Do mutualisms matter? A case study of the sausage tree (*Kigelia africana*) in Kruger National Park, South Africa.

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PLAGIARISM DECLARATION

I know the meaning of plagiarism and declare that all of the work in this thesis, save for what is properly acknowledged, is my own.

Jayaneesh Namah

Signed on the 20th day of November 2013 in Cape Town.

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Chapter 1: Introduction

1.1 What are mutualisms?

From the nitrogen-fixing bacteria in the root nodules of legumes, to the algae that power reef systems, to the myriad pollinators that mediate sexual reproduction in plants, mutualisms are ubiquitous and often ecologically dominant (Leigh & Rowell, 1995). For example, in tropical rainforests the majority of plants depend on animals for pollination and seed dispersal (Bronstein et al., 2006), two of the most conspicuous mutualisms (Howe, 1984). Mutualisms are particularly critical to understanding evolutionary diversification since most organisms are either directly or indirectly involved in mutualistic interactions (Herre et al., 1999; Bronstein, 2001).

Seed dispersal

Seed dispersal is a key process in plant communities (Wills et al., 1997; Harms et al., 2000). The effectiveness of dispersal lies within the fruit traits and its interaction with the dispersers. Large fruits, for instance are more likely to be dispersed by larger animals (Janzen & Martin, 1982). Some fruits actually reflect anachronisms, linking them to groups of now extinct animals (Janzen & Martin, 1982; Jordano, 1995). Examples include *Hymenaea courbaril (Fabaceae), Lacunaria jemmani (*Quiinaceae)*, Genipa americana* (Rubiaceae) which still produce predominantly brown, large and heavy fruits (Guimarães. et al., 2008), characteristics of those previously dispersed by large extinct mammals like native horses, gomphotheres, ground sloths, and other Pleistocene megafauna (Janzen & Martin, 1982). Understanding the persistence of these plants gives an indication of the different evolutionary paths that a plant can potentially undergo to survive without their main seed dispersers (Janzen & Martin, 1982; Chapman & Chapman, 1995).

Plant-animal interaction

The majority of mutualisms including plant-pollinator and plant-disperser relationships have been found to be more generalized, involving multiple interacting partner species in each case (Bronstein, 1994; Geber & Moeller, 2006; Guimarães et al., 2006). However, there are a handful of highly specialized mutualisms such as the fig-pollination mutualism (Machado et al., 2005) and the myrmecochores (Giladi, 2006). One mutualistic relationship that has been given much attention in the past decades includes mutualisms with native ant species (Giladi, 2006). For example, native ants in the Cape fynbos of South Africa are keystone mutualists that various myrmecochorous Proteaceae (e.g. *Leucospermum*, *Paranomus*, *Mimetes*) depend on for seed dispersal and establishment (Bond & Slingsby, 1984).

The ability for mutualisms to persist is closely related to the partners' life histories, behaviour and abundances. For instance, any form of impact to these variables will threaten the mutualistic relationships. In Hawaii, e.g. invasion of Argentine ants have been reported to drastically reduce insect-pollinator abundances, affecting the persistence of many native plants (Cole et al., 1992). Other anthropogenic threats to mutualisms include agriculture which poses the problem of introgression from genetically engineered organisms into related wild species where the wild species crosses with the modified one, thus losing genetic material (Snow & Palma, 1997); pollutants (e.g. Lawrey & Hale, 1979); habitat fragmentation which can cause severe isolation by limiting pollinator and dispersers, for example and eventually loss of mutualisms (Washitani, 1996; Donaldson et al., 2002).

1.2 Do mutualisms matter?

The idea that a species of vertebrate-dispersed fruits can collapse in the absence of their main seed dispersers was first proposed by Temple (1977). He suggested that the tambalacoque tree (*Sideroxylon grandiflorum*) relied on the extinct dodo (*Raphus cuculatus*) for successful seed dispersal and establishment, describing an example of an obligate mutualism. It is now recognized that Temple's analysis was erroneous with no solid evidence that the tambalacoque tree was driven to extinction due to the absence of the dodo since the plant has, in fact, been regenerating (Witmer & Cheke, 1991). Studies have now proven that local extinction of some frugivores can severely reduce seedling recruitment in vertebrate-dispersed plants (Cordeiro & Howe, 2001; Traveset & Riera, 2005) but the populations are rarely driven to extinction (Herhey, 2004).

There is little doubt that the community of mutualists is being increasingly altered, especially through anthropogenic actions (Cole et al., 1992; Herre et al., 1999). In view of the imminent decline of mutualistic relationships, Bond (1994) from an ecological perspective, argued that mutualisms do not matter since plants with more intense mutualisms (i.e. plants depending on a specific pollinator or disperser) compensate for this reliance by having a low dependence on them, buffering them from both pollination and dispersal failures. For example, self-incompatible plants with rare specialist pollinators often propagate vegetatively (Bond, 1994).

1.3 Mutualisms and conservation

Mutualisms are a complex issue for conservation; the preservation of one partner species without the other is difficult (Kearns and Inouye 1997). Because mutualisms bind several species to a common fate, they are important. Thus, our efforts need to encompass both the mutualists and other factors that can affect their densities. While there are no mutualism-focused conservation efforts, mutualistic relationships are now strongly considered in conservation plans (Kiers et al., 2010).

As such *Kigelia africana* is a useful species to study mutualisms. It has large conspicuous flowers and fruits, suggesting that both pollination and dispersal are via a small group of animal vectors (Rønne & Jøker, 2005). There is not much ecological information on this species except for some pollination studies which suggested that the flowers are pre-dominantly pollinated by bats (Harris & Baker, 1958; Baker, 1961; Ayensu, 1974).

In a conservation context, it would be a wise step to gather information on the sausage tree since it is rather rare with a possibly declining density. It is also a big tree that can grow up to 25 m (Rønne & Jøker, 2005) and the fact that big trees are in decline for various reasons is a conservation concern (Turner et al., 1996) especially for the Kruger National Park which tries to maintain heterogeneity throughout its ecosystems (Du Toit et al., 2003).

1.4 Aims of study

The reproductive biology of the sausage tree is relatively unexplored. The aim of this study is to produce a sufficient understanding of the breeding system and population distribution in Kruger National Park. We sought to address the following questions for a more in-depth insight on the ecological functioning of the sausage tree.

1. What pollinate(s) and disperse(s) *K. africana*?
2. Are there any major shifts such as loss in bigger trees or lack of recruits in the population dynamics of *K. africana* in Kruger National Park?

The subsequent chapters investigate the reproductive biology and the population dynamics in relation to recruitment, dispersal, herbivory and elephant damage of *K. africana* in Kruger National Park.

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Chapter 2: The reproductive biology of the sausage tree (*Kigelia africana*) in Kruger National Park, South Africa

Abstract

Hand pollination experiments showed *Kigelia africana* to be self-incompatible. The species relies on large vertebrates for successful cross pollination. Surprisingly, this apparently bat flower is mostly pollinated by many bird species in Kruger National Park. Variation in fruitset was found to be negatively correlated with distance to nearest conspecific individual. We found that there was much less successful pollination if trees were more than 45 m apart.

Keywords

Kigelia africana, self-incompatible, pollination

2.1 Introduction

Kigelia africana (Bignoniaceae) is a semi-evergreen indigenous to Africa (Rønne & Jøker, 2005). It has large wine-colored flowers that are strong-smelling and bell-shaped (Schmidt et al., 2004) and produces sausage-shaped fruits that can grow up to a meter long (Rønne & Jøker, 2005). These conspicuous characteristics suggest a dependence on mutualisms with large animals both for pollination and dispersal. Understanding the nature of plant-pollinator interactions is of particular importance to conservation efforts since the conservation of one may essentially include the conservation of the other (Johnson & Steiner, 2000). Thus, the sausage tree is a useful species to study for the importance and maintenance of mutualisms in a conservation context as it would undoubtedly be associated with an assemblage of species.

The flowers are often quoted as being chiropterophilous (Baker, 1961; Stebbins, 1970; Palgrave, 1981) since they have an unpleasant odor (Harris & Baker, 1958; Pettersson et al., 2004) and produce copious nectar with around 18% sucrose equivalence in sugar composition, which provides a large amount of energy per blossom (Scogin, 1980). There are several studies describing bat visits to the sausage tree in some tropical areas (e.g. Harris

& Baker, 1958; Baker, 1961; Ayensu, 1974) but there is no observational evidence of bats successfully pollinating the flowers in southern Africa (Johnson, 2004). Also, the pollination of this species is not restricted to bats since the sausage tree has been reported to reproduce even in the absence of bats (Harris & Baker, 1958). Though some birds such as sunbirds have been reported to visit the flowers, there are no studies substantiating their role as successful pollinators.

The sausage tree may be dependent on its pollinator availability and density for seed-set. A change in the population dynamics of a pollinator will influence the plant's reproduction and, ultimately, survival (Holland & DeAngelis, 2000). For instance, a decrease in pollinators will lead to a low seed set and low recruitment of the plant species. Small populations, subject to Allee effects (Allee & Rosenthal, 1949) are often at greater risk of extinction (Gilpin & Soulé, 1986). Isolated trees, for example, are less likely to reproduce since pollen exchange between individuals is constrained by pollinator visitation over large distances and abundance of pollinators (Ghazoul et al., 1998; Burrows, 2000). Thus, low tree density may have an adverse effect on the reproductive output of self-incompatible trees.

The risk of extinction of plant species due to the collapse of mutualisms is varied, especially because of their phenotypic plasticity (Crawley & Ross, 1990; Le Maitre & Midgley, 1992). For instance, species with strict mutualistic pollinators may resort to self-pollination to maintain their population (Bond, 1994; Qu et al., 2007). Though self-pollination is rare in the Bignoniaceae family, some species are self-compatible in certain cases (e.g. Bertin et al., 1989). Another buffer against pollination and/or disperser failure is to persist through resprouting, common in many woody plants (Bond & Midgley, 2001).

Here, we investigate the reproductive biology of *K. africana* in South Africa. The aim of this study was three-fold. Firstly, we explored a range of potential pollination vectors of the plant and measured their role in seed set. Second, we sought to determine whether selfing is a possibility in *K. africana*, making it able to reproduce in areas where pollinators have declined or are not present. Thirdly, we examined whether isolated trees have a low fruit-set, indicating reproductive failure (i.e. Allee effects). We also measured the floral attributes such as flower openings, length of flower life, amount of nectar produced.

2.2 Materials and methods

2.2.1 Study site

The study was conducted inside and around Skukuza village in Kruger National Park between October and December 2012, during the flowering period of the sausage tree. Since *K. africana* grows mostly along riverine systems, three rivers (N'waswitsontso, Sabie, N'waswitshaka) having the largest populations of sausage trees around Skukuza were sampled (Fig 1). Also, to avoid working amongst dangerous animals and at night time, most pollination experiments were conducted on sausage trees found in the village itself.

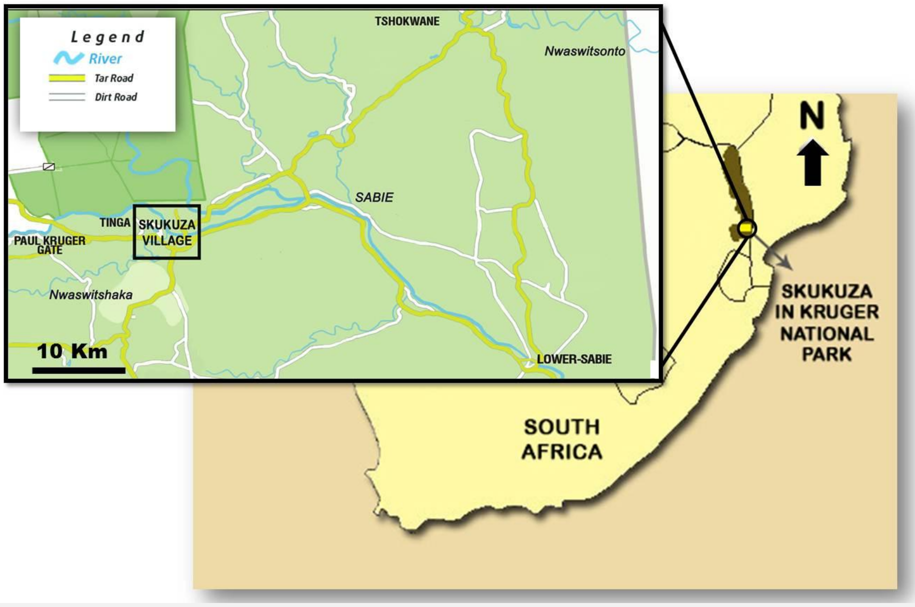

Fig. 2.1 Map showing Skukuza village and the three rivers (N'waswitsontso, Sabie, N'waswitshaka used around Skukuza in Kruger National Park

2.2.2 Measuring floral attributes

Throughout the study we observed the opening time of the flowers and noted how long they stayed in the tree before falling off.

We bagged 122 flowers from nine different trees (three to ten flowers per tree) in Skukuza (Fig. 1). When these opened, they were plucked to quantify the nectar volume, both at dawn (60 flowers in all) and dusk (62 flowers in all). We used a 100 ml syringe with needle to remove the nectar from the base of the perianth and measure the volume. We also measured the sucrose content of the nectar in these flowers using a portable refractometer (Portable Brix Sucrose Refractometer, RF15, Extech, China).

2.2.3 Exploring potential pollination vectors

We put eight infrared camera traps (TrailMaster, TM1550, Goodson & Associates, Inc, United States of America) in three sausage trees around Skukuza and Tinga, a private Game Reserve next Skukuza village and 20 km from the Paul Kruger Gate (Fig. 1) for a period of 16 days from September 20 to October 5. The trees were chosen because they were highly accessible and intensively branched, thus we could easily attach the cameras. These were focused on opened inflorescences and the footage was checked every day, refocusing the camera traps on newly opened flowers each time.

From September 24 to September 26, 2012, we put fine-meshed exclosure bags around newly opened flowers (on three trees which were in close proximity to one another in Skukuza village) at dusk and labeled them. The following day, these were opened at dawn between 05 30–07 30 when we observed and identified bird visitors. We then plucked these flowers to examine the stigma, using a magnifying lens (X 10), noting whether the birds were successful in moving pollen to the stigma while feeding on the flowers’ nectar.

2.2.4 Measuring success of potential pollination vectors

Unopened flowers from 13 individual trees in Skukuza village were bagged for this experiment, carried out from September 26, 2012 to October 04, 2012. Once the flowers opened, the bags were removed to expose them to different potential pollinators: birds only, nocturnal animals only (e.g. bats), and both diurnal (e.g. monkeys) and nocturnal visitors, as explained below.

- 150 bagged flowers were opened, exposing the flowers to any potential pollinator, diurnal and nocturnal. These were not re-bagged and were thus exposed to the full complement of floral visitors.
- 150 bagged flowers were opened at dawn and left for one hour after which they were re-bagged. These were exposed to bird visitors only.
- 150 bagged flowers were opened at dusk and re-bagged one hour before dawn, exposing the flowers to nocturnal animals only.
- 123 flowers remained bagged until they fell. These were the controls.

All flowers were labeled by sticking masking tape around the pedicel of the flower, stating the tree location, flower number, experiment type and date (Fig. 2). After around five weeks, we visited the 13 trees to identify the flowers that were successfully pollinated and had developing fruit. Since the pedicels (and masking tape label) fell off in cases where the flowers did not develop into fruits, we collected the masking tape that were still attached (now to the fruit stalk) and calculated the proportion of fruiting for each pollination vector.

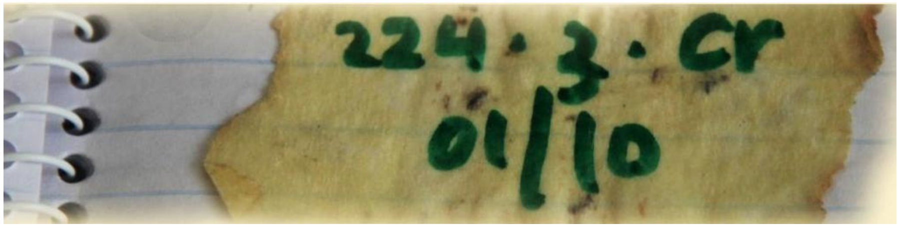

Fig. 2.2 An example of labeled masking tape that was collected from a fruit stalk in November 2012. 224 is the street location of the tree; 3 is the flower number tagged in this particular tree; cr the acronym used for cross-pollinated; and the date of the experiment was October 01, 2012.

2.2.5 Measuring self-incompatibility

We bagged 320 flower buds from 11 different trees for this experiment, carried out from October 01 to October 04, 2012. When the flowers opened (307 flowers opened and the 13 other buds fell off without opening), we crossed a set of five to ten flowers per tree (a total of 102 flowers), using a fine paint brush to remove pollen from flowers of a different tree and placing them on the stigma of the flowers of the experimental tree. The brush was washed between each use to avoid contamination of pollen grains from the same tree. The flowers were re-bagged to avoid visits by pollinators.

We also manually selfed (autogamous) another set of five to ten flowers per tree (a total of 102) and the flowers were re-bagged. Control flowers (a total of 103) were bagged without any manipulation. All flowers used in this experiment were labeled as described above (Fig. 2), using masking tape. The exclosure bags were left on until we re-visited the 11 trees on November 21, 2012 to collect the masking tape from the flowers that were successfully pollinated and calculated the proportion of flowers that produced fruit.

2.2.6 Measuring reproductive success versus degree of isolation

During the month of November 2012, we used stratified random 500 X 50 m transects on the three river banks (Fig. 1) to identify sausage trees growing in the area. We investigated 30 transects, 10 from each river and five on each bank. Transects on the same bank were at least 550 m apart. Since the riparian area was relatively sparse and we were working as a pair of observers, we each sampled parallel, side-by-side 25 m wide transects (thus combined into 50 m wide transects) where we identified a total of 139 reproductively active sausage trees. These were trees bearing fruit and/or remains of the flower stalks (which were still visible, though there were no flowers). The number of fruit per individual tree was noted. Fruit were counted in clusters of five when number of fruit exceeded 20 on an individual tree. We also measured the distance in metres to the nearest conspecific individual (also reproductively active) using a range finder (Callaway Rangefinder, LR550, Nikon, Japan).

2.2.7 Data analysis

All statistical tests were done using R (Version 2.15.2). We used a Mann-Whitney U test to measure the differences in successful pollination between the various groups of vectors. The proportion of successful fruiting resulting from selfed and crossed flowers was analyzed using the Kruskal-Wallis test. In cases where no fruits were produced, we altered the null value to a small insignificant value (10^{-6}) for statistical tests.

For the reproductive success versus isolation experiment, we correlated number of fruits with distance to the nearest conspecific individual. For the trees that were less than 50 m apart, we logged the data to show the relationship between number of fruits and distance. A regression analysis was used to examine the relationship.

2.3 Results

2.3.1 Floral attributes

Out of the 777 flowers used in the pollination experiments, 96.4% lasted only one day while a small number (28 flowers) persisted for two days, after which the corolla fell. All the flowers that were observed and/or used during this study opened only slightly before, at or after dusk. When the corolla opens, both stigma and anthers are fully developed (Fig. 3A), with the bi-lobed stigma opened. Only the manually selfed flowers' stigma opened again after a few hours though the lobes of all manipulated flowers closed when dusted with pollen. The average amount of nectar in the 62 flowers selected at dusk was 52.8 ± 4.3 ml while the average in those selected at dawn (60 flowers) was 14.8 ± 1.5 ml. The nectar (from all 122 flowers) had an average of 15.4 ± 0.7 % sucrose of sugar content (Appendix A).

2.3.2 Potential pollination vectors

We identified 12 different bird species visiting the flowers and 10 of these were observed feeding on the nectar (Table 1 & Fig. 3). We noted as many as 15 bird visitations to a single flower during a one-hour observation. Out of the 90 flowers we plucked from the three different trees, 70% had pollen on their stigma, and only one flower had a missing stigma (Appendix B). Many (53%) had major corolla lacerations such as large holes, ripped petals (Appendix B).

We analyzed between one to three hours of video footage from all the cameras each day. Table 1 summarizes the potential pollinators observed (through cameras and direct observation) in the act of visiting the flowers, noting whether they fed on nectar. Fig. 3B-F displays some of these species. Bees have also been observed entering the flowers but they were not perceived as potential pollinators as they did not touch the stigma at all.

Table 2.1 Direct and camera observations of various animal species that visit the flowers of *K. africana*.

Species		Observation type	Nectar feeding
Common name	Scientific name		
Brown-headed parrot	*Poicephalus crptoxanthus*	Direct	No
Purple-crested turaco	*Tauraco porphyreolopha*	Direct	Yes
Red-faced mousebird	*Urocolius indicus*	Direct	Yes
White-eared barbet	*Stactolaema leucotis*	Direct	No
Black-headed oriole	*Oriolus larvatus*	Direct	Yes
Dark-capped (Black-eyed) bulbul	*Pynonotus tricolor*	Direct + Camera	Yes
Cape glossy starling	*Lamprotornis nitens*	Direct + Camera	Yes
Scarlet-chested sunbird	*Chalcomitra senegalensis*	Direct	Yes
Southern masked weaver	*Ploceus velatus*	Direct	Yes

Village weaver	*Ploceus cucullatus*	Direct	Yes
Yellow-fronted canary	*Crithagra mozambica*	Direct	Yes
Vervet monkey	*Cercopithecus pygerythrus*	Direct + Camera	Yes
Green (Red-billed) wood-hoopoe	*Phoeniculus purpureus*	Camera	Yes
Thick-tailed bushbaby	*Otolemur crassicaudatus*	Camera	Yes
Large-spotted genet	*Genetta tigrina*	Camera	Yes

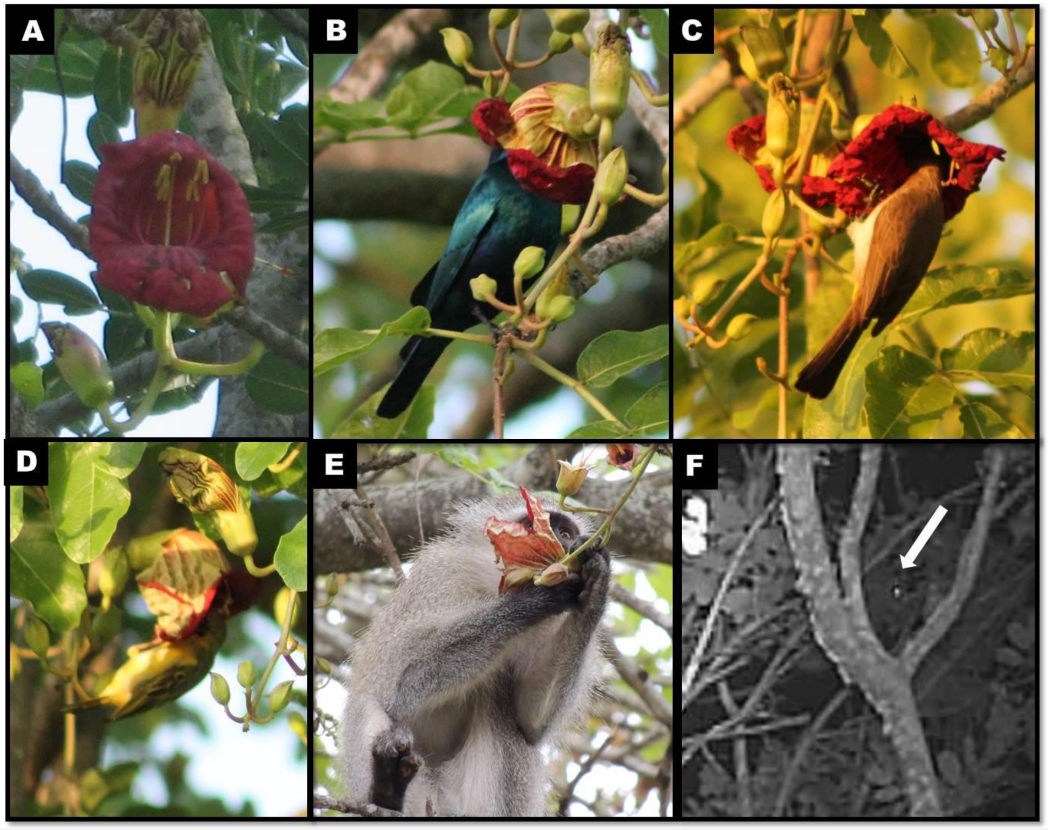

Fig. 2.3 *K. africana* and its various pollination vectors. Plate A shows an open flower and two buds, suspended on their stalk. Plate B depicts the Glossy starling (*Lamprotornis nitens*). Plate C shows a Dark-capped bulbul (*Pycnonotus tricolor*), perching on the stalk and reaching for the nectar. Plate D illustrates a Southern masked weaver (*Ploceus velatus*), clumsily perching on the flower petal to get to the nectar. Plate E portrays the Vervet monkey (*Chlorocebus pygerythrus*) lapping at the nectar. Plate F is a still of a video shot, illustrating the genet (*Genetta tigrina*) sniffing at one of the flowers before placing its snout into the flower.

2.3.3 Pollination success between different vectors

Both diurnal and nocturnal animals (W=0, p<0.0001; comparing control and all) play a significant role in the pollination of *K. africana* (Fig. 4). Though birds (W=6.5, p<0.0001) and nocturnal animals (W=52, p=0.0356) can both be successful pollinators, the former is significantly more important than the latter as pollinating agents for this species (W=16, p=0.000409). Birds successfully pollinated a mean of 60% of the flowers exposed to them (Fig. 2.4). Nocturnals, on the other hand, successfully pollinated only 10 out of the 150 flowers (6.7%) exposed to them. We did not detect a substantial difference between the proportion of flowers pollinated by birds and those pollinated by all vectors (W=55, p=0.135).

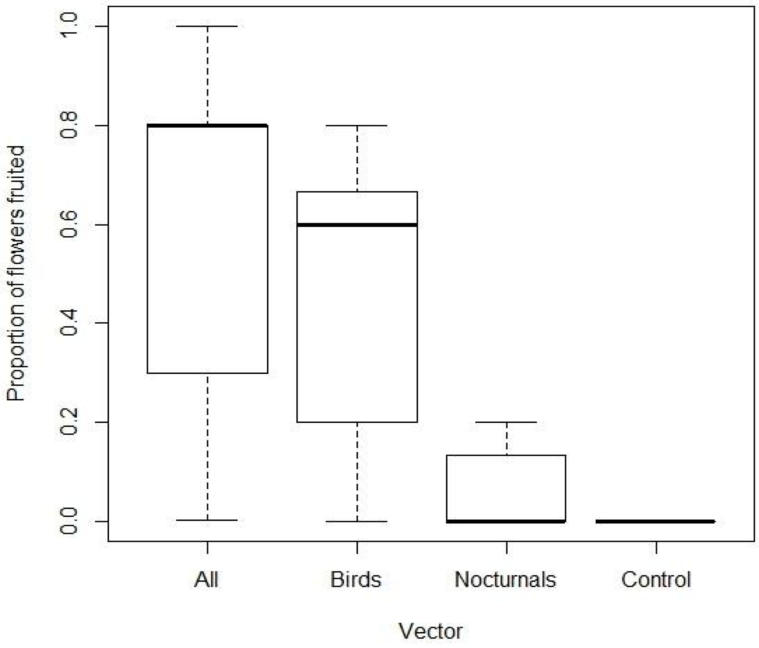

Fig. 2.4 The proportion of flowers that developed fruits as a result of pollination by several vectors: all (both diurnals and nocturnals), birds only and nocturnal animals only. The control was bagged flowers.

2.3.4 Self-incompatibility

K. africana proved to be an obligate outcrosser, with no success of fruiting when the flower was selfed or bagged (Fig. 5). An average of 80% of the flowers that we crossed successfully developed fruits. Using the Kruskal-Wallis test ($H(2)=24.1$; $p<0.0001$), a significant difference was found between the control and crossed proportion of flowers that fruited.

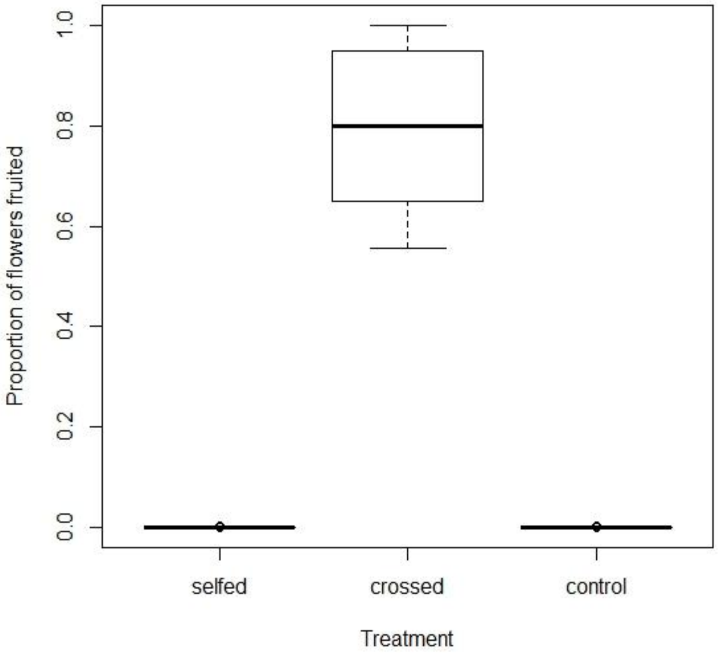

Fig. 2.5 The proportion of flowers that developed fruits when selfed and crossed.

2.3.5 Reproductive success versus degree of isolation

When the distance to the nearest reproductively active individual was more than 45 m, trees produced no fruits (Fig. 6A). We noticed that only six out of 111 trees (5%) that had a neighbor less than 45 m away had no fruits.

We logged the data for the trees within 50 m of each other and noticed a highly significant negative correlation ($r^2=0.51$, $p<0.0001$) between number of fruits and distance (Fig. 6B).

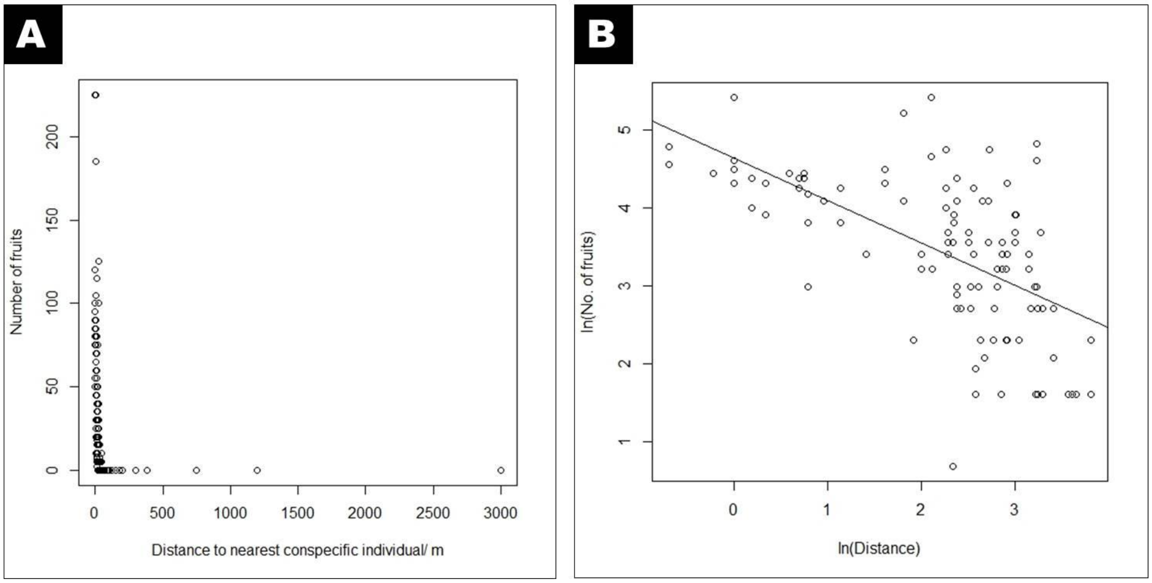

Fig. 2.6 Plate A is a scatter plot of distance to the nearest reproductively active tree and number of fruits. Plate B is a scatterplot of the logged distance versus logged number of fruits for the first 50 m only, showing a regression line.

2.4 Discussion

K. africana has many properties indicating that it is an outcrosser. The flowers are large, produce large amounts of nectar and they open in such a way that one of the petals act like a platform possibly to facilitate the entrance of its pollinator and, thereby, exposing both anthers and stigma. In fact Fig. 1A shows marks left on the ‘platform’ petal and Fig. 1C and 1D show birds perching on flowers using the described petal as anchor. Also, the style is longer than the anthers and placed in such a way that they do not touch at all (Fig. 5A). Besides, the stigma appears to be able to identify and reject pollen from self-pollination. Characteristic of the Bignoniaceae, the bilamellate stigma closes its lobes when pollen is deposited (Gentry, 1974) but in the self-pollinated flowers, the lobes opened again, indicating self-incompatibility.

Even though there is a higher nectar volume at dusk when the flowers open, this study shows that *K. africana* is heavily visited and successfully pollinated by birds rather than bats or other nocturnal animals (Fig 4), indicating that much of the copious nectar produced is lost to evaporation. Also, the fact that more than 50% of the flowers we examined (Appendix B) suffered major damage, such as tearing of the reproductive parts and ripped and punctured corolla, indicates that birds are not the natural pollinating agents of this species. Thus, we argue that this apparently bat-pollinated species is being somewhat rescued by birds. Since, there has been no up-to-date data found on the nectarivorous bat species, Wahlberg's epauletted fruit bat (*Epomophorus wahlbergi*) (Monadjem et al., 2010), populations in KNP, we cannot say for sure that this is a result of a decline in the availability of the 'natural' pollinating agents.

Our study indicates that the generalist birds we observed tend to be very clumsy pollinators, almost always tearing the flowers they visit (Appendix B). In contrast, Harris and Baker (1958) observed no damage to the flowers that were visited by bats. Although *K. africana* is widely assumed to be a bat flower, its plant-pollinator interactions in KNP indicate a more generalized system, which is now buffered against loss and/or unavailability of a bat mutualist.

Though other animals besides birds do contribute in the pollination of *K. africana* (Table 1), they are usually opportunistic, acting as pollinators more by accident. For example, the genet is an opportunistic omnivore (Virgós et al., 1999) and the vervet monkey's aggressive behavior (Frost & Frost, 1981) often tends to destroy the flowers' reproductive parts. Though, the opportunists cannot be trusted for the continued pollination of the sausage tree, their role as agents of pollination is crucial. Being an obligate outcrosser, *K. africana* completely depends on external vectors for pollination and, thus, fruitset.

Therefore, small populations and/or isolation of individuals are detrimental to seed-set of the sausage tree – the Allee effect (Allee & Rosenthal, 1949). Visits by all the observed pollinators (Table 1) would be constrained by large distances between conspecifics since it is essential for them to move back and forth between trees for successful pollination. Our study shows that the trees are affected when the nearest conspecific lies more than 45 m away (Fig. 6), terming a tree as “isolated” beyond this distance. Since the nearest conspecific individuals were reproductively active ones, this indicates that pollen became a limiting factor beyond 45 m and seed set was reduced to zero. Thus, even though birds can easily fly this distance, our study suggests that the longer the flight, the more pollen is lost and it could also be possible that isolated trees are rarely visited by the pollinators.

2.5 Conclusion

Our study shows that *K. africana* is an obligate outcrosser. Thus, maintenance of pollination is important for this species. However, even if *K. africana* has numerous characteristics of being a nocturnal or crepuscular flower, it has a generalized plant-pollinator interaction. Surprisingly, bird species, though clumsy, were the most successful pollinators of the sausage tree in KNP. Similar spectacular rescues are not unheard of. There are about 528 species of angiosperms which depend on nectarivorous bats for pollination (Fleming et al., 2009) but as the populations of the latter decline, such generalized interaction becomes crucial for the plants. One such example is the pollination of the dioecious liana, *Freycinetia baueriana* which is essentially a bat-pollinated plant in New Zealand being rescued by an invasive possum, *Trichosurus vulpecula* (Lord, 1991).

Allee effects were identified in the populations around Skukuza where isolated trees failed to set seeds. Our study shows that a maximum distance of 45m to the nearest conspecific individual is needed for reproductive success. We believe that pollen dispersal becomes a limiting factor beyond this distance and no seed is set. This drastically reduces the individual reproductive output, making isolated trees more vulnerable to stochastic effects, thus more prone to localized extinction (Gilpin & Soulé, 1986).

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Chapter 3: The population dynamics of the sausage tree (*Kigelia africana*) in relation to recruitment, dispersal, herbivory and elephant damage in Kruger National Park.

Abstract

The size class distribution of *Kigelia africana* was investigated and a very low recruitment category (eight recruits out of 151 trees surveyed) was observed in Kruger National Park. Camera traps did not capture any acts of dispersal. Herbivory was found to cause significant seedling mortality. There are indications that smaller herbivores might be damage recruits. Elephant damage through bark stripping though present was not an extensive.

Keywords

Kigelia africana, disperser, recruitment, herbivory, elephant damage

3.1 Introduction

Some woody species are experiencing demographic declines in Kruger National Park (KNP). These are a result of factors such as extensive elephant damage, fire (Whyte et al., 1999; Mapaure & Campbell, 2002; Edkins et al., 2008) and excessive herbivory (Eckardt et al., 2000). It has been suggested that several areas of the east and southern Africa are undergoing a shift in their vegetation from woodlands to open grasslands (Beuchner & Dawkins, 1961; Laws, 1970; Augustine & McNaughton, 1998). Analyses of fixed-point photographs in KNP, for example, have shown a distinct decrease in the number of larger trees (Eckardt et al., 2000). *Kigelia africana*, being one of the larger trees that can grow up to 25 m in height (Rønne & Jøker, 2005), might be one of the affected trees in the riverine system of southern Africa.

The idealized size class distribution of an all-aged population forms an inverse J-shaped curve when frequency is plotted against size class (Meyer, 1953 in Johnson & Bell, 1975), showing abundant recruits relative to adults. An absence in recruitment indicates a declining population (Miller, 1998).

K. africana does not suffer from pollination limitation, as discussed in Chapter 2, and most individuals set seeds. It has large fruits that can weigh up to 10 kg (Rønne & Jøker, 2005), thus, is possibly dependent on mutualisms for seed dispersal. Poor dispersal can contribute to regeneration limitation as was observed in *A. rubrostipa* (Metcalfe et al., 2007). There have been no studies done on the dispersal of the sausage tree but the large sausage fruits have been reported to be dispersed by African elephants (*Loxodonta africana*) and baboons (Mduma et al., 2007; Katende et al., 1995 in Omejaa et al., 2011). Seedling herbivory can heavily impact recruitment (Belsky, 1984). No such study was done to investigate how this affects the regeneration of *K. africana*. Adult trees can also be affected through herbivory. For instance, Ihwagi et al., (2010) observed that the African elephants debarks the sausage tree, thus damaging many trees in Kenya.

The primary aim of this study is to determine the size class distribution of *K. africana* in KNP and factors that may determine the size class structure. We sought to determine whether elephant damage through bark stripping is an issue. The canopy herbivory of the trees was considered and we correlated this with height, assuming that a younger tree (less tall) will be more impacted than an older tree (taller) since the former is more accessible to a browser. Suspected browsers included Giraffe (*Giraffa camelopardalis*), Kudu (*Tragelaphus strepsiceros*), Impala (*Aepyceros melampus*), with the Giraffe being the main herbivore of the adult trees. We also investigated the impacts of herbivory on the seedlings and current patterns of seed dispersal.

3.2 Materials and methods

3.2.1 Study site

The study was carried out around Skukuza in Kruger National Park (Fig. 1) from October 2012 to January 2013. Since *K. africana* grows mostly along riverine systems, three rivers (N’waswitsontso, Sabie, N’waswitshaka) having the larger population of sausage trees around Skukuza were sampled. Though these three rivers are completely different with different sources, soil types, flood histories and vegetation structure (Gertenbach, 1983), they were the only rivers with sets of known sausage trees growing along them. The banks of N’waswitsontso below Orpen Dam were the furthest we investigated outside Skukuza.

The seedling herbivory experiment was partially carried out in Skukuza village which is an exclosure for megaherbivores.

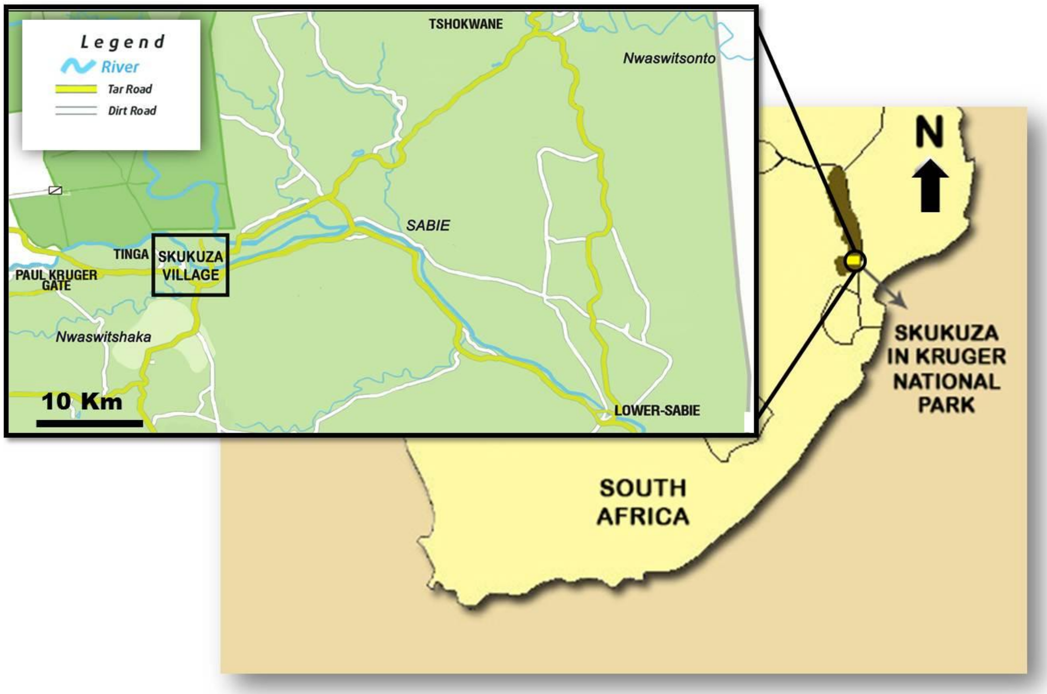

Fig. 3.1 Map of showing Skukuza village and the three rivers (N’waswitsontso, Sabie, N’waswitshaka used around Skukuza in Kruger National Park

3.2.2 Transects for size class distribution

To determine the size class distribution, we used 10 stratified random 500 X 50 m transects on each of the river banks, five from each bank (Fig. 1), where we identified all sausage trees. Transects on the same bank were at least 550 m apart. Since the riparian area was relatively sparse and we were working as a pair, we each did parallel, side-by-side 25 m wide transects (thus combined into 50 m wide transects). We measured the diameter at breast height (DBH) of each tree. The diameter of the younger trees (<1.3m in height) was taken at the base. The trees were then grouped into three categories: recruitment (DBH<15cm), intermediate (15<DBH<30cm) and large (DBH>30cm).

3.2.3 Estimating elephant damage

We estimated the percentage (%) of bark stripped by assessing the damaged area in proportion to the whole tree trunk and branches. We call this % estimated elephant damage. This was done for each tree identified in the transects.

3.2.4 Estimating canopy herbivory

We measured the height of each tree and seedling using a rangefinder (Callaway Rangefinder, LR550, Nikon, Japan). This was done by pointing the rangefinder at the topmost of the tree with no obstructions between the rangefinder lens and the tree. We also estimated the percentage (%) of canopy leaves browsed for each individual in the transects. This was done by assessing the eaten leaves in proportion to the whole canopy. We used a pair of binoculars (10 X 42) to identify the herbivory in the canopy. Herbivory was assumed to be where the axil was left with only part of the petiole attached and no leaves. An example of this is shown in Fig. 2.

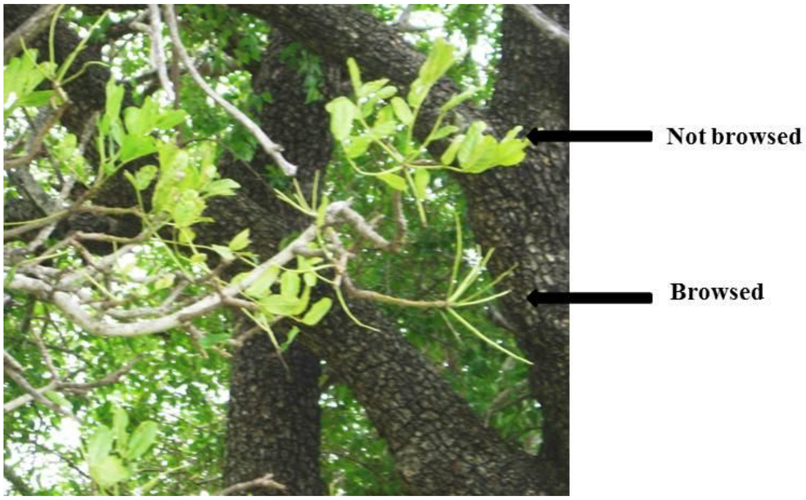

Fig. 3.2 An example where part of the canopy was browsed.

3.2.5 Measuring seedling herbivory

In October 2012, around 500 seeds from fallen sausage fruits were collected and planted in paper cups (Fig. 3A). The fruits had to be hammered open to get the seeds since we did not take decaying fruits. The substrate for germination was soil from the Sabie river bank (Fig. 1). The 483 seedlings that germinated were grown and hardened (Fig. 3B) in the nursery in Skukuza for seven weeks. Then the seedlings were planted in groups of 10 (one group of 10 seedlings = a plot) (Fig. 3C) as detailed below.

- Eight plots were planted outside Skukuza village where they were accessible to all herbivores, including mega-herbivores like elephants.
- Eight plots were planted inside Skukuza village, where mega-herbivores are excluded.
- Ten plots were planted inside a partial enclosure in the village, where only small animals such as rodents and warthogs could enter.
- As control, eight plots were planted outside the village and eight plots inside the village, all under enclosureswhere no herbivores can get to the seedlings. Figure 3D shows one of the enclosures

The planted seedlings were left for around nine weeks, from November 15, 2012 to January 14, 2013, after which we counted the live seedlings to investigate the extent of herbivory.

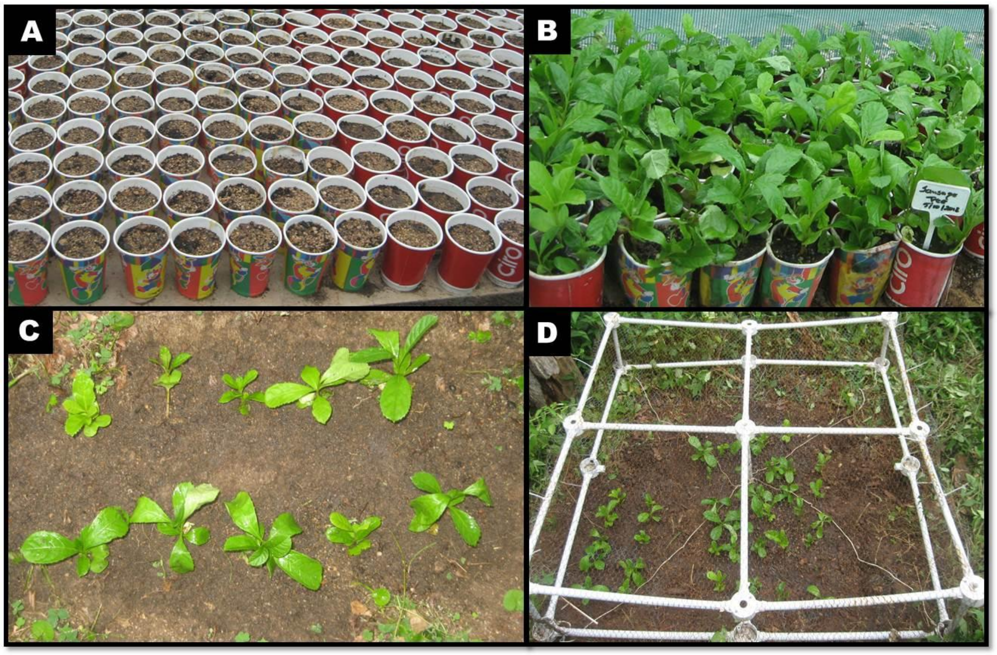

Fig. 3.3 **A** shows the paper cups used for germination of *K. africana*. **B** depicts the seedlings before they were transferred to the ground for the purpose of this experiment. **C** demonstrates a plot of planted seedlings. **D** shows the fine-meshed enclosure used to exclude all herbivores.

3.2.6 Fruit dispersal

Seven camera traps (TrailMaster, TM1550, Goodson & Associates, Inc, United States of America) were placed in four sausage trees around Skukuza and Tinga, a private Game Reserve (Fig. 1). The trees were selected since they were fruiting and had extensive and broad branches on which we could attach the camera traps securely. We collected fallen sausage fruits throughout the region and placed them at the base of these trees to attract any potential disperser. The cameras were left in the trees both during the day and night from

November 2012 to January 2013. The footage was checked on a weekly basis for potential dispersers.

3.2.7 Data analysis

The size-class distribution, having only three categories, is analyzed using simple ratios. The data for elephant damage and herbivory was analyzed in R (Version 2.15.2). Linear regression was used to evaluate % elephant damage through bark stripping and size as well as % canopy herbivory and height. A Mann-Whitney U test was used to compare the extent of seedling herbivory in the different situations.

3.3 Results

3.3.1 Size class distribution

A total of 151 sausage trees were identified, having diameter ranging from 0.9-170 cm. We found the distribution dissimilar on the three river banks. On N'waswitsontso, the ratio of recruitment: intermediate: large is 0.08: 0.14: 1 (n=122) whereas on Sabie it is 0:0.04: 1 (n=26), with no recruits and 0: 0:1 on N'waswitshaka (n=3) (Fig. 4).

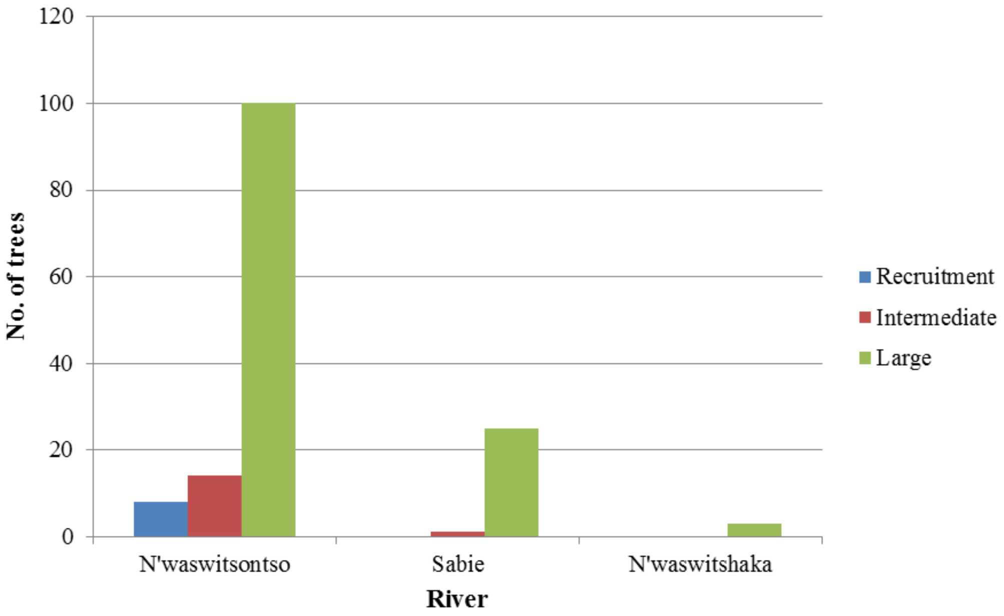

Fig. 3.4 The size class distribution on three river banks in Kruger National Park. Recruitment are trees having DBH <15cm; intermediate 15<DBH<30cm and large DBH>30cm.

3.3.2 Elephant damage through bark stripping

We did not find any significant elephant damage in relation to tree size (r^2=0.00594, p=0.736) suggesting that elephant damage does not accumulate with increasing size of trees (Fig. 5). Only 22.5% of the trees (n=151) were found to have bark stripping marks on them and the average percentage of damage was low (Table 1). Most of the damage to the trunks was old and no trees were found to have been uprooted or otherwise fatally damaged by the elephants.

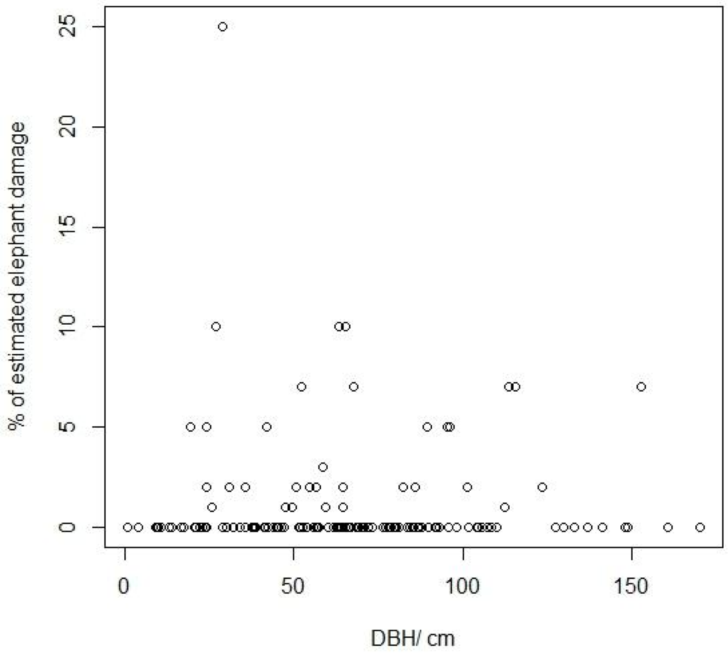

Fig. 3.5 A scatterplot, showing the relationship between % elephant damage by bark stripping and tree size.

Table 3.1 Average % of elephant damage

Average % bark stripped (n=151)	1
Average % bark stripped for damaged trees only (n=34)	4.6

3.3.3 Canopy herbivory

The canopy of younger trees (less tall) experience more browsing than older trees (r^2=0.35, p<0.0001) (Fig. 6). Trees less than five metres are usually affected with more than 10% canopy loss while trees higher than seven metres have less than 15% canopy loss by herbivores.

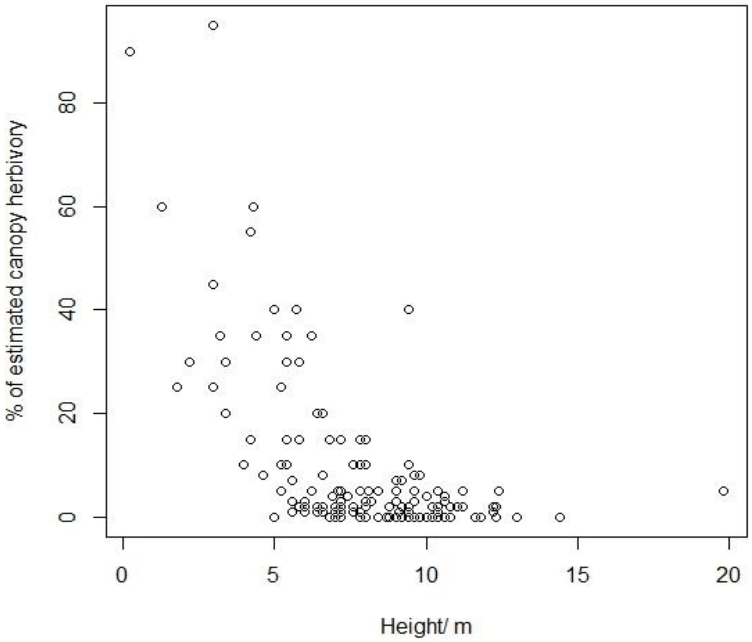

Fig. 3.6 The relationship between % canopy herbivory and tree height.

3.3.4 Seedling herbivory

We found that natural mortality in *K. africana* seedlings was low (about an average 15% in the control, i.e. about 7% per month). There is also evidence of herbivory on the planted seedlings, where average mortality was higher between 35-55% (where herbivores were present) (Fig. 7). We found a significant difference in the proportion of live seedlings remaining after the two months both between the control and those left in the open for all herbivores (W=59.5, p=0.004), and between the control and those in the partially enclosed area (for small animals) (W=5, p=0.0168). However, we did not detect a significant difference between the proportions of live seedlings between the different groups of herbivores.

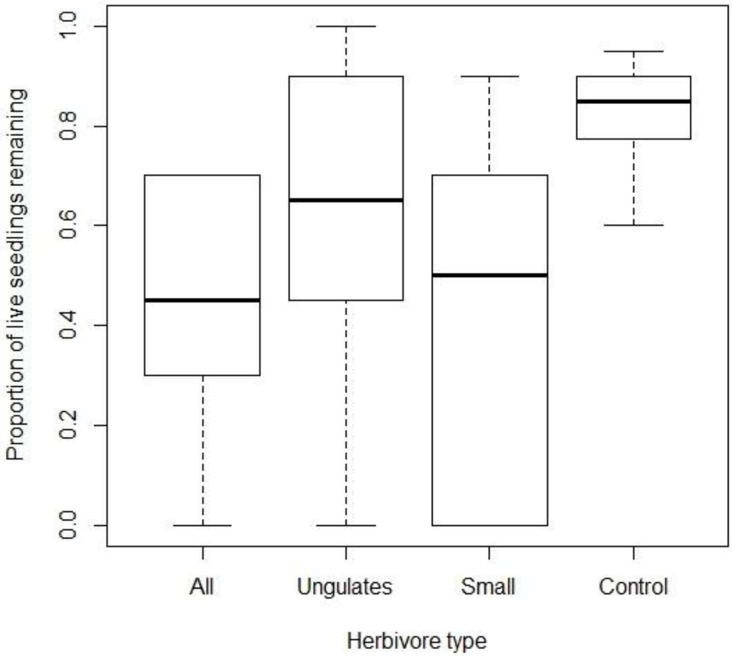

Fig. 3.7 Boxplot showing the difference between the proportions of live seedlings after two months of being exposed to different types of herbivores: All (all herbivores), Ungulates (excluding mega-herbivores) and Small (small animals, such as rodents, only). The control was seedlings left under an enclosure, thus mortality was of natural causes only.

3.3.5 Dispersal

Despite analyzing an average of 30.2 hours of video footage from the camera traps, we found no animals directly taking the fruits or seeds from the base of the trees. Nevertheless we did see elephants sniffing at the fruits though no feeding or dispersal was observed. We also noticed a baboon carrying a wrinkled fruit but not one we had placed out.

3.4 Discussion

3.4.1 Size class distribution

The inverse J-shaped size class distribution (SCD) is generally used by biologists as an indication of a healthy, regenerating population and a deviation from this is a cause of concern (Wilson & Witkowski, 2003). Therefore, the lack of recruitment and skewed size class distributions of *K. africana* should be a concern for the KNP.

Of the three rivers we sampled, recruits, albeit low in numbers, were found only on N'waswitsontso; where most of the trees also happen to occur (Fig. 4). We suggest that this difference could be linked to the soil type on the different river banks. Both Sabie and N'waswitshaka have shallow and sandy soils (Venter 1986) while the banks of N'waswitsontso are more undulating with the soils particles being more compact and clayey (Gertenbach, 1983) but no study has been done on the soil characteristic requirements for the establishment of *K. africana* seeds.

The main reasons for a lack of recruit could be that *K. africana* suffers from disperser and germination limitation. Since the camera traps had no concrete proof of any dispersal actions, we assume that the sausage fruit is not a favorite diet among frugivores. Baboons might be interested in the fruit but this is also anecdotal. Elephants and rhinoceros have been reported as seed dispersers (Rønne & Jøker, 2005). However, for a more in-depth study on dispersal, we propose that the camera traps be left longer than just the summer season, when food is no longer abundant, to see whether the seeds are taken then.

Germination does not seem to be an issue since 96.6% of untreated seeds we planted germinated. Thus the seeds are viable but the successful establishment could be attributed to irrigation. The paper cups in which the seeds were planted (Fig. 3.3A) were watered daily in the nursery for an optimum result but it is uncertain whether the seeds receive such large amounts of water in the wild. However, around 85% of the seedlings in the control plots survived the two months (Fig. 7) after being transferred to the soil where they were not watered manually. This suggests that once germinated, the sausage tree has a high probability of survival.

Intense damage through herbivory can also explain the recruitment bottleneck. The seedling herbivory experiment ascertained that mortality of seedling is increased through herbivory though we cannot say which herbivores damage the seedlings the most (Fig. 7). Our results may be slightly biased since six of the plots (60 seedlings) of the partial enclosure accessible to only small animals were flooded in January 2013. However, mortality in this situation was still significantly higher which suggests that small herbivores may be affecting the seedlings most. We suggest a duplication of this experiment, with a larger sample size as a further study for an improved understanding of herbivory on *K. africana* seedlings.

3.4.2 Canopy herbivory

We observed that trees under five metres were always damaged, most of them having more than 20% estimated canopy loss due to herbivory (Fig. 6), possibly because more new shoots were accessible to browsers. Young leaves of many species are more nutritious with higher protein content and more palatable than mature leaves (Feeny, 1970). Trees above that range were less targeted since the new shoots were higher, thus they suffered mostly on the more readily available lower part of the canopy. We have no evidence of the identity of the browsers but the empirical result of this study suggests that giraffes might be one of the main browsers since they have a browse height between two and five metres (Bond & Loffell, 2001).

3.4.3 Damage to trunks of sausage trees

Though elephants have been found to be damaging many tree species such as *Sclerocarya birrea* (marula trees) and *Acacia nigrescens* (knobthorn trees) in KNP (Whyte et al., 2003), especially by bark stripping (Jacobs & Biggs, 2002; Mapaure & Campbell, 2002), our data suggest that they do not specifically target the sausage tree in KNP. Most of the elephant damage we observed was not fresh. We noticed that flood could be much more damaging. Many canopy trees were found toppled over as a result of flooding. However, most of those trees (10 out of the 12 large trees we found toppled over) were found to be fiercely resprouting, proving that *K. africana* is a persistent species.

3.5 Conclusion

Due to its extensive distribution (Rønne & Jøker, 2005), the sausage tree is probably not going be extinct for centuries even if left to its fate. However, it can be locally endangered since it is experiencing low regeneration. Recruits were found on only one bank out of the three rivers sampled. Poor seed dispersal could be a factor limiting recruitment but further study is needed to confirm this.

Floods seem to have a heavy impact on the trees, especially on the Sabie river banks. The Sabie has experienced a series of flood events, the most recent and severely damaging being in February 2000 (Smithers et al., 2001). We suggest further studies to establish to what extent flood, groundwater and/or general disturbance affect the SCD of *K. africana*.

Neither elephants nor canopy herbivores lethally damage adult plants. Seedling herbivory, however, seems to be an important key to unlocking the mystery of the ‘missing’ size class. Though this study ascertains that a large proportion of seedlings are targeted by herbivores, further experiments are needed to confirm whether herbivores actually limit the regeneration of the sausage tree population.

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Chapter 4: Synthesis

In a changing world where anthropogenic impacts are changing landscapes and environmental degradation is prominent, mutualisms are very threatened (Brook et al., 2008). Kiers et al., (2010) argue an evolutionary perspective whereby mutualistic relationships slowly shift to accommodate the paradigm either by shifting from mutualisms to antagonisms (Sachs & Simms, 2006) or encompassing new partners (West et al., 2007) or abandoning mutualism (Bronstein et al., 2004) completely. Looking at the ecological perspective, this study indicates that mutualisms do matter though it can be flexible, depending on how tightly partners are bound.

Mutualisms are central to the reproduction and continued survival of myriad organisms (Bronstein et al., 2004). Out-crossers, especially obligate out-crossers are totally dependent on mutualisms for successful reproduction. However, pollination syndromes do not essentially exclude a range of pollinators in favour of one (Johnson & Steiner, 2000). For example, *K. africana*, obligate out-crosser, is often quoted as a bat-flower but its most successful pollinator in Kruger National Park was bird species (Chapter 1). The plant-pollinator mutualism was found to be more flexible, not tightly binding the species to a specific vector.

Following pollination, seed dispersal is the key mechanism for the continued reproduction (Cain et al., 2000), thus, population dynamics of a species. Many plants have mutualistic relationships with animals, relying on their mobility to be able to propagate (Schupp, 1993). *K. africana,* having large and heavy fruits, is one such species (Rønne & Jøker, 2005). Our study undertaken in KNP provides no evidence of fruit dispersal (Chapter 2). This has been attributed to potential dispersers having other sources of food in the summer months.

Effective seed dispersion is usually measured through recruitment (Nathan & Muller-Landau, 2000), a low recruitment suggesting that there is a problem with either seed set or seed dispersal. Though *K. africana* seed dispersal remains undetermined after this study, we have established that pollination is successful and seeds are set; though the closer the trees are to conspecifics the more likely they are to have substantial seed set (Chapter 1). The lack of recruitment in this case was argued to be partly due to herbivory on the seedlings (Chapter 2).

In the context of conservation efforts, understanding which species are involved in plant-pollinator and/ or plant-disperser interactions is especially important, since a plant species may not be able to sustain its population in the absence of its partner(s) and vice-versa. Although it is unrealistic to study mutualisms in minute ecological and evolutionary details, key studies such as those with keystone mutualists serve as guides to the range of both extant and extinct interactions.

One major conservation concerns in Parks and Reserves is the decline of the big trees (Turner et al., 1996). The sausage tree which can grow up to 25 m in height (Rønne & Jøker, 2005) should be one such case of apprehension in the Kruger National Park. *K. africana* should be viewed and treated as a rather rare species due to declining density and unhealthy size class distribution. It, undoubtedly, provides shelter for an array of animals, nectar to differing diurnal and nocturnal fauna, especially an array of birds (Chapter 1), fruit possibly to elephants, baboons and rodents, leaves for some herbivores. Dunham (1980) notes that even the fallen flowers are eaten by Impala.

In the past, Kruger National Park has arisen to various novel techniques to manage heterogeneity in its various ecosystems (Du Toit et al., 2003). In this case the problem(s) behind the cause of *K. africana*’s unhealthy size class distribution still remain(s) mostly unidentified. Is it a loss of disperser or a case of massive seedling herbivory? The substrate in which the trees grow could also affect the population. Flood events could be a contributing factor. There are many unanswered questions that need to be addressed that provides opportunities for myriad further studies.

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APPENDICES

Appendix A A summary of nectar attributes. Three to ten flowers from nine different *K. africana* trees were used for this experiment. A total of 60 flowers were plucked to calculate the average nectar present in the flowers at dawn and a total of 62 flowers were used to calculate average nectar present at dusk. Drops of nectar from all of the 122 flowers plucked were used to estimate the average nectar sugar content.

Tree No.	No. of flowers plucked at dawn	Average Dawn Nectar/ ml	No. of flowers plucked at dusk	Average Dusk Nectar/ ml	Average Nectar sugar content/ % sucrose
1	5	9	7	30	12
2	8	10	10	49	19
3	4	14	5	35	15
4	10	12	8	57	17
5	3	12	5	64	15
6	9	22	10	68	13
7	5	20	6	52	17
8	10	18	7	58	14
9	6	16	4	62	17

Appendix B A summary of bird damages on the observed flowers (n=90).

Laceration type	**% flowers affected**
Ripped	18.9
Large hole	24.4
Small punctures	38.9
Stigma missing	1.1
None	17.8