Journal of Tropical Ecology (1992) 8:275–283.

Balanites wilsoniana: elephant dependent dispersal?

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ABSTRACT. This study demonstrates that forest elephants (*Loxodonta africana*) play a key role as seed dispersal agents for the upper canopy forest tree, *Balanites wilsoniana*. Seed that passed through elephants had a much greater probability of germinating (50.7%) than seeds from fruits collected directly from the tree (3%). Of 515 seeds that were collected from under parent trees, 89.1% were rotten at the time of collection, 2.6% had been eaten by forest pigs, 2.8% had been killed by squirrels, and 0.7% had been killed by insect damage. The remaining 4.8% of the seeds were still alive. In 150 hours of focal observations on *B. wilsoniana* trees, two fruits were seen to be destroyed by squirrels, no fruits were seen to be consumed by potential dispersers, and no evidence of scatter hoarding was found. Experimental seedling stations placed out under parent trees and away from parent trees indicated no significant effect of dispersal on seedling survival. Although elephants are not essential for the successful germination of *B. wilsoniana* seeds, they do greatly increase probability of germination and play a vital role in their dispersal, suggesting that this is a highly interdependent plant-animal seed dispersal system.

KEY WORDS: *Balanites wilsoniana*, coevolution, elephants, *Loxodonta*, seed dispersal, Uganda.

INTRODUCTION

Many early studies of seed dispersal proposed tight coevolutionary relationships between plants and their seed dispersers (Howe & Estabrook 1977, McKey 1975, Snow 1965, 1971). However, these early hypotheses have received little support from many recent investigations (Herrera 1984, 1986, Howe 1984a, Howe & Smallwood 1982). This has largely been attributed to factors that limit the mutualistic coevolution between plants and their animal dispersers. These factors include: slow evolutionary rates of plants relative to changes in their dispersers, extensive plant gene flow, and weak selective pressures on dispersers (Herrera 1985, 1986, Howe 1984a). There are, however, some species that do seem to be dependent on only one or perhaps a few species of animal disperser (e.g. *Hymenaea courbaril* and agoutis *(Dasyprocta punctata)*, Hallwachs 1986; tambalacoque trees *(Calvaria major)* and dodos *(Raphus cucullatus)*, Temple 1977; the nitre bush

(*Nitraria billardieri* and emus (*Dromaius novaehollandiae*), Noble 1975; tomatoes (*Lycopersicon esculentum*) and Galapagos tortoises (*Testudo elephantopus*), Rick & Bowman 1961; *Trewia nudiflora* and rhinoceros (*Rhinoceros unicornus*), Dinerstein & Wemmer 1988); *Cucumis humifructues* and aardvarks (*Orycteropus afer*), Patterson 1975). Although present day dependency on a single disperser does not necessarily require a tight coevolutionary relationship between the plant and its seed disperser species (Howe 1985), studies of these highly interdependent systems are of great importance in understanding factors which both limit and promote dependency between plants and their animal dispersers.

In a description of the seeds in elephant (*Loxodonta africana* Blumenbach) dung from Bia National Park, Ghana, Lieberman *et al.* (1987) found *Balanites wilsoniana* (Dawe & Sprague) seeds in 52% of the dung samples they examined (N = 31). Further, they were able to germinate seeds collected from the dung (N = 47), but failed to germinate any fresh seeds collected from beneath the tree (N = 24). They suggested that elephants may play a vital role as a seed dispersal agent for *B. wilsoniana*. Since, the seeds of *B. wilsoniana* are large (8.8 cm long, 4.7 cm wide), there are probably few animals capable of passing and dispersing the seeds. Based on such evidence, we concluded that *Balanites wilsoniana* was a good candidate for a plant currently dependent on a few animal dispersers.

The objective of this study was to provide a quantitative description of the dispersal and fate of *Balanites wilsoniana* seeds. Following Lieberman *et al.* (1987) (see also Alexandre 1978, and Short 1981), we compare the viability of seeds that have passed through elephants with the viability of seeds collected from beneath parent trees. In addition, we assess seed predator damage to fallen fruits and the percentage of fallen seeds that perish under parent trees. Focal tree observation is used to document the species of frugivores that feed in *B. wilsoniana* trees. Seedling survival is assessed both under the parent tree and away from the parent tree. In addition, we document the abundance and distribution of *B. wilsoniana* trees and seedlings using a series of belt plots in each of two study areas. Finally, since elephant populations are declining in many areas of Africa (Douglas-Hamilton *et al.* 1980), we discuss the implications of highly interdependent disperser-plant relationships for the development of effective conservation strategies.

METHODS

Study Site

The study was conducted between March and December 1990 in the Kibale Forest Reserve, located in western Uganda (0° 13′-0° 41′ N and 30° 19′-30° 32′ E) near the base of the Ruwenzori Mountains. The 560 km^2 reserve is a moist, evergreen forest transitional between lowland rain forest and montane forest (Skorupa 1988, Struhsaker 1975, Wing & Buss 1970). About 60% of the Kibale Forest is characterized by tall forest with the canopy generally 25-30 m high, with some trees exceeding 50 m (Butynski 1990). The remainder of the reserve is comprised of a mosaic of swamp, grassland, plantations of exotic softwood, thicket, and colonizing forest (Butynski 1990, Wing & Buss 1970). We studied the dispersal of *B. wilsoniana* seeds in two study areas in the reserve that were 12 km apart, Kanyawara and Ngogo.

A description of Balanites wilsoniana *(Balanitaceae)*

Balanites wilsoniana is an upper canopy tree that can reach a height of 40 m. It produces fruits that are green-brown in colour and average 9.1 cm (SD = 0.67, N = 18) in length, 5.9 cm in width (SD = 0.44, N = 18), and weigh 171 g (SD = 9.2, N = 18). The fruits contain a single large seed averaging 8.8 cm in length (SD = 0.70, N = 18), 4.7 cm in width (SD = 0.56, N = 18), and 159 g in weight (SD = 13.4, N = 18). It is a relatively rare tree in both study areas, found at a density of 0.77 trees ha^{-1} at Kanyawara and 1.67 tree ha^{-1} at Ngogo (density established using a randomly stratified belt plot transect system that enumerated 4733 trees > 10 cm DBH).

Elephant populations in the reserve

The African elephant (*Loxodonta africana*) populations in Uganda have been declining rapidly as a result of habitat destruction, increased rates of human interaction, and hunting. Brooks & Buss (1962) estimated that elephants occupied approximately 70% of Uganda in 1929. Thirty years later, this value had declined to 17%. Between 1926 and 1958 over 40,000 elephants were shot by game guards, control workers, and trophy hunters (Brooks & Buss 1962, Wing & Buss 1970). Elephants visit all parts of the reserve. From tracks and sightings it has been estimated that at least 300 elephants inhabit Kibale. In recent years and during the period of study, they spent more time at Ngogo than at Kanyawara.

Elephant dung and germination trials

Each dung pile encountered was examined *in situ* for seeds. Seeds were stored in individually labelled bags and returned to the Kanyawara camp for identification and the determination of viability. *B. wilsoniana* seeds were separated from those of other species and planted (approximately three quarters buried) in individually labelled cups with soil. To compare the probability of germination of elephant dispersed seeds to non-dispersed seeds, 457 freshly fallen fruits were collected from the ground, stripped of pulp, and the seeds were planted as just described. Because of the height of the tree crowns, such fruits would have been the only ones available for elephant consumption. Seeds were watered daily and examined for evidence of germination. Germination trials were conducted in a walled building with subdued sunlight coming through clear plastic. Germination success was recorded for an average of 117 days (range 76-161 days) by which time germination had ceased. At the end of the study, all of the seeds that had not germinated were opened. No viable embryos were discovered.

Tree follow

Focal tree observations on three *B. wilsoniana* trees were used to document the species of frugivores that eat *B. wilsoniana* fruits and to quantify the relative importance of each animal species to the fruit removal. The species of birds and mammals present in the tree, the number of individuals of each species that were feeding, and their feeding rate were scored every 15 minutes. Since elephants are thought by local people to be dangerous, focal tree observations were generally not conducted while elephants were in the area. Thus, observations provide information on other animals attending *B. wilsoniana* trees. A total of 150 h of observations was conducted on three trees, between 0700 h and 1800 h. No nocturnal observations were attempted, but *B. wilsoniana* seeds were not found in civet middens (N = 12), and no bat wadges of *B. wilsoniana* pulp were found.

Fruits under the tree

The survival of non-dispersed seeds was evaluated by placing freshly fallen fruit on the ground at the base of four trees at Kanyawara in concentric circles at 5 m intervals until 10 m past the canopy of the parent tree (see Howe *et al.* 1985). One fruit was placed at each of four radii, with the degree of the radius chosen randomly. The position of each fruit was marked with a staked flag and monitored approximately twice a week. Seedlings grown in the laboratory were planted under the parent tree using the same method.

To determine the success of seedling establishment away from the parent tree, seedlings were planted in the forest of Kanyawara. Forty experimental stations were established 2 m off three existing trails at 5 m intervals, and both the survival and growth of the seedlings were monitored twice a week. No adult tree was within 100 m of any of these experimental stations.

Seeds from fallen fruits were collected from under seven different trees in April, June, September, and December 1990 (total N = 515 seeds). Each seed was opened to determine if the embryo had perished, and the damage from different types of seed predators was assessed. Seed damage from three types of seed predators was evident. Squirrels, including probably *Protoxerus stangeri*, *Heliosciurus rufobrachium,* and *Funisciurus* sp., opened seeds by gnawing around the middle (shortest cicrumference). Bush pigs (*Potamochoerus porcus*) cracked seeds lengthwise along sutures, and an insect bored holes through the outer seed coat. Under each of these trees a search was made for *B. wilsoniana* seedlings.

Estimation of tree and seedling density

The abundance and distribution of *B. wilsoniana* trees were determined along a series of belt plots in the study area. Fifty belt plots, 200 m long, have been built along the existing trail systems at the two sites: 26 transects at Kanyawara and 24 transects at Ngogo. In the search for seedlings a 4 m strip width was used, providing a sampling area of approximately 2 ha at each study site. For each seedling, we recorded its size, whether or not it was under the parent tree, and noted evidence of leaf damage. For trees greater than 10 cm DBH, a 10 m strip width was used, providing a total sampling area of approximately 5 ha at each study site. Thirty seedlings found under adult *B. wilsoniana* trees were uprooted to verify that they did not represent root sprouts.

RESULTS

A total of 184 elephant dung piles was examined over the duration of the study. Twenty-five (13.6%) of the piles contained *B. wilsoniana* seeds, with an average of 10.7 seeds per dung pile (range = 1-28) producing a total of 267 seeds. There were marked differences between Ngogo and Kanyawara in the frequency of occurrence of *B. wilsoniana* seeds in the dung samples. Twenty-four of the 25 dung piles containing *B. wilsoniana* seeds were found at Ngogo. At Kanyawara there was only one seed found in 74 dung piles examined (0.01 seeds per dropping), while at Ngogo there were 266 seeds in 110 dung piles (2.4 seeds per dropping).

In the Kibale Forest there are very few animals, other than elephants, large enough to swallow *B. wilsoniana* seeds. Chimpanzees (*Pan troglodyes*) may represent the one exception; however, *B. wilsoniana* seeds were not found in 1558 chimpanzee dung samples examined (Chapman & Wrangham unpublished data). In thousands of hours of observations on chimpanzees, they have never been seen to eat *B. wilsoniana* fruits, even though chimpanzees are known to commonly eat fruit from tree species that occur at much lower densities (Chapman & Wrangham unpublished data). In addition, there was no evidence of baboons or other monkeys eating this tree's fruits. No evidence was found of animals scatter-hoarding the seeds.

The germination success of 232 seeds collected from elephant dung was monitored for an average of 117 days after planting. Over this time 118 (50.9%) germinated. It is difficult to state accurately the length of time it takes for a seed to germinate, for it was often not possible to determine how long the seed had remained in the dung before we found it. However, based on the speed with which the dung disintegrates, we thought that it was rarely more than 15 days before we encountered the dung. The average time between seed planting in the laboratory and germination was 59 days (N = 118, range = 2-92).

Similarly, 457 seeds collected directly from parent plants were planted and followed for an average of 117 days (range 76-161 days). Of these seeds, only three germinated by the end of the study (mean time to germinate = 83 days, range = 60-121). Passage through the elephant significantly increased the probability of germinating from 0.7% for those seeds not passed by elephants to 50.9% for those seeds passed by elephants ($X^2 = 123.9$, $P < 0.0001$).

A total of 515 seeds were collected from under seven trees. Of these, 89.1% were rotten at the time of collection, 2.6% had been eaten by bush pigs (*Potamochoerus porcus*), 2.8% had been killed by squirrels, and 0.7% had been killed by insect damage. The remaining 4.8% of the seeds were still alive.

At each of four trees, 20 seeds were placed at marked stations and monitored for an average of 122 days (range = 120-124). Only 5% had disappeared by the end of the study (average date of disappearance = 92 days, range = 60-112 days), and no seeds had germinated.

Twenty seedlings, that had reached an average height of 14.4 cm, were placed under each of three adult *B. wilsoniana* trees. Of these 60 seedlings, only two died in the 100 days they were monitored (3%). Of the 40 seedlings planted away from adult *B. wilsoniana* trees, 10% died in the 100 days they were monitored. The mortality rate of seedlings under parent trees was not significantly different from those planted away from *B. wilsoniana* trees ($X^2 = 1.89$, $P>0.10$).

In 150 hours of observations at *B. wilsoniana* trees, two seeds were seen to be eaten by squirrels, and none were seen to be dispersed. In addition, when the observer approached the tree, prior to the collection of systematic data for that day, squirrels were seen on three occasions. On no occasion were squirrels seen to take *B. wilsoniana* fruits away from the tree.

The density of *B. wilsoniana* trees (>10 cm DBH) is 1.67 trees ha^{-1} at Ngogo, and 0.77 trees ha^{-1} at Kanyawara. At Kanyawara, 133 seedlings were found in the 2 ha that were searched. All of these seedlings were under large conspecifics. At Ngogo, 43 seedlings were found, and 70% were located under conspecific trees, while 30% had been dispersed away from large conspecific trees. There was no significant difference in the percentage of seedlings that had suffered notable leaf damage between those seedlings found under large conspecific trees and those found away from large conspecifics (seedlings under: 60% damaged, seedlings away: 54% damaged, $X^2 = 0.20$, df = 1, $P>0.50$).

DISCUSSION

There are several lines of evidence to suggest that elephants significantly increase the probability of germination of *Balanites wilsoniana* seeds, and that they are vital to the dispersal of their seeds. First, since *B. wilsoniana* seeds are large, there are few animals other than elephants capable of ingesting the seeds. This was reflected in the very infrequent attendance of frugivores observed in the focal tree observations. Although scatter hoarding by squirrels cannot be ruled out as a possible dispersal mechanism, no evidence of scatter hoarding was found. Secondly, although passage through an elephant's gut is not essential for germination, it greatly increases the germination potential of the seeds. Finally, differences in the distribution of seedlings between the two study sites supports elephant-dependent dispersal. At Kanyawara, where elephants were rare, seedlings were only found under conspecific adult trees. At Ngogo, where elephants were common, a good proportion of *B. wilsoniana* seedlings were found some distance from large conspecific trees. Whether elephants were the only dispersers for *B. wilsoniana* in the past is difficult to ascertain (Howe 1985, Janzen & Martin 1982). However, elephants appear to be significant in the removal of seeds away from parent plants at the present time.

There may be a number of features about *B. wilsoniana* fruits that discourage consumption by other frugivores. Hardman (1969) determined that *Balanites* fruits contain diosgenin; a plant steroid that can be used by manufacturers as a precursor to cortisone or sex hormones used in birth control (Janzen 1978). It is used locally as a fish poison and in shampoos to remove hair lice (Abbiw 1990, Hardman 1969), suggesting other toxic properties. Secondly, the most apparent feature that may exclude many frugivores is the extremely large size of the seed. It contains a large store of endosperm which may allow the seedling to grow to a larger size than small seeds in the deep shade of the understorey before becoming energetically self-sufficient. Correspondingly, it is this energy store that attracts seed predators and hence necessitates the thick seed coat and possibly the need for passage through the disperser's gut to weaken the seed coat. This combination of characteristics is less likely to occur in small or medium sized seeds.

A very small portion of the fallen *B. wilsoniana* fruit appears to be capable of germinating and surviving directly under an adult tree. Whether this occurs at a sufficiently high rate to allow the long-term maintenance of the population is not known. However, for many tropical tree species, the survival of fallen fruit does not appear to be sufficient to maintain the population. For *Virola surinamensis*, Howe *et al.* (1985) documented that 99.96% of the fruits that drop under the parent are killed within 12 weeks by weevils and rodents. Connell *et al.* (1984) showed similar density-dependent mortality among seedlings of many Australian trees. It seems probable that a decline in the elephant population in the Kibale forest would lead to a decline in the number of *B. wilsoniana* trees. A similar example is described by Dinerstein & Wemmer (1988). They demonstrated the significance of rhinoceros (*Rhinoceros unicornis*) in the dissemination and maintenance of the floodplain plant *Trewia nudiflora*. They documented heavy seed loads of *Trewia nudiflora* in rhinoceros (*Rhinoceros unicornis*) dung, low germination probabilities of uningested fruit, and rapid growth of seedlings in grassland latrines. Such studies illustrate that systems of interactions in tropical forests may be complex. For tree species which depend on a single species of animal disperser, the removal of the animal can have profound consequences on the maintenance of the tree species population. Thus, for the maintenance and preservation of tropical forests as a whole, it seems critical to maintain animals that facilitate seed dispersal (Howe 1984b, Pannell 1989).

ACKNOWLEDGEMENTS

The authors would like to thank all of the Ugandan Field Assistants for helping in the field work. Permission was given to conduct this research from the Office of the President, Uganda, the National Research Council, and the Ugandan Forest Department. We express our gratitude to the Department of Zoology, Makerere University, to the present and past Directors of the Makerere University Biological Field Station (T. Struhsaker, A. Johns, & G.I. Basuta), and the New York Zoological Society for providing logistical support, without which this research would not have been possible. Funding for this research was provided by grants from NSERC (Canada, LJC), NSF (RWW & M. Hauser), National Geographic (CAC, RWW, Marc Hauser), and from the MacArthur Foundation (RWW). We would like to thank D. Clark, K. Fischer, D. Levey, D. Lieberman, M. Lieberman, F.E. McKenzie, and T.T. Struhsaker for helpful comments on this project.

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Accepted 11 December 1991

Book review

RAMAKRISHNAN, P. S. (ed.). 1991. *Ecology of biological invasions in the tropics*. National Institute of Ecology; International Scientific Publications, New Delhi. viii + 195 pages. Price: US$40.00 (hardback). Available from: International Scientific Publications, 50-B, Pocket C, Siddhartha Extension, New Delhi – 110 019, India.

Thirty-three years have passed since the appearance of Charles Elton's classic, *The ecology of invasions by animals and plants* (1958). Throughout much of the intervening period this was virtually the only integrated treatment of the subject, and is remarkable in that even now it is still relevant and useful. Although new investigations and insights were rather few during the first 20 of these years, the situation changed in the 1980s as a result of increased awareness of the importance of the topic and of the economic, social and environmental problems often created by biological invasions. This awareness was responsible for a SCOPE programme on the Ecology of Biological Invasions, which has resulted in a number of books and papers reporting new work in this field. The present volume contains the proceedings of a conference on biological invasions in the tropics, co-sponsored by SCOPE and the Govind Ballabh Pant Institute, India, which was held in Nainital in September 1989.

Other publications on this theme have concentrated very largely on the temperate regions, and this is the first to deal with the special problems created by biological invasions in tropical environments. It contains 12 papers by distinguished authors, concluding with a chapter of Conclusions and Recommendations by the Editor, who also contributes an introductory overview. The volume reflects current attitudes in seeking not only to present the results of scientific research but also to relate them to the economic and social contexts in which the problems have arisen.

In the first paper, on biological invasions in nature reserves, M. B. Usher shows that all reserves contain some invasive alien species and challenges the view that pristine tropical environments are largely free from invasions. In this respect he is not wholly supported, at least as far as woody species and primary tropical rain forests are concerned, by T. C. Whitmore, writing about invasive woody plants in perhumid tropical forests. As indicated also in the Introduction by Ramakrishnan, the habitats which are most susceptible to invasions are very often those which are man-made or disturbed. Successful invaders are shown to have a 'weedy' biology, and this aspect is further explored in E. H. Rapoport's comparison of tropical and temperate weeds. R. G. Saxena reviews the whole range of plant invasions in the Indian subcontinent, while J. K. Egunjobi deals with some of the effects of exotic plant species on soil factors in Africa.

The hypothesis that tropical environments are less readily invaded than the 'simpler' temperate ecosystems is rejected by G. Fryer, at least in the context of invasions by introduced fishes in African waters. C. H. Fernando and J. Holcik also write on the impacts of fish introductions into tropical freshwaters, while transfers of freshwater fishes into India are covered by A. Sreenivasan. These three papers furnish useful comparisons between aquatic systems, which are further considered in a paper by D. S. Mitchell and B. Gopal on the invasion of tropical freshwaters by