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Frugivory and the fate of dispersed and non-dispersed seeds of six African tree species

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ABSTRACT. The relationship between seedling recruitment (under and away from parent trees) and the behaviour of seed dispersers and predators, was explored in a three-year study in Kibale National Park, Uganda. On the basis of 1261 hours of observation, the foraging activity of the diurnal frugivores which fed on fruit from six tree species was quantified. The fate of dispersed and non-dispersed seeds and seedlings was examined experimentally. The findings suggest that a trade-off exists between factors that promote seedling growth in areas with high seedling density and factors that promote dispersal by frugivores. For example, dispersal of *Mimusops bagshawei* increases both seed and seedling survival; seeds placed away from adult conspecifics had a 8% lower probability of disappearing than seeds placed under adults and seedlings away from adults had a 30% greater probability of surviving than seedlings grown under adults. In contrast, for *Uvariopsis congensis,* dispersed seeds had a 56% greater probability of disappearing than seeds directly under a parent tree, while the survival of dispersed and non-dispersed seedlings was similar. Non-dispersed seed and seedling disappearance were correlated with the percentage of the fruit crop removed from focal trees, suggesting that the ability to survive under an adult maybe related to other aspects of the tree's life history.

KEY WORDS: Africa, Kibale National Park, life history, recruitment, seed dispersal, tropical forests, Uganda

INTRODUCTION

Several lines of evidence suggest that the recruitment ability of tropical fruiting trees varies as a function of the distance from the parent tree, that the nature of this function is highly variable between species, and that selection can act on this variation. Some studies document high levels of mortality and low recruitment under conspecific adults. For example, Howe *et al.* (1985) documented that 99.96% of the seeds from fruit that dropped under *Virola surinamensis* trees died within 12 weeks. Similarly, over a 28-week period, Schupp (1988) documented approximately 93% mortality of *Faramea occidentalis* seeds under the parent crown, but only 76% mortality for seeds 5 m away from the parent tree. In contrast, other studies have revealed relatively small differences in the probability of survival between seeds under parent trees and those dispersed away. For example, DeSteven & Putz (1984) found that seeds of *Dipteryx panamensis* placed 50 m from the parent tree did not have a greater chance of survival than those beneath the parent tree. Similarly, Terborgh *et al.* (1993) found that the distance from the parent tree did not affect the level of seed predation for four of five species examined. Certainly the monospecific dominance in some tropical forests suggests that seedlings of these dominant species can build their way to the canopy near or under conspecific adults (Hart 1990, Hart *et al.* 1989).

There are a number of selective forces that may influence a seed's ability to recruit under or near a parent tree. Studies by Howe & Vande Kerckhove (1980, 1981) and Howe & Richter (1982) on seed dispersal and seedling survival of *Virola surinamensis* have provided one framework for understanding the selective basis of this variation. These researchers found that birds favoured *V. surinamensis* plants with small seeds and avoided those with large seeds (Howe 1993, Howe & Richter 1982; Howe & Vande Kerchove 1980, 1981). However, Howe & Richter (1982) demonstrated that large seeds have a growth advantage over small seeds. These authors suggest that selection may alternately favour small seed size, with an increased probability of dispersal when frugivores are common, and large seed size with an enhanced seedling vigor when frugivores are rare and the probability of seeds being dispersed is reduced. They suggest that a trade-off exists between (1) growth in areas with high seed density, high levels of pathogen attack, and increased seed and seedling predation, and (2) small seed size that promotes dispersal by frugivores (Howe 1989, Howe & Richter 1982). Studies on intraspecific variation in *V. surinamensis* should have application to interspecific variation in the probability of removal and ability to recruit under or near parent trees. We predict that tree species with predictably low rates of removal should have seeds that are more successful at recruitment under or near conspecifics than tree species with high frugivore attendance.

Other selective forces may influence the ability to recruit under or near parent trees on a broader spatial scale (Schupp 1992). One such factor may be the spatial patterning of resources suitable for survival, germination, establishment and growth (e.g., soil type and moisture). Recent studies on spatial patterning of resources have shown that if resources are patchily distributed, the predictability of finding resources equivalent to the ones at the starting location decreases with distance from the starting site (Bell 1992, Grace 1991, Lechowicz & Bell 1991). If resources are randomly distributed there is no relationship between predictability and distance (Bell 1992, Grace 1991, Lechowicz & Bell 1991). These studies may help us understand how the distance from a parent influences seedling establishment. If resources are patchily distributed, the probability of finding a suitable site for establishment, growth, and so forth, will decrease with increasing distance from the parent. Thus, a plant should have a strategy permitting recruitment under or near the parent. In contrast, if resources important to the successful recruitment of a tree are randomly distributed, there should be no relationship between predictability and distance and the plant should have a strategy always favouring dispersal. For example, consider a landscape with undulating hills and swampy valley bottoms. For a tree species adapted to living in the moist conditions of the valley bottoms, the probability of finding a moist site suitable for establishment and growth, will decrease with increasing distance from the parent tree. This will occur simply because the likelihood of being dispersed out of the valley bottom will increase with distance. In contrast, for a plant species that relies on tree fall gaps, which are probably more randomly distributed than moist valley bottoms, there should be no relationship between predictability and the distance dispersed.

Of special interest are predictors of fitness as a function of distance. If we combine our understanding of the relationship between resources and distance with possible density-dependent mortality near the parent tree (Augspurger 1984, Connell 1971, Connell *et al.* 1984, Hubbell 1979, Hubbell *et al.* 1990, Janzen 1970), it is likely that fitness will initially increase with distance for both species capable of recruiting under or near the parent and for those that cannot. Subsequently, however, as a result of the spatial patterning of resources, fitness will decrease with distance for species dependent on patchy resources, and fitness will plateau for species dependent on randomly-distributed resources. Theoretical models of dispersal have demonstrated that at least some dispersal is advantageous when colonization of empty sites enhances reproductive potential (Comins *et al.*, 1980, Hamilton & May 1977, Stamps & Lucas 1990). If it is difficult to select for traits associated with high dispersal potential, while simultaneously selecting for traits permitting recruiting under the parent then, selection may produce a dichotomy in which some species always disperse away from the parent and other species that can both disperse away from the parent and recruit under or near adults.

The relationship between the ability of species to survive under parent trees (the most extreme expression of short distance dispersal) and the behaviour of frugivores and seed predators is explored in this study. We present the results of a three-year study of fruit removal, seed predation, seedling establishment, and seedling survival for six species of trees in Kibale National Park, Uganda. On the basis of 1261 hours of observation, we determined which diurnal frugivores processed fruit from the six tree species and quantified the proportion of the each tree's fruit crop that was removed by frugivores. The fate of dispersed and non-dispersed seeds and seedlings was examined experimentally, focusing on interspecific variation in the probability of seed disappearance and seedling mortality. We examine whether the probability of seed removal is negatively related to seed and seedling survival under parent trees.

METHODS

Study site and focal trees

The Kibale National Park (766 km^2), located in western Uganda (0° 13′–0° 41′ N and 30° 19′–30° 32′ E) near the base of the Ruwenzori Mountains, is a moist, evergreen forest (Skorupa 1988, Struhsaker 1975). The study site, known as Kanyawara, is situated at an elevation of 1500 m. Mean annual rainfall has averaged 1726 mm (1987–1994; annual range = 1570 –1859 mm, annual mean daily maximum temperature 1987 to 1991 = 23.9 ± 0.6°C). The rainfall tends to be well dispersed, falling on an average of 166 days each year; however, there are distinct biannual wet and dry seasons.

Long-term observations of fruit removal, and the fate of dispersed and non-dispersed seeds and seedlings were conducted for a set of six tree species (12 individual trees). The choice of species was made to provide variation in the types of fruit considered, and to permit sequential focal tree observations. *Mimusops bagshawei* is a canopy level to emergent tree with a drupe that averages 1.7 cm in length (S.D. = 1.7, n = 25 fruits from 6 trees). The seeds are oval, with the longest axis averaging 1.1 cm (S.D. = 1.8, n = 25). *Parinari excelsa*, a major hard wood timber tree in the region, has a green-grey 3.2 cm long drupe (S.D. = 4.8, n = 20 fruits from 6 trees) that contains a single large seed 2.6 cm long (S.D. = 3.5, n = 20). *Balanites wilsoniana* is an upper canopy tree that can reach a height of 40 m. It produces a green-brown drupe that averages 9.1 cm (S.D. = 0.67, n = 18 from 6 trees) in length and contains a single large seed averaging 8.8 cm in length (S.D. = 0.70, n = 18). *Uvariopsis congensis* is a common understorey tree that may reach up to 20 m in height. It has a simple fruit that averages 3 cm in length (range 1.5 to 5.0 mm, S.D. = 4.2, n = 30 from 6 trees) and contains between 2 and 7 seeds (mean = 4.5, SD. = 1.36, n = 30). The seeds average 1.3 cm along their longest axis (S.D. = 1.2, n = 30). *Pseudospondias microcarpa* produces a purple drupe, 1.9 cm in length (S.D. = 0.17, n = 30 from 6 trees) with a single spherical seed that averages 1.6 mm in length (S.D. = 1.1, n = 30). *Monodora myristica* is a canopy level tree that produces a large green spherical fruit (16 cm in diameter) which contains many seeds averaging 1.8 cm in length (S.D. = 1.8, n = 30 from 6 trees). Plant taxonomic nomenclature follows Hamilton (1991).

Fruit removal

To quantify fruit removal by diurnal frugivores, 12 trees of the 6 focal species were observed for a total of 1261 h over 237 d (mean number of hours of observation per tree = 101 h, range = 41–226 h, Table 1). Dense foliage precluded detailed quantification of the proportion of the fruit processed in different ways. However, it was possible to categorize frugivores into three groups, species that: (1) swallow fruit and defecate seeds intact, occasionally carry seeds out of the tree that are subsequently dropped, and drop fruit under the canopy, (2) species that kill all seeds handled, but also promote fruit fall by moving through the tree or sampling fruit, and (3) species that only drop intact seeds after processing the fruit at the tree (Table 1).

The data collected on fruit removal involved intermittent observations at specific focal trees over the fruiting cycle from the initiation of fruit ripening to the point when frugivores ceased visiting. The number of individuals of each frugivore species in the tree, the rate they processed fruit, and the number of feeding animals were recorded every 15 minutes. The sum of these values over

Table 1. The sampling effort, crop size of fruit, and proportion of fruit of twelve trees (six species) processed by different frugivores determined by focal tree observations in Kibale National Park, Uganda. Removal is considered as those fruit that were ingested, or processed and dropped away from the tree; it does not include those dropped below the tree or seeds killed by animals such as grey parrots. The column 'Frugivore Present' is the percentage of the days when the frugivore known to eat the fruit was sighted or heard in the vicinity of the focal tree.

							Percent Processed by Each Frugivore									
Species	Tree	Hours	Days	% of Fruit Removed	Crop Size	Frugivore Present	*Pan troglodytes*[a]	*Psittacus erthacus*[b]	*Cercopithecus ascanius*[a]	*C. mitis*[a]	*Cerocebus albigena*[a]	*Tauraco schutti*[c]	*Bycanistes subcylindricus*[a]	Squirrel[b]	*T. schuetti*[c]	Other
Pseudospondias microcarpa	1	66	16	64.7	36276	100	47.2	35.0	9.3	0	0.5	6.0	0	0	2.0	0.1
(Anacardiaceae)	2	79	18	—	—	100	—	—	—	0	—	—	—	—	—	—
	3	185	36	40.3	13133	100	78.5	0	5.7	0	0	12.4	0.8	1.2	1.4	0
Species Average		110	23	52.5	24705	100	62.9	17.5	7.5	0	0.3	9.2	0.4	0.6	17.0	0.05
Uvariopsis congensis	1	266	45	9.0	1397	89	0	0	59.5	11.9	28.6	0	0	0	0	0
(Annonaceae)	2	41	9	—	—	100	0	0	0	100.0	0	0	0	0	0	0
	3	85	16	0.0	452	100	0	0	0	0	0	0	0	0	0	0
Species Average		131	23	4.5	925	96	0	0	13.8	37.3	9.5	0	0	0	0	0
Monodora myristica	1	139	23	0.0	6	75	0	0	0	0	0	0	0	0	0	0
(Annonaceae)																
Balanites wilsoniana	1	42	10	0.1	2002	—	0	0	0	0	0	0	0	100.0	0	0
(Balanitaceae)	2	58	12	0.0	590	—	0	0	0	0	0	0	0	0	0	0
	3	50	7	0.0	797	—	0	0	0	0	0	0	0	0	0	0
Species Average		50	10	0.03	1130	—	0	0	0	0	0	0	0	33.3	0	0
Parinari excelsa	1	195	35	11.5	4295	94	0	0	27.3	42.4	25.9	1.4	0	0	0	3.0
(Rosaceae)																
Mimusops bagshawei	1	51	9	57.8	5933	100	34.5	0	0.6	6.6	10.2	16.3	23.2	0	7.7	0.9
(Sapotaceae)																

Fruit processing categories: [a]swallow fruits, carry them out of the tree and subsequently drop them, and just drop fruits, [b]kill all seeds handled, but also cause fruits to drop, and [c]just drop fruits after processing them.

all species and over the entire fruiting period provided an estimate of the number of fruit removed by frugivores. The number of fruit that were not consumed or processed by frugivores and fell to the ground was estimated daily by collecting fruit along two perpendicular transects (0.5 m wide) below the tree. To calculate the number of fruit falling to the ground each day, the number on the two transects was multiplied by the proportion of the crown that was encompassed by the transects. Crop size was calculated as the sum of the estimated fruit eaten and estimated fruit falling over the fruiting period.

The fate of dispersed and non-dispersed seeds and seedlings

To quantify the fate of dispersed seeds and seedlings, transects were established along an existing grid system of trails. For seeds, sets of five seeds, collected from frugivore dung, were placed on the forest floor at 5 m intervals and 1 m off the sides of trails. Transects were established as seeds from frugivore dung became available. The seed species placed at each station was randomly selected. Stations were monitored the day after they were established, then every second day for 1 month and subsequently, once a month. We recorded the number of seeds remaining, evidence of damage to the seed (e.g., rodent tooth marks on the seed coat), and any sign of germination. A total of 3170 seeds (*M. bagshawei* n = 1515 seeds (from chimpanzee and baboon dung), *U. congensis* n = 720 (from chimpanzee dung), *M. myristica* n = 560 (from chimpanzee and baboon dung), *P. excelsa* n = 225 (from elephant dung, civet dung, and bat processed seeds), *P. microcarpa* n = 90 (from chimpanzee dung), *B. wilsoniana* n = 60 (elephant dung) were placed along the transects (Table 2). The transects were monitored for an average of 6.5 months; 45% of the stations were monitored for 2 years. It seems probable that the passage through different frugivore's guts, differentially effects germination probability for the seeds. However, the sources we selected were all from major dispersers for these plants and offer the only logistically feasible source for such seeds.

To quantify the fate of seedlings, we grew 260 seedlings of the focal tree species until they reached a height of approximately 11 cm and transplanted them 1 m off the sides of transects at 5 m intervals, one per site (Chapman 1989, Wrangham *et al.* 1994). Survival and growth of the seedlings were monitored once a month for 24 months. We were only able to obtain a large sample

Table 2. The percentage of seeds disappearing from seed stations established in the Kibale National Park, Uganda

Species	Number of seeds	Mean number of months monitored	Number germinating	Percent (%) disappearing after 1 wk	1 mo	6 mo
Pseudospondias microcarpa	90	6.2	0	100	100	100
Monodora myristica	560	5.7	1	49	68	95
Uvariopsis congensis	720	6.3	2	15	67	95
Balanites wilsoniana	60	8.0	1	0	0	10
Parinari excelsa	225	6.9	0	1	30	38
Mimusops bagshawei	1515	6.1	2	74	80	100

of seedlings for *M. bagshawei* (n = 56), *U. congensis* (n = 64), *P. microcarpa* (n = 64), *M. myristica* (n = 22), and *B. wilsoniana* (n = 54). For *P. excelsa*, we conducted germination trials on seeds collected from parent trees (n = 60 seeds), on seeds processed by bats, civets, and elephants (n = 42), on seeds that had been soaked for various periods in acid (n = 40), and on seeds whose seed coat had been filed (n = 50). However, we were only able to germinate 2 of 192 seeds processed (one that had been treated by filing the seed coat, and the other seed had been soaked in acid, mean time to germination = 620 d).

Twenty months following planting, the following data were recorded for each surviving seedling: the number of leaves with herbivore damage (expressed as a proportion of the total number of leaves, n = 153 seedlings) and whether or not there was an adult tree of the same species directly above it. In addition, a relative measure of the amount of light reaching the seedling was obtained using a booklet of 10 light sensitive diazo papers set out in a closed petri dish for one week (Friend 1961). The level of exposure of the papers was ranked on a 1 to 10 scale. We used this technique once in the wet season and once in the dry season, during the first year of the seedling's growth.

We evaluated the survival of non-dispersed seeds and seedlings planted under an adult conspecific (parent) trees following the methods of Howe *et al.* (1985). For seeds, we placed freshly fallen and cleaned seeds systematically along four radii from the tree's trunk in random directions. For large trees (all species except *U. congensis*), seeds were placed at 1, 3, 5, 7, 9 m along radii, producing a total of 20 seeds per tree. For *U. congensis*, which has a small canopy, seeds were placed at 1 m and 3 m from the trunk, producing a total of eight seeds per tree. For each species, this protocol was replicated using a number of different trees (*P. microcarpa* n = 9 trees, *P. excelsa* n = 5, *B. wilsoniana* n = 4, *M. bagshawei* n = 3, *U. congensis*, n = 2, *M. myristica* n = 1). Typically, seeds were monitored every two days during the fruiting cycle for signs of damage, germination, or establishment. Subsequent to fruiting, the seeds under parent trees were monitored once week for an average of 110 days (*P. excelsa* 170 d, *U. congensis* 143 d, *B. wilsoniana* 122 d, *M. myristica* 103 d, *P. microcarpa* 63 d, *M. bagshawei* 58 d).

For seedlings planted under the parent tree, we used the same procedure. As a result of the difficulties in germinating *P. excelsa* seeds and growing *M. myristica* seedlings, trials on these species were not performed. For the other four species, the number of adult conspecific trees under which seedlings were planted depended on the number of seedlings available (*B. wilsoniana* n = 60 seedlings, *U. congensis* n = 25, *M. bagshawei* n = 15, *P. microcarpa* n = 15).

Once a week, the condition of the seedling was monitored, its height was measured, and signs of damage described (duration of monitoring *M. bagshawei* 127 d, *U. congensis* 112 d, *B. wilsoniana* 100 d, *P. microcarpa* 92 d).

For each of the focal species, both types of seed treatment (seeds away *vs* seeds under) were initiated soon after the tree had been fruiting and sufficient seeds could be collected from the frugivore's dung. Seedlings of a particular species were planted once a sufficient number could be grown to a height of approximately 11 cm. As a consequence of these two protocols, the onset and duration of sampling varied between species. Seedlings for the transects and for placement under the parent trees were transplanted at approximately the same time (i.e. within a week). Since sample size progressively increased to n = 4001, the seed and seedlings under the parent trees could not be monitored for the same duration as seeds and seedlings on the transects.

RESULTS

Fruit removal

The proportion of the fruit crop estimated to have been removed from each of the focal tree species by frugivores averaged 21%, but ranged from <1% for *B. wilsoniana*, and *M. myristica* trees to 53% for *P. microcarpa* trees (Table 1). For some of the trees, frugivores were never observed to enter the focal tree, but it is probable that some fruit were removed while the observer was not present. However, since *M. myristica* bears only a few large fruit, it was possible to count the fruit each day and determine that no fruit were removed. The low level of removal was not a result of frugivores not being in the area. With the exception of *B. wilsoniana*, frugivores known to eat the fruit of the focal tree, were seen or heard in the area of the focal tree, on an average of 95% of the days for which observations were made (range between trees 75% to 100%, Table 1). *B. wilsoniana* is heavily dependent on elephants for dispersal (Chapman *et al.* 1992) and observations were not made when elephants were in the area.

The fate of dispersed and non-dispersed seeds and seedlings

The proportion of seeds that disappeared from the transects and the time period over which they disappeared varied dramatically between species (Table 2). For some species, many seeds disappeared during the first night (e.g., *P. microcarpa* and *M. bagshawei*), while for *B. wilsoniana* no seeds had disappeared after one month. Six months after the seeds were placed along the transects, disappearance averaged 73% among the species (mode = 100%, range 10–100%). The pattern of disappearance was bimodal, with two species showing a very low probability of disappearance after six months (*B. wilsoniana* 10%, *P. excelsa* 38%) and the other four species exhibiting an extremely high probability of seed removal ⩾95% (Table 2). Signs of rodent activity were observed at 43% of the stations, but this is an under-representation of the actual level of rodent activity, since they carry seeds away. Germination at seed stations along the transects was very low; only six out of 3170 seeds were observed to germinate and two became established (Table 2).

Seeds placed under parent trees (non-dispersed seeds) also showed a bimodal pattern of disappearance. Some species disappeared very quickly. For example, on average 100% of *P. microcarpa* seeds placed under a parent tree disappeared in three days. Other species showed very low rates of disappearance. For example, no *M. myristica* seeds disappeared in the 103 d they were monitored

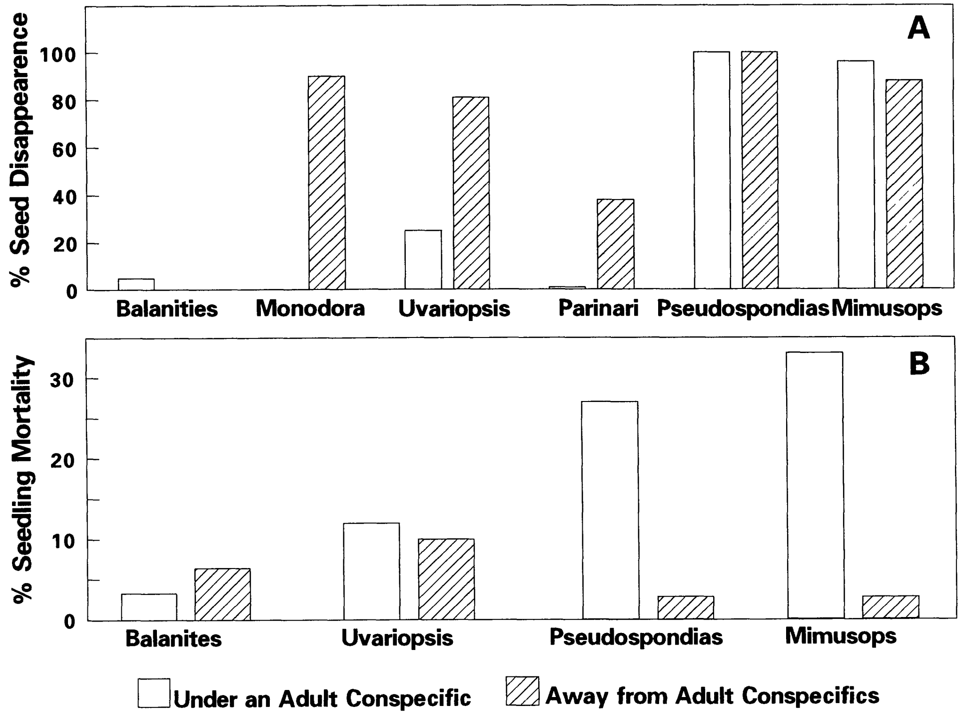

Figure 1. The percentage of the seeds placed under and away from adult conspecifics that disappeared (A), and the percentage of the seedlings planted under and away from adult conspecific that died (B) (all comparisons are made over a comparable number of days).

(Figure 1a). No germination was observed for any species during the time the seeds were monitored (mean duration = 110 d).

The pattern of removal for dispersed (transects) and non-dispersed (under parent trees) seeds varied between species (Figure 1a). We contrasted the proportion of seeds removed from under the parent trees with the proportion removed during the same time from the transects. For *U. congensis* and *P. excelsa*, seed disappearance was higher away from the parent than under the parent (*P. excelsa* – disappearance under = 1%, away = 38%, $\chi^2 = 48.80$, $P < 0.005$; *U. congensis* – 25, 81%; $\chi^2 = 30.36$, $P < 0.005$). For *M. bagshawei* and *B. wilsoniana* there was no difference in seed disappearance from under the tree versus seed disappearance away from parents (96, 88%; $\chi^2 = 2.35$, $0.5 > P > 0.1$; *B. wilsoniana*, 5, 0; $\chi^2 = 3.07$, $0.1 > P > 0.5$). All *P. microcarpa* seeds placed under the parent and all of the seeds on the transects disappeared after two months. However, seeds under parent trees disappeared sooner than seeds on the transects.

Mortality of seedlings 24 months after they had been transplanted along the transect averaged 30% across species (n = 260 seedlings, range 9 to 38%). 115 seedlings of four of the six focal tree species were planted under conspecific adult trees. Mortality rates were relatively low (*B. wilsoniana* – two out of 60 seedlings died during 100 d of monitoring; *U. congensis* – three out of 25 died in

112 d; *P. microcarpa* four out of 15 seedlings died in 92 d; and *M. bagshawei* – five out of 15 seedlings died in 127 d). Comparison of mortality rates between seedlings under conspecifics and seedlings grown away from adult conspecifics over similar time periods varied between species (Figure 1b). For *B. wilsoniana* (mortality under = 3.3%, away = 6.4%, $\chi^2 = 0.376$, $P > 0.5$) and *U. congensis* (12, 10%; $\chi^2 = 0.189$, $P > 0.5$) seedling mortality under a conspecific adult was similar to that of seedlings on the transects (Figure 1b). In contrast, the mortality of *M. bagshawei* (33, 2.7%; $\chi^2 = 11.78$, $P > 0.01$) and *P. microcarpa* seedlings (27,2.8%; $\chi^2 = 9.59$, $P > 0.001$) was much higher under an adult conspecific than away from conspecifics.

Over the 24 months that measurements were made, monthly growth rates of seedlings on the transects (not randomly placed under a parent tree) averaged 4.3 mm across species (*B. wilsoniana* 8.7 mm, *M. myristica* 5.2, *U. congensis* 3.2, *M. bagshawei* 2.9, *P. microcarpa* 1.4). When measured 20 months after planting, seedlings on the transects had an average of 7.2 leaves (range among species 4.8 to 12.7, Table 3). On average, 51.9% of the leaves exhibited damage that was indicative of insect herbivory (range 46.3% *M. bagshawei* to 68.2% *P. microcarpa*; $F = 4.94$, $P < 0.001$). A seedling was considered to have experienced severe damage indicative of mammal foraging if there was evidence of loss of leaves and sections of the stem, or if the seedling decreased in height by >10 cm. The percentage of the seedlings that experienced one episode of such damage ranged from 0 to 11% (Table 3). Some *P. microcarpa* and *B. wilsoniana* seedlings experienced two episodes of severe damage (Table 3). Contrary to what might be expected, there was a tendency for seedlings randomly placed under a parent tree on the transects to have less damage (proportion of leaves with damage = 45%, $n = 19$), than seedlings not growing under an adult of that species (proportion of leaves with damage = 58%, $n = 196$; $t = 1.84$, $0.05 < P < 0.10$). Increasing levels of leaf damage were correlated with a decrease in growth rate ($r = 0.175$, $P < 0.01$, $n = 199$). There was a trend for increased growth with increased light for *M. bagshawei* ($r = 0.461$, $0.05 < P < 0.10$), and *B. wilsoniana* ($r = 0.348$, $0.05 < P < 0.10$), however growth rate did not increase with increasing light for *U. congensis* ($r = -0.177$, $P > 0.10$), or *M. myristica* ($r = 0.288$, $P > 0.10$).

Table 3. The damage experienced by seedlings planted in the Kibale National Park, Uganda.

SPECIES	Sample[1] Size	Average Number of Leaves	% of Leaves with Damage	Percent (%) Suffering Drastic Damage[2] Once	Twice
Pseudospondias microcarpa	45	7.1	68.2	3	2
Monodora myristica	10	4.8	51.1	0	0
Uvariopsis congensis	32	5.4	47.6	0	0
Balanites wilsoniana	33	12.7	46.5	11	2
Mimusops bagshawei	33	6.0	46.3	2	0

[1] Observations were made after 1 year 8 months, thus the n reflects only those surviving to that date.

[2] Drastic damage was considered whenever (1) observations were made of whole leaves or sections of the stem being eaten, or (2) when the plant was recorded to have decreased in height by 10 cm or more.

Traits associated with recruiting under the parent's canopy

For the six focal species, the percentage of the fruit crop removed was correlated with the probability of disappearance for seeds placed under the parent's canopy (Spearman's rank $r = 0.829$, $n = 6$, $P < 0.05$) and with non-dispersed seedling mortality ($r = 0.989$, $n = 4$, $P < 0.01$), suggesting that species that experience high seed and seedling mortality under the parent have high rates of dispersal away from the parent. The proportion of non-dispersed seeds that disappeared was also related to seedling mortality under the parent ($r = 1.00$, $n = 4$, $P < 0.01$). Similarly, both the number of frugivore species that were seen at a focal tree and the proportion of the observation days on which frugivores fed were related to the probability of seed disappearance under the parent's canopy (frugivore richness, $r = 1.00$, $n = 6$, $P < 0.0001$; frugivore attendance, $r = 1.00$, $n = 6$, $P < 0.001$).

DISCUSSION

The positive relationship between the proportion of the fruit crop removed and both seed disappearance and seedling mortality under the parent's canopy suggests that the ability to survive under or near an adult may be linked with other aspects of the tree's life history. Frugivores avoid carrying large seeds away from fruiting trees (Levey 1987), but large seeds enhance seedling vigor under or near the parent tree (Foster & Janson 1985). This suggests a trade-off between traits increasing the probability that seeds will be removed from the tree and traits permitting recruitment under or near adults. These results expand on the original suggestion made by Howe & Vande Kerckhove (1980, 1981) and Howe & Richter (1982) to explain variation in *V. surinamensis* seed size. The basic premise is that a trade-off exists between selection for large seed size that promotes growth in areas with high seed density, which have high levels of insect and pathogen attack and seed and seedling predation and small seed size that promotes dispersal by frugivores (Howe 1989, Howe & Richter 1982, Stamp & Lucas 1983, Terborgh *et al.* 1993).

Schupp (1992) provides one example of seed survival that illustrates the complexity of the relationships that may determine optimal dispersal distance. For *Faramea occidentalis*, seed survival beneath adults was significantly lower than survival away from the canopy. However, at the population level the number of seeds surviving increased with the density of adult trees, probably the result of seed predator satiation. For this species, the best dispersal distance may be away from the parent's canopy, but not so far away that the seed is placed in an area where it becomes a novel food resource to seed predators that have not been satiated by local abundance of these seeds.

The findings of this study suggest that the ability to survive under or near an adult are linked with other aspects of the tree's life history, such as traits associated with encouraging fruit consumption and seed dispersal. This raises intriguing questions as to the nature and extent with which fruit and seed traits represent a compromise between competing selective pressures. Past research on fruit syndromes has pointed out that, in addition to attracting dispersers, some fruit traits may represent a response to other selective pressures or may perform more than one function (Fischer & Chapman 1993). For example, it has been suggested that, in addition to attracting specific dispersers, green fruits reduce the energetic costs of reproduction through photosynthesis (Cipollini & Levey 1991, Wheelwright & Janson 1985). Similarly, red fruit is suggested to both attract specific vertebrate dispersers and provide protection from arthropod predation through crypsis (Willson & Thompson 1982).

If fruit and seed traits, seedling survival abilities, and traits associated with attracting frugivores are all part of a coadapted complex, it may be inappropriate to examine the adaptive significance of seed or fruit traits only in terms of dispersal. Rather, investigations should examine consequences of variation in traits on a number of different life history stages. For example, it seems reasonable to speculate that selection might favour seeds that are ovate and elongate, like many pills. Seeds of this shape would have sufficient volume that they would encourage the initial growth of the seedling, but the elongated shape would increase the likelihood that the seed was swallowed. However, it is also conceivable that the probability of such elongated seeds being incorporated in the dung beetle's ball might be lower than a round seed of similar volume. Investigations of how specific seed traits influence primary seed dispersal, subsequently secondary seed dispersal, and seedling establishment may prove to be an intriguing area of future study.

The complex nature of interactions among environmental parameters, seed dispersers, and plants in tropical forests is illustrated in this study. If there is a general trade-off between growth in areas with high seed density and small seed size that favours dispersal, it seems likely that trees that cannot recruit under adults may be in jeopardy. In many tropical forests, subsistence or commercial hunting have impacted large tracks of forest by removing the majority of the large-bodied seed dispersers, but have left the forest's physical structure relatively unaltered (Redford 1992). In areas where the frugivore community is no longer intact, the long-term persistence of tree species that are unable to recruit under conspecific adults in areas is questionable and may be a profitable area for future investigation (Chapman & Chapman 1995). Such findings support the idea that seed dispersal by frugivores is vital to the survival of some fruiting tree populations, since the survival of fallen fruit does not appear to be sufficient to maintain populations of many tropical tree species (Chapman *et al.* 1992, Howe 1984, Pannell 1989).

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