., Sinsin, B., Gheysen, G., Van Damme, P., 2006. Patterns of genetic and morphometric diversity in babobab (*Adansonia digitata*) populations across different climatic zones of Benin (West Africa). Ann. Bot. 97, 819–830.

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. Journ. Bot. 138, 47–56.

Ayre, D.J., Whelan, R.J., 1989. Factors controlling fruit set in hermaphroditic plants: studies with Australian proteaceae. Tree 4, 267–271.

Barrett, S.C.H., 2002. The evolution of plant sexual diversity. Nature 3, 274–284.

Baum, D.A., 1995a. The comparative pollination and floral biology of baobabs (*Adansonia - Bombacaea*). Ann. Mo. Bot. Gard. 82, 322–348.

Baum, D.A., 1995b. A systematic revision of Adansonia (Bombacaea). Ann. Mo. Bot. Gard. 82 (3).

Baum, D.A., Small, J.L., Wendel, F., 1998. Biogeography and floral evolution of baobabs *Adansonia*, Bombacaceae as inferred from multiple data sets. Syst. Biol. 47, 181–207.

Borchert, R., Rivera, G., 2001. Photoperiodic control of seasonal development and dormancy in tropical stem-succulent trees. Tree Physiol. 21, 213–221.

Burd, M., 1998. "Excess" flower production and selective fruit abortion: a model of potential benefits. Ecology 79, 2123–2132.

Chapotin, M.S., Razanameharizaka, J.H., Holbrook, M.N., 2006. Baobab trees (*Adansonia*) in Madagascar use stored water to flush new leaves but not to support stomatal opening before the rainy season. New Phytol. 169, 549–559.

Charlesworth, D., Guttman, D.S., 1999. The evolution of dioecy and plant sex chromosome systems. In: Ainsworth, C.C. (Ed.), Sex Determination in Plants. BIOS Scientific Publishers Ltd, Oxford.

Charnov, E.L., 1979. The genetical evolution of patterns of sexuality: Darwinian fitness. Am. Nat. 113, 465–480.

Chidumayo, E.N., 2001. Climate and phenology of savanna vegetation in Southern Africa. J. Veg. Sci. 12, 347–354.

Chidumayo, E.N., 2015. Dry season watering alters the significance of climate factors influencing phenology and growth of saplings of savanna woody species in central Zambia, southern Africa. Austral Ecol. 40 (7), 794–805.

Childes, S.L., 1989. Phenology of nine common woody species in semi-arid, deciduous Kalahari Sand vegetation. Vegetatio 79, 151–163.

Craparo, A.C.W., et al., 2015. *Coffea arabica* yields decline in Tanzania due to climate change: global implications. Agric. For. Meteorol. 207, 1–10.

Cron, G.V., Karimi, N., Glennon, K.L., Udeh, C.A., Witkowski, E.T.F., Venter, S.M., Assogbadjo, A.E., Baum, D.A., 2016. One African baobab species or two? synonymy of *Adansonia kilima* and *A. digitata*. Taxon 65 (5), 1037–1049.

Cuni Sanchez, A., Osborne, P.E., Haq, N., 2011. Climate change and the African baobab (*Adansonia digitata* L.): the need for better conservation strategies. Afr J Ecol 49, 234–245.

De Jong, T.J., Klinkhamer, P.G.L., 2005. Evolutionary ecology of plant reproductive strategies. Cambridge University Press, U.K.

Dhillion, S.S., Gustad, G., 2004. Local management practices influence the viability of the baobab (*Adansonia* Linn.) in different land use types, Cinzana, Mali. Agric. Ecosyst. Environ. 101, 85–103.

February, E.C., Higgins, S.I., 2016. Rapid leaf deployment strategies in a deciduous savanna. PLoS ONE 11 (6), e0157833. https://doi.org/10.1371/journal.pone.0157833.

Fenner, M., 1980. Some measurements on the water relations of baobab trees. Biotropica 12, 205–209.

Gentry, A.H., 1974. Flowering phenology and diversity of tropical Bignoniaceae. Biotropica 6, 64–68.

Johnson, S.D., Neal, P.R., Peter, C.I., Edwards, T.J., 2004. Fruiting failure and limited recruitment in remnant populations of the hawkmoth-pollinated tree *Oxyanthus pyriformis* subsp. *pyriformis* (Rubiaceae). Biol. Conserv. 120, 31–39.

Larsen, S.A., Vaillant, A., Verhaegen, D., Kjaer, E.D., 2009. Eighteen SSR-primers for tetraploid *Adansonia digitata* and its relatives. Conserv. Genet. Res. 1, 325–328.

Meagher, T.R., 1988. Sex determination in plants. In: Doust, J.L., Doust, L.L. (Eds.), Plant reproductive ecology: patterns and strategies. Oxford University Press, U.K., pp. 125–138.

Mucina, L., Rutherford, M.C. (Eds.), 2006. The vegetation of South Africa, Lesotho and Swaziland. South African National Botanical Institute, Pretoria.

Ollerton, J., Lack, A.J., 1992. Flowering phenology: an example of relaxation of natural selection. Tree 7, 274–276.

Pannell, J.R., 2002. What is functional androdioecy? Funct. Ecol. 16, 858–869.

Pardy, A., 1953. Indigenous trees and shrubs of S. Rhodesia. *Adansonia digitata* (Bombacaceae). Rhodesia Agric. J. 50, 5–6.

Ramsey, J., Schemske, D.W., 2002. Neopolyploidy in flowering plants. Annu. Rev. Ecol. Syst. 33, 589–639.

Rathcke, B., Lacey, E.P., 1985. Phenological patterns of terrestrial plants. Annu. Rev. Ecol. Syst. 16, 179–214.

Richards, A.J., 1986. Plant breeding systems. George Allen & Unwin, London.

Ryan, C.M., Williams, M., Grace, J., Woollen, E., Lehmann, C.E.R., 2017. Pre-rain green-up is ubiauitous across southern tropical Africa: impliations for temporal niche separation and model represenation. New Phytol. 213, 625–633.

Schlessmann, M.A., 1988. Gender diphasy ("sex choice"). In: Doust, J.L., Doust, L.L. (Eds.), Plant reproductive ecology: patterns and strategies. Oxford University Press, U.K., pp. 139–153.

Schulze, R.E., 1997. South African Atlas of Agrohydrology and -Climatology. Water Research Commission, Pretoria.

Schumann, K., Wittig, R., Thiombiano, A., Becker, U., Hahn, K., 2010. Impact of land- use type and bark- and leaf-harvesting on population structure and fruit production of the baobab tree (*Adansonia digitata* L.) in a semi-arid savannah, West Africa. For. Ecol. Manage. 260, 2035–2044.

Sidibe, M., Williams, J.T., 2002. Baobab *Adansonia digitata*. International Centre for Underutilized Crops, Southhampton, UK.

Sutherland, S., 1987. Why hermaphroditic plants produce many more flowers than fruits: experimental tests with *Agave mckelveyana*. Evolution 41, 750–759.

Sutherland, S., Delph, L.F., 1984. On the importance of male fitness in plants: patterns of fruit-set. Ecology 65, 1093–1104.

Swanepoel, C., 1993. Baobab phenology and growth in the Zambezi Valley, Zimbabawe. Afr. J. Ecol. 31, 84–86.

Tsy, J.L.P., Lumaret, R., Mayne, D., Vall, A.O.M., Abutaba, Y.I.M., Sagna, M., Raoseta, S.O.R., Danthu, P., 2009. Chloroplast DNA phylogeography suggests a West African centre of origin for baobab, *Adansonia digitata* L. (Bombacoideae, Malvaceae). Mol. Ecol. 18, 1707–1715.

Venter, S.M., Glennon, K.L., Witkowski, E.T.F., Baum, D., Cron, G.V., Tivakudze, R., Karimi, N., 2017. Baobabs (Adansonia digitata L.) are self-incompatible and 'male' trees can produce fruit if hand-pollinated. S. Afr. J. Bot. 109, 263–268.

Venter, S.M., Witkowski, E.T.F., 2010. Baobab (*Adansonia digitata* L.) density, size-class distribution and population trends between four land-use types in northern Venda, South Africa. For. Ecol. Manage. 259, 294–300.

Venter, S.M., Witkowski, E.T.F., 2011. Baobab (*Adansonia digitata* L.) fruit production in communal and conservation land-use types in Southern Africa. For. Ecol. Manage. 261, 630–639.

Venter, S.M., Witkowski, E.T.F., 2013a. Where are the young baobabs? factors affecting regeneration of *Adansonia digitata* L. in a communally managed region of southern Africa. J. Arid Environ. 92, 1–13.

Venter, S.M., Witkowski, E.T.F., 2013b. Fruits of our labour: contribution of commercial baobab (*Adansonia digitata* L.) fruit harvesting to the livelihoods of marginalized people in northern Venda, South Africa. Agrofor. Syst. 87, 159–172.

Von Breitenbach, F., Von Breitenbach, J., 1974. Baobab Flower. Trees S. Africa 26, 14–15.

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. Springer, Madagascar and Australia.

Wilson, M.F., 1994. Sexual selection in plants: perspectives and overview. Am. Nat. 144, S13–S39.

Whitecross, M.A., Archibald, S., Witkowski, E.T.F., 2012. Do freeze events create a demographic bottleneck for *Colophospermum mopane*? S. Afr. J. Bot. 23, 9–18.

Whitecross, M.A., Witkowski, E.T.F., Archibald, S., 2016. No two are the same: assessing variability in broad-leaved savanna tree phenology, with watering, from 2012–2014 at Nylsvley, South Africa. S. Afr. J. Bot. 105, 123–132.

Whitecross, M.A., Witkowski, E.T.F., Archibald, S., 2017a. Assessing the frequency and drivers of early-greening in broad-leaved woodlands along a latitudinal gradient in southern Africa. Austral Ecol. 42, 341–353.

Whitecross, M.A., Witkowski, E.T.F., Archibald, S., 2017b. Savanna tree-grass interactions: a phenological investigation of green-up in relation to water availability over three seasons. S. Afr. J. Bot. 108, 29–40.

Witkowski, E.T.F., 1990. Nutrient limitation of inflorescence and seed production in *Leucospermum parile* (Proteaceae) in the Cape fynbos. J. Appl. Ecol. 27, 148–158.

Witkowski, E.T.F., Lamont, B.B., 1996. Disproportionate allocation of mineral nutrients and carbon between vegetative and reproductive structures in *Banksia hookeriana*. Oecologia 105, 38–42.

Wright, S.J., van Schaik, C.P., 1994. Light and the phenology of tropical trees. Am. Nat. 143, 192–199.

Zimmerman, M., 1988. Nectar production, flowering phenology and strategies for pollination. In: Lovett Doust, J., Lovett Doust, L. (Eds.), Plant reproductive ecology: patterns and strategies. Oxford University Press.