

available at [www.sciencedirect.com](http://www.sciencedirect.com)journal homepage: [www.elsevier.com/locate/biocon](http://www.elsevier.com/locate/biocon)

# Balanites wilsoniana: Regeneration with and without elephants

Fred Babweteera<sup>a,\*</sup>, Peter Savill<sup>b</sup>, Nick Brown<sup>b</sup>

<sup>a</sup>Budongo Forest Project, P.O. Box 362 Masindi, Uganda

<sup>b</sup>Department of Plant Sciences, University of Oxford, South Parks Road, Oxford OX1 3RB, United Kingdom

## ARTICLE INFO

### Article history:

Received 21 March 2006

Received in revised form

8 August 2006

Accepted 16 August 2006

Available online 2 October 2006

### Keywords:

Tropical rainforest

Disturbance

Fruit size

Large vertebrates

Dispersal and predation

## ABSTRACT

Tropical forest trees that produce large fruits and/or large seeds are believed to be dependant on a few and often rare large vertebrates for dispersal. However, little is known about the population dynamics of such trees when they lose their specialised dispersers. This study examines the juvenile spatial distribution of *Balanites wilsoniana*, Dawe & Sprague, which is believed to be dependant solely on elephants for dispersal, in forests with and without elephants. Using camera traps, elephants were confirmed to be the only frugivores feeding and thus dispersing *Balanites wilsoniana* fruits. There was a high density of seedlings beneath adult trees in one forest without elephants, which was attributed to low seed and seedling predation in this forest. Nevertheless, it was only in the forest with elephants that juveniles were established away from adult trees. Analysis of the spatial distribution of these juveniles by size revealed that saplings and poles are more likely to be found away from adult trees thus providing evidence that dispersal enhances juvenile survival. This study underlines the importance of seed dispersal for trees that cannot maintain their populations through seedlings germinating and surviving beneath adult conspecifics. The study also demonstrates that loss of vertebrates has ramifications for tree species dynamics above and beyond loss of seed dispersers.

© 2006 Elsevier Ltd. All rights reserved.

## 1. Introduction

Many tropical forest tree species are dependant on animals for dispersal (Gautier-Hion et al., 1985; Corlett, 1996; da Silva and Tabarelli, 2000). Animals disperse seeds of tree species that provide them with a direct reward such as fleshy fruit or arillate seeds. Among the tree species that produce fleshy fruits, it is presumed that frugivores often specialise on particular fruit traits (e.g. Gautier-Hion et al., 1985). Perhaps of greater importance for tree population biology, are the limits that are set by fruit allometry to the range of frugivores that are capable of dispersal. Only large-bodied animals have the capacity to swallow or carry large seeds intact. As both the

richness and abundance of animals declines with increasing body size, large-seeded tree species may have limited rather than specialised animal dispersers. There may also be limited capacity for disperser substitution if an important animal disperser is lost. There are a number of well-known examples where it has been hypothesised that the loss of a large vertebrate has led to the decline of tree species dependant on it for dispersal. Examples for such narrow mutualisms are *Trewia nudiflora* and Rhinoceros (*Rhinoceros unicornus*) (Dinerstein and Wemmer, 1988); *Balanites wilsoniana* and elephants (*Loxodonta africana*), (Chapman et al., 1992); and *Calvaria major* and dodos (*Raphus cucullatus*) (Temple, 1977).

\* Corresponding author. Tel.: +44 1865 275 810; fax: +44 1865 275 084.

E-mail addresses: [fred.babweteera@plants.ox.ac.uk](mailto:fred.babweteera@plants.ox.ac.uk), [bfp@africaonline.co.ug](mailto:bfp@africaonline.co.ug) (F. Babweteera), [peter.savill@plants.ox.ac.uk](mailto:peter.savill@plants.ox.ac.uk) (P. Savill), [nick.brown@plants.ox.ac.uk](mailto:nick.brown@plants.ox.ac.uk) (N. Brown).

0006-3207/\$ - see front matter © 2006 Elsevier Ltd. All rights reserved.

doi:10.1016/j.biocon.2006.08.002

It is well known that hunting and habitat fragmentation have a disproportionate effect on large vertebrates (Pimm et al., 1988; Peres, 2001). This is because large vertebrates are more attractive to hunters and often have a lower reproductive rate (Bodmer et al., 1997). Large vertebrates cannot adjust to persistent hunting pressures by becoming more behaviourally inconspicuous. Also, they require large contiguous habitats (Laidlaw, 2000), which means they are vulnerable to fragmentation.

Despite the growing awareness that some tree species are dependant on one or a few, often rare, large vertebrate seed dispersers, there is limited information on whether their loss from tropical forests would result in restricted regeneration and possibly eventual extinction of the tree species dependant on them for dispersal. This study examined dispersal and recruitment of *B. wilsoniana* Dawe and Sprague (Zygophyllaceae), a tree species believed to be dependant on elephants (*L. africana* Blumenbach) for dispersal and germination (Chapman et al., 1992; Hawthorne and Parren, 2000; Cochrane, 2003). This tree species was selected because it is widely distributed in many tropical rain forests across West, Central and Eastern Africa (Lieberman et al., 1987; Hamilton, 1991; Hawthorne and Parren, 2000). However, some of these forests have lost their elephant populations over the past years (Howard, 1991; Alers et al., 1992). Thus, the study of *B. wilsoniana* in forests with and without elephants would provide an insight into the effects of loss of a specialised disperser.

In previous studies of *B. wilsoniana* (hereafter *Balanites*) it was observed that elephants are their sole seed dispersers (Cochrane, 2003). It is also believed that passage through the guts of an elephant increases the proportion of seeds that germinate as well as reducing time to germination. Seed predators of *Balanites* can destroy up to 80% of undispersed seeds (Cochrane, 2003). The reduced germination time may increase germination by reducing exposure to seed predators. These observations have led to the belief that elephants provide the only means by which *Balanites* can maintain its population over the long-term. However, none of the studies of the *Balanites*–elephant mutualism examine the effects of loss of elephants on the population dynamics of *Balanites* by comparing forests with and without elephants. The recruitment and survival of tropical trees may not be entirely dependant on dispersal but post dispersal survival of seeds and seedlings (Forget, 1993).

Consequently, this study attempted to assess three issues. Firstly, it examined whether there is any kind of disperser substitution in forests where elephants have been lost. Secondly, the study assessed the regeneration and spatial distribution of juveniles of *Balanites* in forests with and without elephants, to determine whether the juveniles were recruiting from dispersed seeds or not. Thirdly, the study examined the spatial distribution of juveniles by size to determine whether the dispersed juveniles had a higher probability for survival. In conclusion, the results of the study are discussed in a wider context of the implications of loss of large vertebrates for seed dispersal and population dynamics of the large fruited and/or large seeded tree species in tropical rain forests.

## 2. Methods

### 2.1. Study sites

This study compared three tropical rain forests in Uganda namely: Mabira, Budongo and Kibale Forests. The three forests were selected because they are habitat to *Balanites* trees. In the past, the three forests had an almost similar fauna and floral composition (Hamilton, 1991; Howard, 1991), however, the animal populations in the three forests have been subject to very different intensities of disturbance. Mabira Forest Reserve is a medium altitude moist semi-deciduous forest in Central Uganda (32°52′–33°07′E and 0°24′–0°35′N), covering an area of 306 km<sup>2</sup>. The forest has been subjected to intense anthropogenic disturbances such as logging and hunting which have led to loss of most of its animal populations (Howard, 1991). In addition, vast areas of formerly forested land have been converted to agriculture land. For example over a period of 15 years (1973–1988) it is estimated that 29% of the forest cover was lost and the total forest edge-to-area ratio increased by 29% over the same period (Westman et al., 1989). This resulted in severe forest fragmentation with an estimated fifty thousand people living in the associated enclaves. Budongo Forest Reserve is also a medium altitude moist semi-deciduous forest in western Uganda (31°22′–31°46′E and 1°37′–2°03′N), covering an area of 853 km<sup>2</sup>. Although Budongo has been selectively logged since the 1920s, it remains relatively intact with a large population of diurnal primates (Plumptre and Cox, 2006). Mabira and Budongo Forest Reserves are both believed to have had other large vertebrates such as elephants (*L. africana*) and leopards (*Panthera pardus*) but these were driven to extinction between 1950 and 1980 (Howard, 1991). As forest reserves, logging is still permitted in Mabira and Budongo. On the other hand, the 506 km<sup>2</sup> Kibale Forest National Park (30°19′–30°32′E and 0°13′–0°41′N) is a moist evergreen forest, transitional between lowland rain forest and montane forest. Kibale is habitat to approximately 280 elephants and has a higher primate biomass than Mabira and Budongo (Plumptre and Cox, 2006). As a national park, Kibale is granted a better protection status than Budongo and Mabira given that neither logging nor hunting is permitted.

### 2.2. Study species

*Balanites* is an upper canopy deciduous tree that reaches a height of 40 m. Adult trees of *Balanites* have extensive crowns reaching 30 m in diameter ( $N = 46$ ). The tree produces single-seeded fruits c. 90 mm in length and 60 mm in width (Chapman et al., 1992). When mature, the fruits are green-brown with an unpleasant smell. The seeds c. 88 mm in length and 47 mm in width are often found in elephant dung in Kibale Forest (Chapman et al., 1992). The large seed and fruit sizes are thought to exclude other frugivores including many primates, from feeding on them. As a result, *Balanites* is believed to be ingested and dispersed by elephants only. However, scatter hoarding rodents are also thought to disperse *Balanites* seeds although their contribution is insignificant (Cochrane, 2003).

### 2.3. Frugivory

Six individual fruiting trees of *Balanites* (hereafter focal trees) were selected in each of the three forests between April 2004 and July 2005. The focal trees were at least 1 km apart. Three of the six focal trees in each forest were used for direct observation of frugivory activities and these were made at the peak of the ripe fruit for six days for a period of 7–9 h per day. Thus the average observation time for each focal tree was 48 h. The observations were made between 700 h and 1800 h, with breaks during periods of rainfall. The total numbers of direct observation hours were 146, 139 and 157 h for Mabira, Budongo and Kibale respectively. During these direct observations we recorded information on frugivore species visiting the trees, the number of fruits consumed per visit and the time spent feeding for each visiting frugivore species. In addition to the direct observations, we mounted camera traps (DSC-P32 Digital Camtrakkers) close to the remaining three focal trees to record information on frugivores feeding on fallen fruits and the presence of seed and seedling predators. Four cameras were placed within a radius of 30 m from each focal tree and were set to operate during the day and night (24 hourly observations) for a mean duration of 1820 h per tree. The total numbers of camera trap observation hours were 5049, 5292 and 4455 h for Mabira, Budongo and Kibale, respectively. Cameras were programmed with a 5 min delay timer between consecutive photographs in order to limit the probability of photographing the same individual animal. Only photographs with animals were included in the photographic count. Camera traps have been used successfully to study animal populations (Carbone et al., 2001; Silveira et al., 2003) and their use is thought to overcome the limitations of human observation such as failure to observe nocturnal frugivores and shy secondary dispersers, and seed or seedling predators.

### 2.4. Regeneration and juvenile spatial distribution

This was assessed in square 1-ha plots established around adult trees of *Balanites*. We established three plots around three of the six focal trees in each forest. In each plot, we made an intensive search for all juveniles (seedlings 0–50 cm in height; sapling 51–400 cm; and poles >400 cm in height but less than 10 cm DBH) of *Balanites* and the distance to the adult *Balanites* tree measured. It should be noted that *Balanites* propagates both sexually and vegetatively. Consequently, an effort was made to identify whether juveniles originated from root sprouts or seeds. Individuals confirmed to be developing from sprouts were omitted from the analysis. To compare the relative dispersion between forests, the cumulative distributions of distances from juveniles to adult trees in each forest were computed (Hamil and Wright, 1986). Pairwise Kolmogorov–Smirnov tests were then conducted between plots within each forest to determine whether there were significant differences in the spatial distributions among plots within each forest. Thereafter, the spatial distribution data were pooled for each forest to obtain a single distribution function to enable comparisons between forests using Kolmogorov–Smirnov tests. To test for the effect of dispersal on juvenile survival, the cumulative distributions

of distances from seedlings, saplings and poles were compared. The comparison was done for forests where some juveniles were observed to be established further away from the adult tree, thus an indication of dispersal. The underlying assumption of this analysis is that if mortality among juveniles is independent of the distance from the adult tree, then the cumulative distributions of seedlings, saplings and poles should be similar.

## 3. Results

During the direct focal tree observations, no frugivores were observed feeding on the fruits of *Balanites* in any of the three forests. However, using camera traps, elephants were the only animals photographed feeding nocturnally on the fruits of *Balanites*, in Kibale Forest. In addition, *Balanites* seed predators (bush pigs) and seedling predators (duikers) were photographed in Kibale and Budongo Forests only (Table 1).

The recruitment of juveniles was higher in Mabira Forest than Budongo and Kibale Forests. The mean number of juveniles in the plots was 2 298, 39 and 85 per ha in Mabira, Budongo and Kibale, respectively. The high seedling density observed in Mabira was not due to vegetative regrowth, indeed over 80% of the juveniles arose from seeds. However, an analysis of the size class distribution of the juveniles in the three forests indicated a small proportion of seedlings in Mabira and Budongo progress from seedling to sapling and pole stages compared to Kibale. Over 98% of the observed juvenile population in Mabira and Budongo were seedlings whereas the proportion of seedlings in Kibale was 77% (Fig. 1). Although a decrease in number of individuals with increasing age or size is expected (Peet and Christensen, 1987), the proportion of juveniles progressing from seedling to pole stage in Mabira (<2%) and Budongo (0%) is probably low to maintain a stable population of this tree species in the long-term. This is because in the event of stochastic mortality, small populations are more likely to become extinct. The reduced survival rate of juveniles in Budongo and Mabira Forests is reflected in the low density of adult trees in the two forests. Using existing population estimates, the density of

**Table 1 – A comparison of (A) tree density and, (B) number of animals photographed feeding on fruits, seeds and seedlings of *B. wilsoniana*, in Mabira, Budongo and Kibale forests**

Species	Mabira	Budongo	Kibale
<b>(A) Tree density (No./ha)</b>			
Adult tree density	0.14	0.15	1.22
Juvenile density	2298	39	85
<b>(B) Photographic count of animals</b>			
Blue duiker ( <i>Cephalophus monticola</i> ) <sup>b</sup>	0	167	2
Bush pig ( <i>Potamochoerus porcus</i> ) <sup>a</sup>	0	7	11
Elephant ( <i>L. africana</i> )	0	0	62
Weyns duiker ( <i>Cephalophus weynsi</i> ) <sup>b</sup>	0	5	1

a Bush pigs are believed to be the major *Balanites* seed predators (Cochrane, 2003).  
b Duikers are mainly seedling predators.

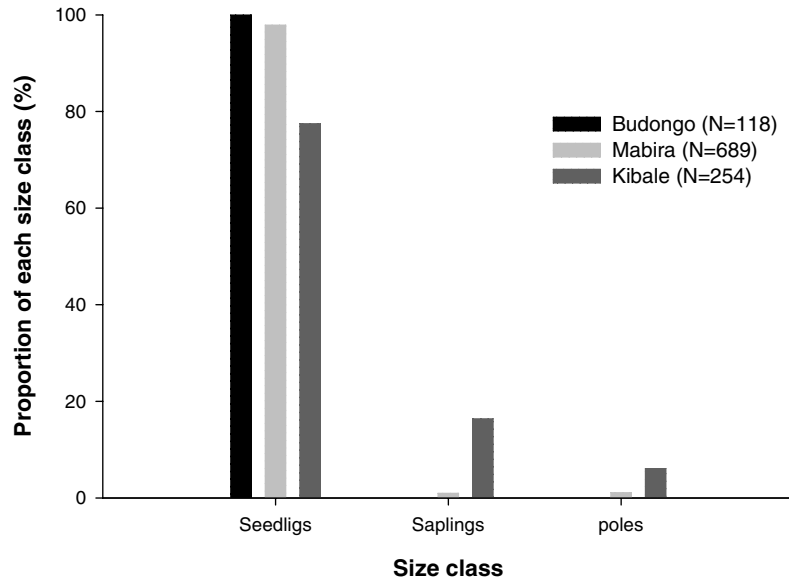


Fig. 1 – Distribution by size class of juveniles of *Balanites* in Budongo, Mabira and Kibale forests.

*Balanites* trees greater than 10 cm DBH in Kibale c. 1.22 tree ha<sup>-1</sup> (total sampled area c. 10 ha) was higher than that of Budongo c. 0.15 tree ha<sup>-1</sup> (total sampled area c. 26 ha) and Mabira c. 0.14 tree ha<sup>-1</sup> (total sampled area c. 125 ha) (Kibale: Chapman et al., 1992; Budongo and Mabira: National Forestry Authority, unpublished data). The extremely low adult tree densities in Budongo and Mabira may not be attributable to the differences in sampling methods used, but probably to the high mortality rate that inhibits seedlings progressing to later life stages. In addition, of the 22 adult trees recorded in Budongo and Mabira only one tree was below 20 cm DBH (Fig. 2). This suggests a lack of recruitment during the past 10–20 years. The density estimates in Kibale (Chapman et al., 1992) did not indicate the size class distribution of trees. However, a number of trees less than 20 cm DBH were seen

during the search for fruiting trees in Kibale (Babweteera, personal observation).

Pairwise Kolmogorov–Smirnov tests between plots within each forest showed no significant differences in juvenile spatial distributions ( $P > 0.05$ ). For brevity, the data were pooled for each forest. The resulting analysis of the pooled data showed that most juveniles were growing beneath adult trees in all three forests (Fig. 3). The juvenile spatial distributions in Mabira and Budongo were not significantly different ( $Z = 0.48$ ,  $P > 0.05$ ). However, the spatial distribution of juveniles in Kibale was significantly different from those of Mabira and Budongo ( $Z = 4.163$ ,  $P < 0.001$ ; and  $Z = 4.484$ ,  $P < 0.001$ , respectively). As illustrated in Fig. 3, over 40% of the juveniles in Kibale were not established beneath adult tree crowns, with some established 80 m from the adult tree. This is an indication of

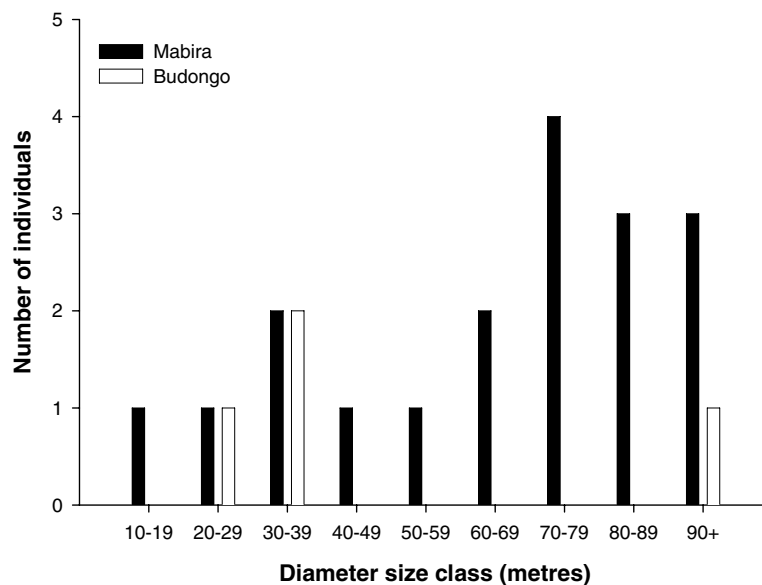


Fig. 2 – Size class distribution of *Balanites* trees in Budongo and Mabira forests.

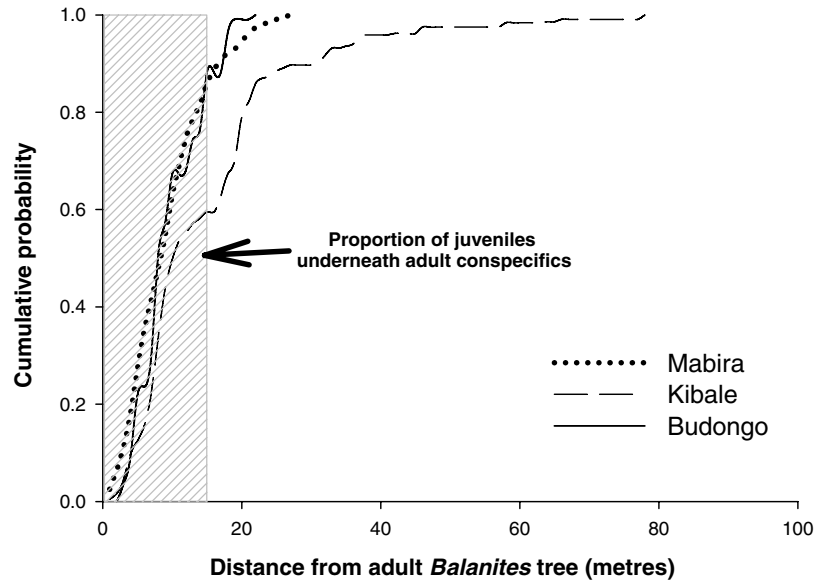


Fig. 3 – Observed spatial distribution of juveniles of *Balanites* around adult conspecifics in Mabira, Budongo and Kibale forests.

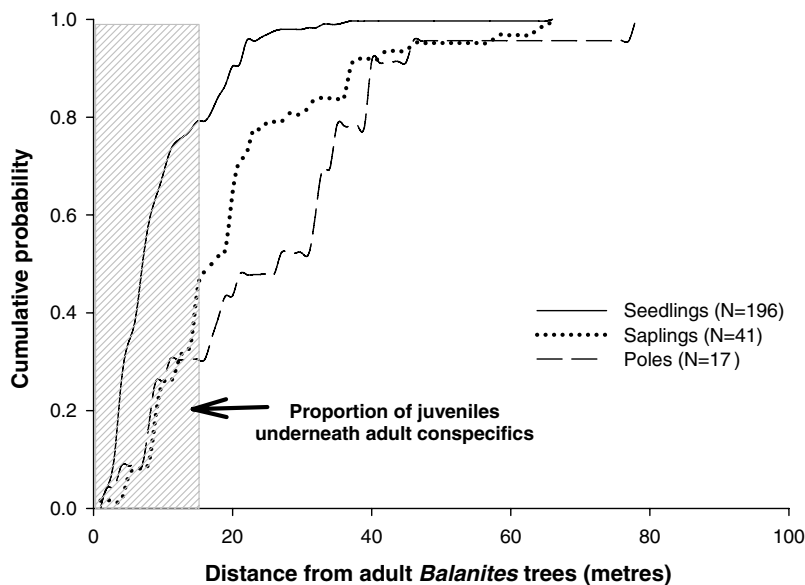


Fig. 4 – Observed juvenile spatial distribution by age of *Balanites* in Kibale forest.

dispersal away from adult trees in Kibale and not Mabira nor Budongo.

Given that it is only in Kibale where the seedlings of *Balanites* are dispersed away from adult trees, we conducted a further analysis on the juvenile distribution in Kibale to determine whether dispersal away from adult trees enhances juvenile survival. This analysis examined the cumulative spatial distribution of *Balanites* seedlings, saplings and poles independently. A Kolmogorov–Smirnov test showed that whereas the spatial distribution of poles and saplings was not significantly different ( $Z = 1.601$ ,  $P > 0.05$ ), the spatial distribution of seedlings was significantly different from that of saplings ( $Z = 3.122$ ,  $P < 0.001$ ) and poles ( $Z = 4.323$ ,  $P < 0.001$ ). Eighty percent of seedlings were established within 15 m of the adult trees, which corresponds to the average canopy ra-

dius of an adult *Balanites*, whereas 45% of saplings and 30% of poles were established beneath the canopies of adult trees (Fig. 4).

#### 4. Discussion

Elephants were confirmed to be the only frugivores feeding and thus dispersing *Balanites*. The large fruits of *Balanites* exclude many small frugivores from feeding on them. Therefore, there is no substitute disperser for *Balanites* in forests where elephants are extinct. Although many seedlings were able to germinate under undispersed environments in forests without elephants, the high mortality rate beneath adult conspecifics constrains the survival of juveniles to later life stages.

Previous experiments on germination of *Balanites* have supported the notion that elephants significantly increase the probability of germination of this species (Chapman et al., 1992; Cochrane, 2003). These studies compared ‘gut passed’ and ‘unpassed’ *Balanites* seeds and deduced that elephant gut treatment enhanced germination by over 50% whereas unpassed seeds had a germination probability of less than 3%. However, the *Balanites* seedlings germinating from seeds in forests where elephants are now extinct provides counter evidence that germination can also be significant without elephant gut treatment. Germination of seedlings in tropical rain forests is influenced by a number of factors including light and moisture regimes, predators, pathogens, forest floor litter and soil disturbance. Our observations suggest that there are other mortality factors which outweigh the importance of the increased germination success attributable to elephant consumption. We recorded a ‘super abundance’ of seedlings in Mabira forest where elephants do not occur, which could be attributed to reduced seed and seedling predation in this forest. Cochrane (2003), noted that bush pigs are the major predators of *Balanites* seeds in Kibale and we have observed ungulates to be regular browsers of seedlings in Budongo. Currently, there is no data on the densities of either bush pigs or other ungulates in these forests. However, using photographic counts of camera trap data in the three forests (Table 1), it is evident that bush pigs (major seed predators) and duikers (seedling browsers) are more common in Budongo and Kibale than in Mabira. Consequently, it is plausible that the presence of bush pigs and duikers in Budongo and Kibale accounts for the low seedling densities observed. Nonetheless, the high density of seedlings observed in Mabira does not appear to persist through to the sapling and pole stages. Likewise, in Budongo the seedlings do not progress to the sapling and pole stages. This could be attributed to the high seedling mortality at high densities beneath the adult conspecifics caused by pathogens and other abiotic factors in Mabira, and possibly a combination of vertebrate predators, pathogens and abiotic factors in Budongo (Wright

et al., 2000; Bell et al., 2006). The constrained progress from seedling to bigger size classes is indeed reflected in the population structure of adult trees where a lack of trees in the smaller diameter classes (<30 cm DBH) is evident. Ideally, most tree species would have a decreasing number of individuals with increasing tree size (reverse J-shape) in order to maintain a stable population. The small population of younger trees in Budongo and Mabira would probably imply a declining population of *Balanites*. Moreover, most trees encountered in the two forests were above 30 cm DBH which might represent a pre-elephant extinction tree population.

Analysing the spatial distribution of juveniles by size class provides an insight into survival probabilities beneath and away from the adult conspecifics. A greater proportion of the population found more than 15 m from adult trees was comprised of saplings and poles in Kibale than was the case for the population found less than 15 m, suggesting that dispersed juvenile survival is greater in this forest. In a study of mortality rates of *Balanites* seedlings planted underneath and away from adult trees, Chapman et al. (1992), found no significant difference in the mortality rates after three months. However, three months is a fairly short observation period to make any explicit conclusions. Since this study examined different size classes of juveniles, some of which could be several years old, it may provide explicit evidence of enhanced survival away from adult trees.

*Balanites* might be one among thousands of tree species and the loss of elephants leading to extinction of this tree species, may not significantly affect the dynamics of a forest ecosystem (Hawthorne and Parren, 2000). However, its study emphasises the need to understand higher-order interactions between loss of large-bodied frugivores and long-term forest dynamics in secondary forest landscapes where the remnant predominantly small-bodied species may not effectively disperse seeds of many large-seeded trees (Tabarelli and Peres, 2002). While some trees can germinate and grow beneath adult conspecifics, others require dispersal to avoid high mortality beneath adult conspecifics or to reach favourable sites

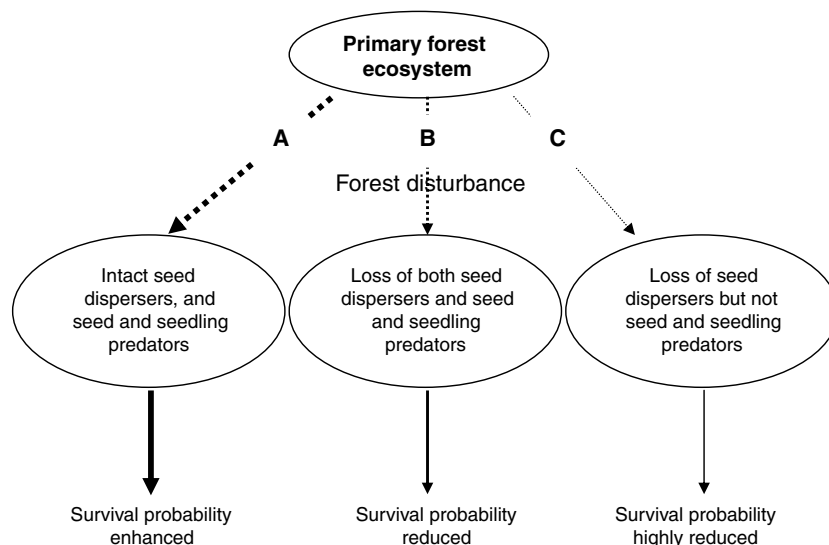


Fig. 5 – Illustration of pathways of tree species survival in the event of loss of vertebrates due to forest disturbances.

such as forest gaps (Melo and Tabarelli, 2003). This study demonstrates that the loss of vertebrates has ramifications for tree species dynamics above and beyond loss of seed dispersers. Particularly, the study highlights the vital role of post dispersal predation on the long term survival of tree species. We postulate that anthropogenic disturbances in a forest landscape that alter the balance between seed dispersers and predators are likely to create shifting survival probabilities of tree species in the long-term (Wright and Duber, 2001; Terborgh et al., 2002). Three possible pathways through which loss of vertebrates in tropical rain forests is bound to affect tree population dynamics are illustrated in Fig. 5.

First, given that dispersal enhances seedling survival, in forests whose seed dispersing community as well as the seed and seedling predation community are intact (Fig. 5 pathway A, analogous to Kibale), the survival probability of tree species in such forests may be enhanced by dispersal to avoid predators and other factors driven by high seed and seedling densities. Consequently, most tree species including those that cannot recruit beneath adult conspecifics due to limited light environments or density driven mortality factors are able to maintain their populations through dispersal. Secondly, in forests where there is a co-occurrence of loss of animal seed dispersers and predators, there is a likelihood for self recruiting tree species to germinate and survive beneath adult conspecifics and thus maintain their populations through self recruiting (Fig. 5 pathway B, analogous to Mabira). Thirdly, in forests whose seed dispersing population is reduced or driven to extinction whereas the seed and seedling predator populations are intact (Fig. 5 pathway C, analogous to Budongo), the tree survival probability in such a forest is highly reduced by predators or other factors attracted by high seed and seedling densities beneath the adult trees. In such forests, tree species dependant on one or a few often rare vertebrate dispersers are likely to experience suppressed recruitment and survival of juveniles to adult stage.

In conclusion, loss of vertebrate seed dispersers from a forest landscape is likely to affect tree recruitment and survival for many species. However, crucially important, is the effect of post dispersal seed and seedling predation (Chiarello, 1999). The heavily disturbed Mabira forest lacks large-bodied frugivores while the population of rodent seed predators is high (Babweteera, 2006). In such frugivore impoverished forest landscapes it is likely that shade tolerant species that invest heavily in defence against herbivores and microbial pathogens (Coley and Barone, 1996) will dominate the landscape. However, the recruitment will increasingly be nearer to adult conspecifics (Wright and Duber, 2001). Light demanding trees that require open environments to establish will experience limited recruitment due to dispersal and establishment limitations. This may in time cause a reduction in tree diversity.

## Acknowledgements

This research was supported by an International Foundation for Science grant. We are grateful to G. Erickson and E. Orijabo who assisted with the field work. Permission to conduct this research was kindly granted by Uganda National Council for

Science and Technology, Uganda Wildlife Authority and National Forestry Authority. We are also grateful to National Forestry Authority who permitted us to use the inventory data for Budongo and Mabira Forest Reserves. Two anonymous reviewers gave useful comments to improve the manuscript.

## REFERENCES

- Alers, M.P.T., Blom, A., Kiyengo, C.S., Masunda, T., Barnes, R.F.W., 1992. Preliminary assessment of the status of the forest elephant in Zaire. *African Journal of Ecology* 30, 279–291.
- Babweteera, F., 2006. Interaction between frugivores and fleshy-fruited trees in primary and secondary tropical forests. D.Phil thesis, Department of Plant Sciences, University of Oxford.
- Bell, T., Freckleton, R.P., Lewis, O.T., 2006. Plant pathogens drive density-dependent seedling mortality in a tropical tree. *Ecology Letters* 9, 569–574.
- Bodmer, R.E., Eisenberg, J.F., Redford, K.H., 1997. Hunting and the likelihood of extinction of amazonian mammals. *Conservation Biology* 11, 460–466.
- Carbone, C., Christie, S., Conforti, K., Coulson, T., Franklin, N., Ginsberg, J.R., Griffiths, M., Holden, J., Kawanishi, K., Kinnaird, M., Laidlaw, R., Lynam, A., Macdonald, D.W., Martyr, D., McDougal, C., Nath, L., O'Brien, T., Seidensticker, J., Smith, D.J.L., Sunquist, M., Tilson, R., Shahrudin, W.N.W., 2001. The use of photographic rates to estimate densities of tigers and other cryptic mammals. *Animal Conservation* 4, 75–79.
- Chapman, L.J., Chapman, C.A., Wrangham, R.W., 1992. *Balanites wilsoniana* – elephant dependent dispersal. *Journal of Tropical Ecology* 8, 275–283.
- Chiarello, A.G., 1999. Effects of fragmentation of the Atlantic forest on mammal communities in south-eastern Brazil. *Biological Conservation* 89, 71–82.
- Cochrane, E.P., 2003. The need to be eaten: *Balanites wilsoniana* with and without elephant seed-dispersal. *Journal of Tropical Ecology* 19, 579–589.
- Coley, P.D., Barone, J.A., 1996. Herbivory and plant defenses in tropical forests. *Annual Review of Ecology and Systematics* 27, 305–335.
- Corlett, R.T., 1996. Characteristics of vertebrate-dispersed fruits in Hong Kong. *Journal of Tropical Ecology* 12, 819–833.
- da Silva, J.M.C., Tabarelli, M., 2000. Tree species impoverishment and the future flora of the Atlantic forest of northeast Brazil. *Nature* 404, 72–74.
- Dinerstein, E., Wemmer, C.M., 1988. Fruits Rhinoceros Eat - Dispersal of *Trewia-Nudiflora* (Euphorbiaceae) in Lowland Nepal. *Ecology* 69, 1768–1774.
- Forget, P.M., 1993. Postdispersal predation and scatterhoarding of *Dipteryx- panamensis* (Papilionaceae) seeds by rodents in Panama. *Oecologia* 94, 255–261.
- Gautier-Hion, A., Duplantier, J.M., Quris, R., Feer, F., Sourd, C., Decoux, J.P., Dubost, G., Emmons, L., Erard, C., Hecketsweiler, P., Mougazi, A., Roussillon, C., Thiollay, J.M., 1985. Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia* 65, 324–337.
- Hamill, D.N., Wright, S.J., 1986. Testing the dispersion of juveniles relative to adults – a new analytic method. *Ecology* 67, 952–957.
- Hamilton, A., 1991. *A Field Guide to Uganda Forest Trees*. Makerere University Printery, Kampala.
- Hawthorne, W.D., Parren, M.P.E., 2000. How important are forest elephants to the survival of woody plant species in Upper Guinean forests? *Journal of Tropical Ecology* 16, 133–150.
- Howard, P.C., 1991. *Nature Conservation in Uganda's Tropical Forest Reserves*. IUCN, Gland, Switzerland.

- Laidlaw, R.K., 2000. Effects of habitat disturbance and protected areas on mammals of peninsular Malaysia. *Conservation Biology* 14, 1639–1648.
- Lierberman, D., Lierberman, M., Martin, C., 1987. Notes on seeds in elephant dung from Bia national park, Ghana. *Biotropica* 19, 365–369.
- Melo, F.P.L., Tabarelli, M., 2003. Seed dispersal and demography of pioneer trees: The case of *Hortia arborea*. *Plant Biology* 5, 359–365.
- Peet, R.K., Christensen, N.L., 1987. Competition and tree death. *Bioscience* 37, 586–595.
- Peres, C.A., 2001. Synergistic effects of subsistence hunting and habitat fragmentation on amazonian forest vertebrates. *Conservation Biology* 15, 1490–1505.
- Pimm, S.L., Jones, H.L., Diamond, J., 1988. On the risk of extinction. *American Naturalist* 132, 757–785.
- Plumptre, A., Cox, D., 2006. Counting primates for conservation: primate surveys in Uganda. *Primates* 47, 65–73.
- Silveira, L., Jacomo, A.T.A., Diniz-Filho, J.A.F., 2003. Camera trap, line transect census and track surveys: a comparative evaluation. *Biological Conservation* 114, 351–355.
- Tabarelli, M., Peres, C.A., 2002. Abiotic and vertebrate seed dispersal in the Brazilian Atlantic forest: implications for forest regeneration. *Biological Conservation* 106, 165–176.
- Temple, S.A., 1977. Plant-animal mutualism – coevolution with dodo leads to near extinction of plant. *Science* 197, 885–886.
- Terborgh, J., Pitman, N., Silman, M., Schlichter, H., Nunez, P.V., 2002. Maintenance of tree diversity in tropical forests. In: Levey, D.J., Silva, W.R., Galetti, M. (Eds.), *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*. CABI, Wallingford, Oxfordshire, pp. 1–17.
- Westman, W.E., Strong, L.L., Wilco, B.A., 1989. Tropical deforestation and species endangerment: the role of remote sensing. *Landscape Ecology* 3, 97–109.
- Wright, S.J., Duber, H.C., 2001. Poachers and forest fragmentation alter seed dispersal, seed survival, and seedling recruitment in the palm *Attalea butyraceae*, with implications for tropical tree diversity. *Biotropica* 33, 583–595.
- Wright, S.J., Zeballos, H., Dominguez, I., Gallardo, M.M., Moreno, M.C., Ibanez, R., 2000. Poachers alter mammal abundance, seed dispersal, and seed predation in a neotropical forest. *Conservation Biology* 14, 227–239.