RUNNING HEADING: COMPARATIVE SEED SHADOWS

COMPARATIVE SEED SHADOWS OF BIRD-, MONKEY- AND WIND-DISPERSED TREES IN A CENTRAL AFRICAN TROPICAL FOREST

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Abstract – Though it is widely assumed that spatial patterns of seed distribution vary greatly among plant species dispersed by different mechanisms (e.g. animals and wind), few studies have directly examined this assumption in tropical forest. We compare patterns of seed rain under and around trees disseminated by large birds, monkeys and wind in a closed canopy forest in the Dja Reserve, Cameroon. Seed traps that collectively represented 5% of the area of the tree crown were placed randomly under the canopies of five individuals from each of nine focal tree species. Additional traps representing 1% of the area at each distance annulus were placed along six rays at 60º intervals 5, 10, 20, 40 and 60 m from the edge of each tree crown.

We compared patterns of seed distribution among trees, species, and vectors using ANOVA. We found no support for the supposition that different vectors yield detectable differences in the distributions of seeds within 60 m of parent trees. We found no differences among vectors in the density of seeds deposited at each distance. Great variability in patterns of seed distribution, both within and among tree species and vectors, suggests that knowledge of a tree’s predominant dispersal mechanism alone is not sufficient to make reliable predictions regarding its seed shadow. Most seeds produced by trees regardless of vector fell directly under the parent canopy (individual tree range: 26.69 – 96.1%). Most seeds disseminated beyond parent canopies fell within 60 m of the parent tree (range: 57.8 – 99.71 %), indicating that long distance dispersal events are relatively uncommon in this forest system. Birds disperse a smaller proportion of the total seed crop beyond 60 m than do monkeys or wind. However, maximum dispersal distances beyond the 60 m trap design were greater for bird-dispersed trees than for monkey-or wind-dispersed trees.

Key words: seed shadows, seed rain, seed dispersal, wind-dispersal, monkeys, frugivorous birds, tropical forests.
INTRODUCTION

Many plant species have developed seed or fruit traits that aid in dissemination, such as fleshy fruits or fatty arils for dispersal by animals, and wings or plumes for dispersal by wind (van der Pijl 1982). Because fruit morphology determines how a seed is transported, seeds that are adapted to dissemination by different vectors are expected to have different seed shadows (the spatial pattern of seeds dispersed from a single plant).

Among species of vertebrates that disperse seeds, many studies show differences among taxa in the morphology of the fruit on which they feed (Howe and Westley 1988, Charles-Dominique et al. 1991, Poulsen et al. 2002). Following feeding, behavioral differences among species of frugivores, such as movement patterns or gut passage times, are expected to produce different seed shadows among the plant species selected for consumption (Howe 1990, Charles-Dominique 1991, Da Silva et al. 1996). For example, trogons (Trogon sp., Pharomachrus sp.) generally leave a fruiting tree immediately after each fruit is consumed, while fruit pigeons (i.e., Ptilinopus sp., Gymnophaps sp.) remain in trees for hours after feeding, dropping seeds under the parent canopy (Pratt and Stiles 1983). Large primates like chimpanzees (Pan troglodytes) and grey-cheeked mangabeys (Lophocebus albigena) can move longer distances after feeding (1930 m and 1010 m, respectively; Goodall 1986, Poulsen et al. 2001) in comparison to smaller primates, such as blue monkeys (Cercopithecus mitus), redtail guenons (Cercopithecus ascanius), or various rodents that move much shorter distances after feeding (30 – 355m, Peterson et al. 1998).

Because of their influence on seed shadows, different vectors might differentially affect seed and seedling survival and recruitment, genetic structure, and the rate of expansion of the geographic range of plant populations (Janzen 1970, Connell 1971, Augspurger 1983, Clark and Clark 1984, Condit et al. 1992, Cain et al. 2000). Therefore, examination of the seed shadows of
plants with different vectors should provide insights into a process that is central to plant population and community structure. Here, we directly compared seed shadows of plants dispersed by different vectors using data collected simultaneously from nine plant species in the same plant community. Field sampling programs specifically designed to compare the seed shadows around trees dispersed by different vectors are rare (but see Ribbens et al. 1994 and Clark et al. 1998 for a different approach to quantifying seed shadows). Rather, comparisons among plant species and dispersal vectors have relied on syntheses from the literature relating seed density to distance from the seed source by fitting data to a variety of statistical models (Willson 1993). However, vast differences in the sampling techniques employed among studies make comparisons among sites, plant species, and dispersal agents difficult (Willson 1993).

We test the hypothesis that tree species with different mechanisms of seed-dispersal will have different seed shadows. Using field data collected in a closed canopy tropical forest, we compare seed shadows of tree species dispersed by large frugivorous birds, monkeys, and wind. Specifically, we address the following questions: 1) Does seed dispersal by vertebrates (birds and monkeys) yield detectably different seed shadows than wind-dispersal? 2) Do the proportions of the total seed crop deposited below the crown of a tree, within 60 m, and at greater distances from the tree, differ among tree species dispersed by different vectors?

Our study is unique in that seed shadow data were collected with a well-replicated sampling design that allowed us to directly examine the generality of seed distribution patterns among tree species representing three categories of dispersal agents. In addition, we estimated seed rain at six distance categories from the parent tree while keeping sampling effort/m$^2$ constant, thus removing a sampling bias inherent in many previous studies.

METHODS
Study Site

Our study took place from January 1998 to May 1999 at the Bouamir Research Station (BRS) in the Dja Reserve, Cameroon. The Dja Reserve, an IUCN Biosphere Reserve protects an area of 526 km². Our study area is a 25-km² site located roughly at the center of the reserve (3°11'27"N, 12°48'41"E). The vegetation is semi-deciduous tropical rain forest, and has never been logged (Letouzey 1968). At the study site, there are two wet and two dry seasons with major and minor rainfall peaks in September and May, respectively (Whitney and Smith 1998). Average annual rainfall is approximately 1600 mm/yr (Laclavère 1980).

Tree species selection

Within each category of dispersal agent (bird, monkey, and wind), tree species were randomly selected from a list of all possible tree species for that category. The list of tree species and their predominant seed dispersal agent was produced from observations made by researchers at BRS from 1994 to 1997 and the knowledge of local Baka guides (Whitney et al. 1998, Clark 2001, Poulsen et al. 2002). To avoid confounding our data set with overlapping conspecific seed shadows, mature trees of the study species were chosen at random, subject only to the constraint that they were at least 180 m from the nearest fruiting conspecific.

Seed rain was sampled around the canopies of five trees from each of nine species, three species predominantly dispersed by large, frugivorous birds: *Cleistopholis glauca* (Annonaceae), *Maesopsis eminii* (Rhamnaceae), and *Staudtia kamerunensis* (Myristicaceae); three dispersed by monkeys: *Gambeya boukokoensis* (Sapotaceae), *Garcinia smeathmannii* (Clusiaceae), and *Uapaca paludosa* (Euphorbiaceae); and three wind-dispersed species: *Terminalia superba* (Combretaceae), *Pteleopsis hylodendron* (Combretaceae), and *Funtumia elastica* (Apocynaceae) (nomenclature follows Hutchinson et al. 1963, Letoutzey 1970, Tailfer 1989).

The bird-dispersed trees, *C. glauca* and *M. eminii*, produce oblong fleshy drupes (1.5 -
2.5 cm and 2.5 - 3 cm in length, respectively) that turn violet or black at maturity. The fruits of *S. kamerunensis* are enclosed in a yellow dehiscent capsule that opens to reveal the seed (2 - 3 cm in length) surrounded by a bright red waxy aril. The monkey-dispersed trees all produce green, yellow or orange fruits, round or oval in shape. *U. paludosa* produces 2.5 – 3 cm long succulent fruits with three oblong seeds. The fruits of *G. boukokoensis* are 2 cm in length with 3-5 seeds surrounded by a resinous pulp. *G. smeathmannii* produces fruits 2 - 2.5 cm in length. Wind-dispersed species were defined by their fruit and seed characteristics and possess classic wind-dispersal syndromes. The fruits of *T. superba* and *P. hylodendron* are samaras measuring 5 - 6 cm and 1.5 - 2 cm in length, respectively. *Funtumia elastica* produces oblong green fruits (12 - 20 cm long) that break open to release plumed seeds, 5 - 6 cm in length.

**Characterization of frugivore dispersal assemblages and estimation of crop size**

To determine which animals visit each tree species and how many seeds animals drop, remove, defecate or regurgitate under the parent canopy, we observed fruiting trees of our study species. A minimum of 20 five-hour watches, one 24-hour watch, and five night watches were conducted for each tree species. During night watches, we viewed trees from hides with a night vision scope for 30 minutes at 2200 hrs, 2400 hrs, 0200 hrs, and 0400 hrs, and recorded all frugivore activity. We recorded the duration of the visit, number of fruits eaten, and the direction and distance moved at departure for each observation of an animal in the tree.

At the beginning of each daylight observation period, we estimated fruit production (standing crop size) by meticulously counting the number of fruits on all completely visible tree branches with a telescope, averaging the number of fruits per branch, and multiplying that number by the total number of branches on the tree. This method is widely used to achieve the best estimate of crop size for canopy trees in tropical forests (Janzen *et al.* 1976, Laman 1996). Because light conditions, fruit ripeness, and observer bias can influence the detection of fruits...
high in the canopy, we averaged multiple crop size estimates obtained by several different observers, rounding to the nearest thousand fruits. When possible, we checked fruit production estimates against extrapolations from the number of husks (*Staudtia kamerunensis*) or bracts (most other species) that fell into seed traps (41 of 45 visual estimates fell within 95% confidence limits of estimates based on husks and bracts).

*Seed trap placement and monitoring*

Seed traps were placed under and around the canopies of each tree prior to fruit maturation. Seed traps that collectively represented 5% of the area of the tree crown were placed randomly under the canopy of each focal tree. Traps placed under tree canopies were constructed of plastic mesh stapled to rattan frames. Traps ranged in size (0.25 m$^2$ - 1.25 m$^2$) and number (2 - 22 traps) to reflect differences in the canopy area of individual trees.

Using the crown edge as the point of origin, additional traps were placed at 5, 10, 20, 40 and 60 m from the crown edge. To avoid sampling bias caused by non-random wind direction or movement patterns of vertebrates away from the canopy, traps were arranged in a radial design at 60° intervals originating from the base of each tree (Fig. 1). We increased trap sizes deployed outside of the canopy to sample 1% of the area at each distance annulus. Each distance annulus was 1 m wide and centered at the target distance. Therefore, the total trap area at each distance was directly proportional to distance from the crown edge but the total number of traps at each distance annulus remained constant. This trap design improves upon constant-area designs that place traps of equal area at each distance sampled or have only slightly increased sampling effort at increasing distances from tree crowns. Such constant-area designs are biased against detecting dispersal at greater distances because a smaller proportion of the potential dispersal sites are sampled at greater distances. We limited our trapping to 60 m from the parent canopy both because of logistical constraints on our proportional-area sampling design and because 60 m
equaled or exceeded the distances sampled in previous studies (Howe et al. 1985, Laman 1996).

Seed traps placed outside the tree canopy were constructed of sheets of heavy cloth suspended between trees by cords attached to each corner. All seed traps were elevated to a height of 1 - 1.5 m from the ground and seeds were collected frequently to discourage the removal of seeds by animals. Traps were installed just before fruits were mature and left in place until after all the fruits had been removed from the tree.

The contents of seed traps were collected at 10-day intervals for the duration of the fruiting cycle for each tree. All conspecific seeds, fruits, and fruit or seed pieces were collected in plastic bags and returned to the field station for processing. Fecal clumps defecated into traps were also collected intact so that their seed contents could be examined and counted.

Following Laman (1996), we calculated the proportion of the estimated seed crop falling under the canopy of each tree by multiplying the density of conspecific seeds recorded in traps under the tree crown by the crown area and dividing this number by the estimated crop size. The proportion of the total seed crop recorded at each distance annulus for each tree was estimated by multiplying the density of conspecific seeds at each annulus by the area of the annulus and dividing by the estimated crop size (Fig.1). The proportion of the estimated seed crop not accounted for within 60 m of the parent canopy was presumed to have dispersed greater than 60 m from the parent canopy. The proportion of seeds deposited beyond 60 m are likely to be overestimates because some seeds accounted for in crop size estimates were probably preyed upon before dispersal, and therefore, not detected in seed traps (Clark et al. 2001).

Estimating dispersal distances beyond 60 m of the tree canopy

Because the distances seeds are dispersed could exceed the maximum distance in our sampling design (60 m), we recorded supplementary observations of long distance dispersal using an additional array of seed traps, which were available from a concurrent study of seed rain
In the concurrent study, traps sampling 5% of the area of the canopy were placed under an additional five to ten individuals of each of the nine species of trees. For each seed from any of the nine focal species of trees, we measured the straight-line distance from the trap to the nearest possible seed source, the closest fruiting conspecific tree. We identified the nearest fruiting conspecific tree using an expanding spiral technique. Between two and four observers searched the area starting at the point of seed collection, circling the collection point in a spiraling fashion until the nearest fruit source was discovered. Because we assumed that seeds originated from the nearest possible seed source, our estimates of long-distance dispersal are conservative. The estimates of dispersal distances beyond 60 m from the parent tree may be biased by the relative abundance of the focal species, with more abundant species being biased to shorter dispersal distances than less abundant species. However, the correlation between dispersal distance and the relative importance of the species on the study site was not significant ($r = -0.35$, $t = -0.991$; df = 7; $P = 0.3547$), suggesting that the dispersal distance of a tree species is not biased by its relative abundance (Table 4).

**Statistical analysis**

We tested the null hypothesis that seed shadows do not differ among trees disseminated by different dispersal agents using a 3-factor mixed-effects ANOVA model with species nested within dispersal type and repeated measures on the distance factor (3 species x 3 vectors x 6 distances x 5 trees per species). Vector and distance were treated as fixed factors, whereas species and trees were treated as random factors. Therefore, the vector effect was tested over the mean square due to species nested within vector, and the distance and distance by vector interactions were tested over the mean square due to the distance by species nested within vector interaction (Keppel 1991). Our use of a mixed-effects model with tree species as a random-effects factor allows us to make inferences about tree species not included in this study (Beck...
For each individual tree, we used data on seed density at each of six distances after averaging among all traps placed in each distance.

To test the hypothesis that the maximum dispersal distances do not differ among tree species dispersed by different vectors, we performed a one-way ANOVA on the observed dispersal distances beyond 60 m using tree species within vector as our source of replication.

RESULTS

Tree and crop characteristics

Fruit production of individual trees ranged widely, both within and between species and seed-dispersal agent (Table 1). Observations on the assemblages of animals feeding on each tree species suggest that our classifications of tree species by seed-dispersal agent are accurate. Based on data collected during tree watches, birds accounted for 92.6, 96.3, and 99.9% of the visits by frugivores to *C. glauca*, *M. eminii*, and *S. kamerunensis*, respectively (Table 2). Likewise, primate visits accounted for 90.7, 94.7, and 100% of all frugivore visits to *U. paludosa*, *G. boukokoensis*, and *G. smeathmannii*. Squirrels act only as seed predators of these species (Clark *et al.* 2001). Although we did not conduct regular tree watches for feeding activity by vertebrates at wind-dispersed tree species, we did observe monkeys to eat the seeds of all three species of wind-dispersed trees. However, the seeds of wind-dispersed tree species comprise a very small proportion of the food consumed by primates (Poulsen *et al.* 2001).

Do wind, monkey and bird dispersal yield different seed shadows?

Patterns of seed distribution for all tree species were strongly leptokurtic (Fig. 2). Seed density generally dropped sharply between 5 and 20 m from the parent tree. Seed densities greater than 20 m from the parent tree show slight differences in pattern. All wind- and monkey-dispersed tree species exhibited a gradual decline in seed density between 20 and 60 m from the parent plant, though this decline is more gradual in *U. paludosa*. Two of three bird-dispersed
tree species, on the other hand, exhibited a slight increase in seed density between 20 and 40 m from the parent canopy, rather than the monotonic pattern of decrease in seed density observed for all other species (Fig. 2). Averaging across distance and tree species, we found no difference among dispersal vectors in the density of seeds deposited under or near trees (vector effect $F_{2,6} = 0.85, p = 0.488$, Table 3). However, we found differences among tree species in the densities of seeds dispersed, independent of vector (species within vector: $F_{6,36} = 10.04, p = 0.00001$; Table 3).

Averaging across species and vector, we detected large differences in seed density among distance intervals (Fig. 3, Table 3). More seeds are deposited under or near than away from the parent tree. More importantly, we found no difference among vectors in the distance seeds are moved away from the parent tree (distance by vector interaction; Table 3 and Fig. 3). However, we found a significant interaction between distance and tree species, which suggests that there is more variation among tree species than among vectors in the distance seeds are dispersed (Fig. 2).

**Deposition patterns of the seed crop**

We also examined seed shadows for each tree by calculating the cumulative proportion of the seed crop that fell beneath the parent canopy or within each distance annulus (5, 10, 20, 40, and 60 m), and the proportion of seeds dispersed beyond 60 m from the canopy edge. For all but one tree species (G. smeathmannii), more than 55% of the seed crop fell to the ground below the parent canopy. Higher percentages of the seed crop fell directly under bird-dispersed tree species than under monkey- or wind-dispersed species (Table 5). The proportion of the seed crop estimated to fall between 5 and 60 m from the parent crown varied among individuals, species, and vectors. The proportion of the seed crop deposited beyond the parent canopy, but within 60 m of the parent crown, was higher for wind (38.48 ± 14.25%) and monkey-dispersed
trees (29.23 ± 23.94%) than for bird-dispersed trees (9.9 ± 8.1%). However, more than 85% of all fruits for all tree species (with the exception of *G. smeathmannii*) were deposited within 20 m of the parent tree. The estimated proportion of seeds disseminated beyond 60 m of the parent canopy was low for all trees (range: 0.21 to 42.18%, N = 45; range: 0.21 to 19.01%, N = 43, with the removal of two outlying individuals). A larger proportion of the seed crops of monkey-dispersed tree species were dispersed beyond 60 m than for the other dispersal agents (Table 5). The estimated long-distance dispersal differed significantly among vectors (*F*₂,₆ = 5.362, *p* = 0.046). Long-distance dispersal distances recorded for all tree species ranged from 90 m (*G. smeathmannii*, monkey-dispersed) to 473 m (*M. eminii*, bird-dispersed). The longest dispersal distances were recorded for bird-dispersed tree species (Table 3). Monkeys dispersed seeds up to 200 m, while the estimated dispersal maximum for wind-dispersed trees was 158 m.

**DISCUSSION**

The great variability in patterns of seed deposition, both among tree species and among dispersal agents, argues strongly that knowledge of a tree species’ dispersal mechanism alone is insufficient to predict reliably its seed shadow. Most seeds, regardless of the vector, fell either under or within 60 m of the parent tree. Thus, long distance dispersal events (distances > 60 m) presumed to result frequently from vertebrate seed-dispersal account for a relatively small proportion of the seed crop. Because we randomly sampled species of trees from all those available, our results should be indicative of most wind-, bird-, and monkey-dispersed species of trees occurring in the study site.

*Do wind, monkey and avian dispersal yield different seed shadows?*

Our data do not support the common assumption that different dispersal agents yield detectable differences in seed distributions around parent trees (no interaction between distance and vector, Table 3). High variability among trees and tree species within vectors accounts for
the lack of differences in seed shadows among trees dispersed by different vectors. Heterogeneity in seed shadow patterns may be extremely important and is certainly understudied. Independent of distance, seed deposition patterns may vary among patch or habitat types and micro-sites. For example, the wind-dispersed trees we examined had different seed types, tree heights, and may have been subject to variable wind conditions or habitat characteristics that affect patterns of seed distribution around tree canopies. Similarly, variability in seed distribution patterns among species of bird- and monkey-dispersed trees are likely driven by animal behavior and reflect post-feeding patch selection of individual vertebrate dispersers (Jordano 1992, Schupp 1995, LePage et al. 2000). For example, we found an increase in average seed deposition at 40 m from the parent trees of two bird-dispersed tree species. This increase in deposition may indicate a common distance large birds move from a tree to process fruits after feeding bouts (Clark 2001). Much current research illustrates that patterns of contagious seed dispersal, higher seed densities deposited in areas frequently used by frugivores, are common and complicate conceptual models of seed shadows (Schupp et al. 2002). For birds, post-feeding patch-selection and the resulting spatial distribution of seeds could depend on the proximity of a tree to other fruiting trees, good perches, nest-cavities, breeding display sites, or forest gaps (Hoppes 1987, Levey 1988, Thomas 1991, Krijger et al. 1997, Kinnaird and O’Brian 1998, Wenny and Levey 1998, Wenny 2000, Clark 2001). Thus, we suggest that seed shadow patterns deposited around plants may be both as much a function of the forest characteristics surrounding fruiting trees as of any single attribute of the fruiting tree itself.

Currently, mechanistic models intended to predict patterns of seed distribution directly from the attributes of plants and their dispersal agents (e.g. wind speed, direction and tree height) are used to explain patterns of seed deposition via wind-dispersal (Anderson 1991, Greene and Johnson 1996, Nathan and Muller-Landau 2000, Nathan et al. 2002). In theory, similar models
incorporating knowledge of animal behavior and plant characteristics should be able to predict seed dispersal patterns associated with vertebrate dispersal. In fact, mechanistic models of the effects of vertebrate dispersal on the seed shadows of trees that are based on the gut passage time of seeds and movement patterns of the dispersal agent have been proposed (Murray 1988, Sun et al. 1997, Holbrook and Smith 2000). Although often referred to as seed shadow studies they do not model the entire seed shadow of a plant, but calculate the hypothetical contribution of one species of dispersal agent to the distance seeds are moved away from the parent plant. However, because we found as much variability in patterns of seed distribution within as among vectors, actual post-feeding behaviors and movements are likely more complex and context-dependent than assumed in these models. Additionally, realistic models of seed shadows need to include all the potential dispersal agents a tree may experience, each with different post-feeding behaviors (Peterson et al. 1998). Finally, our data also indicate that many seeds are not dispersed by the putative primary dispersal agents. Rather, many seeds fall beneath the parent tree where they are dispersed by secondary agents. We suggest that a more comprehensive mechanistic framework to model or predict the effects of vertebrate seed-dispersal on seed shadows should incorporate not only attributes of the fruit being dispersed, the behavior and physiology of the various primary and secondary dispersal agents, but also aspects of the structure of the surrounding forest.

Implications for plant populations and communities

We found that for all tree species, regardless of the predominant dispersal agent, the majority of the seed crop falls to the ground directly below the parent canopy. Thus, in this forest system, we conclude that seed dispersal processes are largely quantitatively-restricted (Schupp et al. 2002). Independent of dispersal agent or seed production, the number of seeds dispersed away from parents is limited by disperser activity, or, in the case of wind-dispersed
tree species, the wind velocities necessary to disseminate most seeds away from the tree crown. However, greater proportions of the seed crops of bird- than monkey- or wind-dispersed species were dropped under the canopies of the parent tree. The high density of seeds deposited under the canopy of the parent tree, especially under the canopies of bird-dispersed trees, may influence the fate of the seeds and subsequent patterns of plant recruitment in two ways. First, far fewer seeds than would be expected based on fruit production estimates will be deposited in potential recruitment sites beyond the canopy (distance-restricted seed dispersal; Clark et al. 1998, Muller-Landau et al. 2002, Schupp et al. 2002). Second, seeds deposited in high density below the parent canopy may be subject to higher rates of mortality reinforcing recruitment limitation (Janzen 1970, Connell 1971, Augspurger 1983, Howe et al. 1985, Schupp and Frost 1989, Condit et al. 1992). On the other hand, some studies suggest that high seed densities near parent crowns may in fact satiate predators, resulting in greater seedling recruitment under or near parents than would occur if seeds were evenly deposited across a landscape (Augspurger and Kitajima 1992). Thus, more thorough studies of the relationship between recruitment success, seed density, and distance from parent tree will be necessary to understand patterns of recruitment.

The proportion of the seed crop deposited beyond the parent canopy, but within 60 m of the parent crown, was greatest for wind (~38%)- and monkey-dispersed (~29%) trees, while birds disseminated the lowest proportion of seed crops (~10%) between 5-60 m. Low proportions of seed crops deposited between 5 and 60 meters of parent canopies offers further evidence that dispersal limitation may contribute to patterns of plant recruitment in this forest system. In other words, we would expect very few seeds to establish far from adults in this forest simply because very few seeds are dispersed far from adults.

Seed dissemination beyond 60 m of the parent crown was a relatively uncommon event
for all species in this study. However, the fact that low proportions of seed crops are disseminated beyond 60 m from the parent tree does not negate the importance of long distance dispersal. Because overall seed production is high for all focal tree species in this study (10,000 to 100,000 seeds), even a small percentage of dispersed seeds translate into an impressive number of seeds in absolute terms (Table 4). Long distance dispersal events may be disproportionately important in determining genetic structure, range expansion rates, and rates of recruitment in plant populations (Cain et al. 2000). Despite the fact that birds disperse lower proportions of the total seed crop beyond 60 m, maximum dispersal distances were greater for birds than for monkeys or wind-dispersed seeds. Birds dispersed seeds as far as 473 m from another conspecific. Nonetheless, our method of calculating dispersal distances of seeds, which assumes the nearest fruiting conspecific individual to be the source, likely underestimates true dispersal distances. Using home range movement as a model of seed dispersal distances, Holbrook and Smith (2000) estimated that hornbills potentially could move seeds as far as 6500 m from the parent tree. Similarly, estimates of monkey-facilitated seed dispersal distances suggest potential seed movement up to 2000 m from a parent canopy (Poulsen et al. 2001).

Thus, in rare instances, vertebrate-mediated seed dispersal can move seeds great distances. In addition, highly mobile frugivorous birds, like hornbills and touracos, can move relatively long distances in short periods of time, enabling them to move seeds farther than monkeys or wind (Sun et al. 1997, Holbrook and Smith 2000).

There are several problems associated with current methods used to examine seed shadows of focal trees. Perhaps the most problematic is that most studies use a single species and variation among conspecific individuals may be largely ignored. Also, most studies use very few sampling intervals and little replication at each distance. Finally, many studies sample a constant area at each distance from the focal tree or only roughly adjust sampling area to the total
area sample with increasing distance from parent plants. Thus, the resulting seed distribution
curves are biased estimates of the actual seed shadow because the probability of trapping any
given seed will be a negative function of the distance of the trap from the tree. More studies that
sample with a constant proportion of the area at each distance should remove this bias and
contribute importantly to our understanding of seed shadows. Alternatively, numerically
intensive modeling techniques can be employed where adult tree populations are mapped and
seed traps are well distributed with respect to distances to possible seed sources (Clark et al.

CONCLUSION

We found no differences among seed shadows of trees dispersed by different agents
because of high variability among trees within species and among tree species within category of
dispersal agent. Our results suggest that knowledge of a tree’s predominant dispersal agent may
not predict reliably the shape of the seed shadow. However, we recognize that long-term studies
conducted over multiple years are necessary to better understand seed shadow function. Our
understanding of patterns of seed dispersal could be improved by conducting studies over
multiple years and sampling with greater replication both within and among species to produce
better estimates of variability in patterns of seed dispersal.

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Table 1. Estimated crop size and tree sizes for the nine study species (species averages ± standard error, N = 5 for each species). Estimated crop size has been rounded to the nearest thousand seeds. DBH = diameter at breast height. CLGL = *Cleistopholis glauca*, MAEM = *Maesopsis eminii*, STKA = *Staudtia kamerunensis*, UAPA = *Uapaca paludosa*, GASM = *Garcinia smeathmannii*, GABO = *Gambeya boukokoensis*, PTHY = *Pteleopsis hyloendron*, FUEL = *Funtumia elastica*, TESU = *Terminalia superba*.

<table>
<thead>
<tr>
<th>Species</th>
<th>Dispersal Agent</th>
<th>Tree Height (m)</th>
<th>DBH (m)</th>
<th>Crown area (m$^2$)</th>
<th>Estimated seed crop</th>
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</thead>
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<tr>
<td>CLGL</td>
<td>Bird</td>
<td>41.9 ± 3.4</td>
<td>0.79 ± 0.08</td>
<td>188.3 ± 29.2</td>
<td>25,200 ± 2010</td>
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<tr>
<td>MAEM</td>
<td>Bird</td>
<td>50.1 ± 2.9</td>
<td>0.96 ± 0.06</td>
<td>302.3 ± 44.7</td>
<td>48,200 ± 8558</td>
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<td>STKA</td>
<td>Bird</td>
<td>36.0 ± 4.7</td>
<td>0.77 ± 0.14</td>
<td>173.7 ± 54.3</td>
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<td>UAPA</td>
<td>Monkey</td>
<td>33.3 ± 1.8</td>
<td>0.60 ± 0.07</td>
<td>224.0 ± 26.8</td>
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<td>10,000 ± 2665</td>
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<td>Monkey</td>
<td>34.1 ± 2.8</td>
<td>0.78 ± 0.07</td>
<td>162.2 ± 24.2</td>
<td>29,400 ± 6961</td>
</tr>
<tr>
<td>PTHY</td>
<td>Wind</td>
<td>45.7 ± 5.5</td>
<td>0.91 ± 0.05</td>
<td>237.4 ± 35.3</td>
<td>13,780 ± 7850</td>
</tr>
<tr>
<td>FUEL</td>
<td>Wind</td>
<td>33.1 ± 1.1</td>
<td>0.42 ± 0.04</td>
<td>49.5 ± 7.7</td>
<td>72,400 ± 15661</td>
</tr>
<tr>
<td>TESU</td>
<td>Wind</td>
<td>43.1 ± 3.6</td>
<td>1.09 ± 0.22</td>
<td>268.1 ± 132.6</td>
<td>51,200 ± 11465</td>
</tr>
</tbody>
</table>
Table 2. List of species of vertebrates observed eating the fruits of the study tree species. Percent removal is the percent of the total number of fruits consumed during all watches of a tree species eaten by a particular animal species. AGP = African grey parrot, APH = African pied hornbill, BCH = Black-casqued hornbill, BPE = Blue plaintain-eater, CHP = Chimpanzee, CRG = Crowned guenon, CVT = Civit, GAL = Galago, GCM = Grey-cheeked mangabey, MM = Mustached monkey, PPH = Piping hornbill, RFP = Red-fronted parrot, SQR = Squirrel, STR = Starling, WNG = White-nosed guenon, WTH = White-thighed hornbill, YBA = Yellow-billed barbet. Due to time and logistical constraints, we were not able to conduct extended tree observations at wind-dispersed tree species.

<table>
<thead>
<tr>
<th>Tree Species</th>
<th>Hrs. Observations</th>
<th>AGP</th>
<th>APH</th>
<th>BCH</th>
<th>BPE</th>
<th>CHP</th>
<th>CVT</th>
<th>CRG</th>
<th>GAL</th>
<th>GCM</th>
<th>MM</th>
<th>PPH</th>
<th>RFP</th>
<th>STR</th>
<th>SQR</th>
<th>WTH</th>
<th>WNG</th>
<th>YBA</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Cleistopholis glauca</em> (BIRD)</td>
<td>222</td>
<td>1</td>
<td>1</td>
<td>92</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>21</td>
<td>91</td>
<td>2</td>
<td>11</td>
<td>0</td>
<td>54</td>
<td>22</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>% removal</td>
<td>&lt;1</td>
<td>&lt;1</td>
<td>34</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>3</td>
<td>37.2</td>
<td>&lt;1</td>
<td>&lt;1</td>
<td>0</td>
<td>19.2</td>
<td>4.9</td>
<td>0</td>
</tr>
<tr>
<td><em>Maesopsis eminii</em> (BIRD)</td>
<td>338</td>
<td>0</td>
<td>51</td>
<td>213</td>
<td>68</td>
<td>0</td>
<td>5</td>
<td>4</td>
<td>0</td>
<td>2</td>
<td>49</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>671</td>
<td>30</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>% removal</td>
<td>2.1</td>
<td>14.2</td>
<td>8.3</td>
<td>0</td>
<td>0</td>
<td>&lt;1</td>
<td>&lt;1</td>
<td>0</td>
<td>&lt;1</td>
<td>3.2</td>
<td>&lt;1</td>
<td>0</td>
<td>68.1</td>
<td>3</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td><em>Staudtia kamerunensis</em> (BIRD)</td>
<td>182</td>
<td>0</td>
<td>4</td>
<td>69</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>68</td>
<td>0</td>
<td>3</td>
<td>0</td>
<td>117</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>% removal</td>
<td>0</td>
<td>0</td>
<td>20.3</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>&lt;1</td>
<td>23.3</td>
<td>&lt;1</td>
<td>0</td>
<td>54.3</td>
<td>&lt;1</td>
<td>&lt;1</td>
<td></td>
</tr>
<tr>
<td><em>Uapaca paludosa</em> (MON)</td>
<td>202</td>
<td>0</td>
<td>0</td>
<td>15</td>
<td>0</td>
<td>0</td>
<td>23</td>
<td>4</td>
<td>33</td>
<td>59</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>5</td>
<td>0</td>
<td>118</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>% removal</td>
<td>0</td>
<td>0</td>
<td>2.6</td>
<td>0</td>
<td>0</td>
<td>6.5</td>
<td>&lt;1</td>
<td>12.5</td>
<td>25.5</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>&lt;1</td>
<td>0</td>
<td>52.4</td>
<td>0</td>
</tr>
<tr>
<td><em>Garcinia smeathmannii</em> (MON)</td>
<td>130</td>
<td>0</td>
<td>0</td>
<td>26</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>23</td>
<td>0</td>
<td>41</td>
<td>12</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>% removal</td>
<td>0</td>
<td>0</td>
<td>19.4</td>
<td>0</td>
<td>0</td>
<td>15.7</td>
<td>0</td>
<td>52.1</td>
<td>12.8</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Gambeya boukokoensis</em> (MON)</td>
<td>128</td>
<td>0</td>
<td>0</td>
<td>3</td>
<td>0</td>
<td>2</td>
<td>24</td>
<td>0</td>
<td>15</td>
<td>8</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>48</td>
<td>0</td>
<td>55</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>% removal</td>
<td>0</td>
<td>0</td>
<td>6</td>
<td>1</td>
<td>7.1</td>
<td>0</td>
<td>13.1</td>
<td>9.4</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>46</td>
<td>0</td>
<td>27.8</td>
<td>0</td>
</tr>
</tbody>
</table>
Table 3. Three-factor mixed-model ANOVA on the density of seeds (seeds/m$^2$) deposited by each species and vector at each distance. Species is nested within vector, and distance is a repeated measures factor (each tree is observed at each distance). Species is a random factor and all other effects are fixed factors. The Vector effect was tested over the MS \text{Species(Vector)}$, and the Distance and Distance by Vector effects were tested over the MS \text{Distance x Species(Vector)}. Parentheses indicate levels of nesting of trees and species within vector.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>SS</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>BETWEEN SUBJECTS</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vector</td>
<td>184702.55</td>
<td>2</td>
<td>92351.28</td>
<td>0.85</td>
<td>0.488</td>
</tr>
<tr>
<td>Species(Vector)</td>
<td>650119.25</td>
<td>6</td>
<td>108353.21</td>
<td>10.04</td>
<td>0.00001</td>
</tr>
<tr>
<td>Tree x Species(Vector)</td>
<td>388493.72</td>
<td>36</td>
<td>10791.49</td>
<td></td>
<td></td>
</tr>
<tr>
<td>WITHIN SUBJECTS</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Distance</td>
<td>2064490.50</td>
<td>5</td>
<td>412898.10</td>
<td>7.15</td>
<td>0.00001</td>
</tr>
<tr>
<td>Distance x Vector</td>
<td>202165.80</td>
<td>10</td>
<td>20216.58</td>
<td>0.35</td>
<td>0.965</td>
</tr>
<tr>
<td>Distance x Species(Vector)</td>
<td>1731996.50</td>
<td>30</td>
<td>57733.22</td>
<td>7.19</td>
<td>0.00001</td>
</tr>
<tr>
<td>Distance x Tree x Species(Vector)</td>
<td>1446281.63</td>
<td>180</td>
<td>8034.90</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 4. Maximum dispersal distances observed for each tree species. Maximum dispersal distances recorded show no significant correlation with the importance value of the tree species ($r = -0.35$, $t = -0.991$; df = 7; $P = 0.35$).

<table>
<thead>
<tr>
<th>Species</th>
<th>Importance Value</th>
<th>Dispersal Vector</th>
<th>N</th>
<th>Observed maximum dispersal distance (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Cleistopholis glauca</em></td>
<td>0.354</td>
<td>Bird</td>
<td>530</td>
<td>210</td>
</tr>
<tr>
<td><em>Maesopsis eminii</em></td>
<td>0.047</td>
<td>Bird</td>
<td>763</td>
<td>473</td>
</tr>
<tr>
<td><em>Staudtia kamerunensis</em></td>
<td>0.143</td>
<td>Bird</td>
<td>166</td>
<td>300</td>
</tr>
<tr>
<td><em>Uapaca paludosa</em></td>
<td>3.468</td>
<td>Monkey</td>
<td>2527</td>
<td>124</td>
</tr>
<tr>
<td><em>Garcinia smeathmannii</em></td>
<td>0.273</td>
<td>Monkey</td>
<td>41</td>
<td>90</td>
</tr>
<tr>
<td><em>Gambeya boukokoensis</em></td>
<td>0.390</td>
<td>Monkey</td>
<td>47</td>
<td>200</td>
</tr>
<tr>
<td><em>Pteleopsis hylodendron</em></td>
<td>0.472</td>
<td>Wind</td>
<td>1811</td>
<td>101</td>
</tr>
<tr>
<td><em>Funtumia elastica</em></td>
<td>0.391</td>
<td>Wind</td>
<td>518</td>
<td>105</td>
</tr>
<tr>
<td><em>Terminalia superba</em></td>
<td>2.045</td>
<td>Wind</td>
<td>3860</td>
<td>158</td>
</tr>
</tbody>
</table>

*Importance values from M. Fogeil, unpublished data
Table 5. Average proportion of seed crop (± SD) estimated to fall directly under the parent canopy, between 5-60 m from the canopy and greater than 60 m from the canopy edge.

Proportion of seeds falling directly under the parent canopy was estimated as density of seed/m$^2$ recorded in traps x crown area / estimate of crop size. Proportion of crop per distance is estimated by multiplying the average seed rain density at the limit of each annulus by the area.


<table>
<thead>
<tr>
<th>Tree species</th>
<th>Vector</th>
<th>Under Canopy</th>
<th>5-60 M</th>
<th>&gt; 60 M</th>
<th>Estimated absolute number of seeds dispersed beyond 60 m.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Clgl</td>
<td>Bird</td>
<td>0.90 ± 0.06</td>
<td>0.07 ± 0.05</td>
<td>0.03 ± 0.02</td>
<td>751.24 ± 482.84</td>
</tr>
<tr>
<td>Maem</td>
<td>Bird</td>
<td>0.86 ± 0.09</td>
<td>0.11 ± 0.08</td>
<td>0.03 ± 0.02</td>
<td>1358.43 ± 1094.66</td>
</tr>
<tr>
<td>Stka</td>
<td>Bird</td>
<td>0.84 ± 0.13</td>
<td>0.11 ± 0.11</td>
<td>0.05 ± 0.03</td>
<td>1434.41 ± 1106.08</td>
</tr>
<tr>
<td>Uapa</td>
<td>Monkey</td>
<td>0.71 ± 0.26</td>
<td>0.22 ± 0.28</td>
<td>0.08 ± 0.06</td>
<td>5534.66 ± 4893.59</td>
</tr>
<tr>
<td>Gasm</td>
<td>Monkey</td>
<td>0.30 ± 0.28</td>
<td>0.47 ± 0.19</td>
<td>0.23 ± 0.15</td>
<td>1909.85 ± 1024.82</td>
</tr>
<tr>
<td>Gabo</td>
<td>Monkey</td>
<td>0.70 ± 0.13</td>
<td>0.19 ± 0.15</td>
<td>0.12 ± 0.06</td>
<td>3807.01 ± 3487.46</td>
</tr>
<tr>
<td>Pthy</td>
<td>Wind</td>
<td>0.65 ± 0.13</td>
<td>0.33 ± 0.13</td>
<td>0.01 ± 0.01</td>
<td>149.21 ± 128.75</td>
</tr>
<tr>
<td>Fuel</td>
<td>Wind</td>
<td>0.57 ± 0.17</td>
<td>0.41 ± 0.16</td>
<td>0.02 ± 0.01</td>
<td>1413.45 ± 908.47</td>
</tr>
<tr>
<td>Tesu 5</td>
<td>Wind</td>
<td>0.57 ± 0.15</td>
<td>0.41 ± 0.15</td>
<td>0.01 ± 0.00</td>
<td>563.33 ± 207.09</td>
</tr>
</tbody>
</table>

FIGURE CAPTIONS

Figure 1. Illustration of sampling regime. Beneath the canopy, traps representing 5% of the canopy area were placed randomly. Beyond the canopy, traps were arranged in a radial design of 6 transects at 60º intervals using the crown edge as the point of origin. Traps were placed at 5, 10, 20, 40 and 60 m from the crown edge along each transect and sized to sample 1% of the area of an annulus 1 m in width and centered at the target distance. Therefore, the total trap area at each distance was directly proportional to distance from the crown edge. Estimates of the proportion of the total seed crop falling between, for example, 20 and 40 m from each tree were made by multiplying the average density of conspecific seeds in traps on all six radii at 40 m by the area of the annulus between distances (shaded area) and dividing by the estimated crop size.

Figure 2. Mean seed density (± se) at each distance for tree species within each vector.

Figure 3. Mean seed density (± standard error) at each distance interval for each tree species dispersed by (a) birds, (b) monkeys, and (c) wind. Bird-dispersed species: CLGL = Cleistopholis glauca, MAEM = Maesopsis eminii, STKA = Staudtia kamerunensis; Monkey-dispersed species: GABO = Gambeya boukokoensis, UAPA = Uapaca paludosa, GASM = Garcinia smeathmanni; Wind-dispersed species: FUEL = Funtumia elastica, PTHY = Pteleopsis hylodendron, TESU = Terminalia superba. Because Funtumia elastica produces so many more seeds that all other tree species included in this study, the seed density axis for F. elastica differs from all other species.
Fig. 1
Figure 3