

COMPARATIVE SEED SHADOWS OF BIRD-, MONKEY-, AND WIND-DISPERSED TREES

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Abstract. Although spatial patterns of seed distribution are thought to vary greatly among plant species dispersed by different vectors, few studies have directly examined this assumption. We compared patterns of seed rain of nine species of trees disseminated by large birds, monkeys, and wind in a closed canopy forest in Cameroon. We used maximum-likelihood methods to fit seed rain data to four dispersal functions: inverse power, negative exponential, Gaussian, and Student *t*. We then tested for differences in dispersal characteristics (1) among individuals within species, and (2) among species dispersed by the same vector. In general, an inverse power function best described animal-dispersed species and the Gaussian and Student *t* functions best described wind-dispersed species. Animal-dispersed species had longer mean dispersal distances than wind-dispersed species, but lower fecundities. In addition to these distinct differences in average dispersal distance and functional form of the seed shadow between animal- and wind-dispersed species, seed shadows varied markedly within species and vector, with conspecifics and species within vector varying in their dispersal scale, fecundity, and clumping parameters. Dispersal vectors determine a significant amount of variation in seed distribution, but much variation remains to be explained. Finally, we demonstrate that most seeds, regardless of vector, fall directly under the parent canopy. Long-distance dispersal events (>60 m) account for a small proportion of the seed crop but may still be important in terms of the absolute numbers of dispersed seeds and effects on population and community dynamics.

Key words: animal dispersal; Cameroon; dispersal kernel; inverse power; maximum likelihood; seed dispersal; seed rain; seed shadow; tropical trees; wind dispersal.

INTRODUCTION

Empirical and theoretical research suggests that initial spatial distributions of seed dispersal play a crucial role in determining the structure and dynamics of plant populations and communities (see reviews by Nathan and Muller-Landau 2000, Levine and Murrell 2003). By setting the template for subsequent processes such as predation, germination, competition, and growth, patterns of seed dispersal may ultimately shape the spatial pattern of adult plants (Janzen 1970, Connell 1971, Harper 1977, Willson 1992, Venable and Brown 1993, Schupp and Fuentes 1995). At local spatial scales, the density of seed deposited near vs. far from parent canopies affects seed aggregation, and thus, competition and density-dependent mortality (Janzen 1970, Levin et al. 1984, Augspurger and Kitajima 1992, Venable and Brown 1993, Hurtt and Pacala 1995). At larger spatial scales, the proportion of seeds deposited near vs. far from parent canopies affects the genetic structure of populations, the rate of range expansion, and the ability of plants to colonize new habitats and respond to climate change (Clark 1998, Ouborg et al.

1999, Cain et al. 2000, Caswell et al. 2003). Dispersal at both spatial scales contributes to the seed shadow (the spatial distribution of seed around a parent plant).

Despite the recognized importance of the spatial distribution of seeds, our knowledge of the factors that lead to variation in patterns of seed deposition is limited. These factors include density of adult plants, the mode of dispersal, and characteristics of the plant such as height and fecundity. In addition, many plant species have developed seed or fruit traits that may influence the spatial distribution of their dispersed propagules (Willson 1993). These traits include fleshy fruits or fatty arils for dispersal by animals, and wings or plumes for dispersal by wind (van der Pijl 1982). Therefore, dispersal vectors may influence the distribution of seeds deposited both near and far from parent plants (Janzen 1970, Connell 1971, Augspurger 1983, Clark and Clark 1984, Condit et al. 1992, Cain et al. 2000). Examining the seed shadows of plants with different vectors should identify specific differences in the shape and scale of seed dispersal, and thus, provide insights into a process central to plant population and community structure.

Most seed shadow studies use seed traps to estimate the density of seeds that fall within specified distance categories from the parent plant. Seed shadow shapes

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are then estimated by relating seed density to distance from the seed source using a variety of statistical models (Harper 1977, Okubo and Levin 1989, Willson 1993, Lamen 1996, Clark et al. 1999). Generally, these statistical distributions estimate either local or long-distance dispersal well, but rarely both simultaneously (Clark et al. 1999). Thus, models applied to understand seed dispersal dynamics at small spatial scales often apply the Gaussian distribution because this shape describes the influence of the overhanging canopy, where most seeds fall (Clark et al. 1998). Models applied to understand seed dispersal dynamics at large spatial scales generally employ statistical distributions characterized by a unimodal, leptokurtic distribution with a peak at or close to the source, followed by a rapid decline and a long, relatively "fat" tail (e.g., inverse power functions). More recent studies have proposed distributions that describe seed distributions at both small and large spatial scales, such as the two-dimensional Student t (2Dt; Clark et al. 1999).

Despite the importance of understanding variation in seed dispersion patterns resulting from differences in plant and disperser characteristics, field studies designed to examine seed shadows have been relatively rare (Hoppes 1988, Kitajima and Augspurger 1989, Laman 1996, Clark et al. 1999). Studies designed as direct comparisons of seed shadows among trees with different dispersal mechanisms are rarer still. Comparisons among plant species and dispersal vectors have relied on syntheses of the literature, which either meta-analyze results about which curves fit best for a particular vector (Willson 1993), or fit data collected from different systems at different time periods to statistical models (Clark et al. 1999). However, vast differences in the sampling techniques employed among studies make comparisons among sites, plant species, and dispersal agents problematic (Willson 1993).

Here we explored the factors that influence the spatial patterns of seed distribution by directly comparing seed shadows of tree species dispersed by different vectors at the same study site, during the same study year. Our objectives were fourfold. First, using field data collected in a closed canopy tropical forest, we compared seed shadow shapes and parameter estimates of dispersal distance, fecundity, and clumping among species dispersed by birds, monkeys, and wind. Second, we examined whether characteristics of individual trees (height, crop size, and crown area) were related to seed shadow parameter estimates. Third, because seed mortality is often disproportionately high under the canopy (Janzen 1970, Connell 1971, Augspurger 1983, Howe et al. 1985, Condit et al. 1992), one measure of the relative effectiveness of vectors is the proportion of the entire seed crop that is dispersed away from the canopy. Therefore, we examined the proportion of seed crops dispersed under, up to, and farther than 60 m from the canopy by birds, monkeys, and wind. Finally, we used an approximation of long-dis-

tance dispersal to compare the relative contribution of each of the vectors to dispersal beyond 60 m of the canopy edge.

METHODS

Our study took place from January 1998 to May 1999 at the Bouamir Research Station (BRS) in the Dja Reserve, Cameroon. A detailed description of the study site can be found in previous studies (Poulsen et al. 2001, 2002, Clark et al. 2004).

Tree species selection

Within each category of dispersal agent (bird, monkey, and wind), tree species were randomly selected from a list of all possible species for that category. The list of species and their predominant seed disperser was produced from observations made by researchers at BRS from 1994 to 1997 and by local Baka guides (Poulsen et al. 2002). Observations of animals feeding on each tree species support our classification of species by vector (Appendix A). 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 to decrease the effect of overlapping seed shadows. We do not believe that this constraint limits the results of our analyses to nontypical (i.e., abnormally isolated) individuals of the focal species because tree densities of each species were low (Table 1), and locating individuals that met these criteria was not difficult.

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, Letouzey 1970).

Estimation of crop size

We estimated fruit production (standing crop size) of all focal trees by counting the number of fruits on all completely visible branches with a telescope, averaging the number of fruits per branch, and multiplying that number by the total number of branches. This method is widely used to estimate crop size for 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 hundred fruits. We checked fruit production estimates against extrapolations from the number of husks (*S. kamerunensis*) or bracts (other species) that

TABLE 1. Adult tree density and short- and long-distance seed dispersal.

Tree species	Vector	Density (no. trees/ha) [†]	Proportion of seed crop			No. seeds dispersed >60 m	Maximum dispersal distance	
			Under canopy	5–60 m	>60 m		m	No. seeds
<i>M. eminii</i>	bird	0.13	0.86 ± 0.09	0.11 ± 0.08	0.03 ± 0.02	1358 ± 1095	473	763
<i>C. glauca</i>	bird	0.73	0.90 ± 0.06	0.07 ± 0.05	0.03 ± 0.02	751 ± 483	210	530
<i>S. kamerunensis</i>	bird	1.0	0.84 ± 0.13	0.11 ± 0.11	0.05 ± 0.03	1434 ± 1106	300	166
<i>P. hylo dendron</i>	wind	1.06	0.65 ± 0.13	0.33 ± 0.13	0.01 ± 0.01	149 ± 129	101	1811
<i>T. superba</i>	wind	0.93	0.57 ± 0.15	0.41 ± 0.15	0.01 ± 0.00	563 ± 207	158	3860
<i>F. elastica</i>	wind	1.13	0.57 ± 0.17	0.41 ± 0.16	0.02 ± 0.01	1413 ± 908	105	518
<i>G. smeathmannii</i>	monkey	0.86	0.30 ± 0.28	0.47 ± 0.19	0.23 ± 0.15	1910 ± 1025	90	41
<i>U. paludosa</i>	monkey	2.1	0.71 ± 0.26	0.22 ± 0.28	0.08 ± 0.06	5535 ± 4894	124	2527
<i>G. boukokoensis</i>	monkey	0.33	0.70 ± 0.13	0.19 ± 0.15	0.12 ± 0.06	3807 ± 3487	200	47

Notes: The middle columns of the table report the proportion of seed crop (mean ± SD) estimated to fall directly under the parent canopy, between 5 m and 60 m from the canopy, and >60 m from the canopy edge. The proportion of seeds falling directly under the parent canopy was estimated as no. seeds/m² recorded in traps × crown area/estimate of crop size. The proportion of crop per distance is estimated by multiplying the average seed rain density at the limit of each annulus by the area. See Table 3 for full species names.

[†] Density calculated from 15 randomly established 100 × 100 m² plots (C. J. Clark and J. R. Poulsen, unpublished data).

fell into seed traps under canopies. For the five trees of each species, we estimated the density of bracts in traps and multiplied the density by the area of the canopy. Most (41 of 45) visual estimates of fruit production 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 crown were placed randomly under the canopy of each focal tree. Traps placed under canopies were constructed of plastic mesh stapled to rattan frames and ranged in size (0.25–1.25 m²) and number (2–22 traps) to reflect differences in the canopy area of individual trees. 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 all the fruits had been removed from the tree.

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 radially at 60° intervals originating from the base of each tree. 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. We limited seed traps to 60 m from the parent canopy both because of logistical constraints and because, in the case of tropical trees, previous studies demonstrate that most seeds are deposited within 60 m of the parent

(Howe et al. 1985, Laman 1996, Clark et al. 1999). Thus, this trap design focuses on close and intermediate scales of dispersal, but does not quantify long-distance dispersal. The contents of seed traps were collected at 10-d intervals for the duration of the fruiting cycle for each tree. All conspecific seeds, fruits, and fruit or seed pieces were collected and identified. Fecal clumps defecated into traps were also collected so that their seed contents could be counted.

Modeling the seed shadow

To compare patterns of dispersal among species and vectors, we compared the fit of four different curves (dispersal functions) to the field data (grouped by individual trees and species) and estimated parameters that characterize the seed shadow including fecundity, dispersal distance, and shape. The seed shadow is a two-dimensional probability distribution of seeds that describes the number of seeds dispersed over an area. Most functions to describe the seed shadow are one-dimensional dispersal kernels $k(x)$ that describe the probability that a seed will land a particular distance from its parent (e.g., negative exponential, inverse power law, and Gaussian functions). To find the best functional form of the seed shadow, we compared the fit of seed trap data to four candidate dispersal kernels: negative exponential [$k(x) = (1/a)\exp(-x/a)$], inverse power law [$k(x) = 0$ if $x > c_2$, Cc_1^{-a} if $x < c_1$, Cx^{-a} otherwise, with $C = (1 - a)/c_2^{1-a} - ac_1^{1-a}$], Gaussian [$k(x) = \{2/(a\sqrt{2\pi})\}\exp(-x^2/[2a^2])$], and the Student t [$k(x) = (2/a)\{\Gamma([b + 1]/2)/[\sqrt{b\pi}\Gamma(b/2)]\}(1 + [x/a]^2/b)^{-(b+1)/2}$]. Here, $k(x)$ is the density of seeds as a function of distance x from the source, and a and b are fitted parameters for dispersal scale and seed shadow shape. In each case, we used the one-dimensional, positive form of the distribution so that the probability of a seed traveling any positive distance integrates to 1. Distributions that are usually defined over the entire real line (Gaussian and Student t) therefore include an extra fac-

tor of 2, and we used the usual one-dimensional form of the Student t rather than Clark et al.'s (1999) two-dimensional form. In order to normalize the inverse power distribution (which, despite its frequent use to model seed shadows (Willson 1993, Laman 1996) cannot be used as a probability distribution because its integral diverges), we bounded it at distances of $c_1 = 0.001$ and $c_2 = 100$ m, specifying that seed dispersal was constant for distances closer than c_1 and zero for distances beyond c_2 . Increasing the upper cutoff parameter c_2 had a negligible effect on dispersal scale estimates, but tended to exaggerate fecundities. Using 100 m as the upper cutoff provided fitted fecundities that usually fell within the 95% confidence intervals of our crop size estimates from the field.

Given a dispersal kernel $k(x)$, $k(x) dA$ is the expected proportion of the total seedfall in an area dA at distance x from the parent tree. Dispersal scale a describes the steepness of the seed shadow curve, determining how fast seed density falls off with distance from the source: larger a values imply longer dispersal. (For the inverse power function, a represents a scaling exponent rather than a characteristic length scale as in the exponential, Gaussian, and Student t functions; in this case mean dispersal distance decreases with increasing a). The shape parameter b describes the shoulder of the curve for the Student t distribution. If a tree's total fecundity is f , we find the expected number of seeds in a trap at distance x by multiplying the dispersal kernel by the fecundity and the trap area and then dividing by the area of the annulus $2\pi x$: $N = f \cdot k(x, a, b) \cdot A / (2\pi x)$. (Under-canopy traps were set to a distance of 1 m.) We assumed that observed seed numbers were negative binomially distributed with mean N and dispersion parameter k (we also fitted models with Poisson error; the negative binomial distribution fit better in all cases). Low values of $k < 1$ correspond to high variances in observed values around the expected values (overdispersion) and high values ($k \gg 1$) tend to a Poisson distribution.

We calibrated parameters for these dispersal functions by searching numerically for the combination of parameter values that maximize the likelihood function, using the default Nelder-Mead simplex algorithm in R. Confidence intervals were calculated for each parameter by numerical approximation of the Hessian, the matrix of second partial derivatives of the log-likelihood function with respect to the parameters at the maximum-likelihood estimate. The inverse of the Hessian, also called the observed information, is an estimate of the asymptotic variance-covariance matrix, from which variances were obtained to calculate $\sim 95\%$ confidence intervals for all parameters (Wasserman 2004).

Fixed-effects model for seed shadows

We constructed a fixed-effects model to determine whether parameter values (a , f , b , and k) differ signif-

icantly (1) among individuals within species, and (2) among species within vector. We first found maximum-likelihood estimates for the no-effects model, in which the dispersal kernel was fit to all the data for a particular species or vector (i.e., assuming that all trees within a species or all species with a particular vector have identical dispersal parameters). To test whether parameter values differed significantly among individuals, we fitted a dispersal kernel to the data, allowing a parameter or combination of parameters to be estimated for each individual, while keeping all other parameters constant. We then used a likelihood-ratio test to compare the no-effects model with the individual-effects model to determine whether accounting for inter-individual differences in parameters produced a better fit to the data, taking into account the increased complexity of the individual-effects model (i.e., species within vector differ significantly in dispersal distance; Hilborn and Mangel 1997). This process was repeated for each parameter and combination of parameters and for two levels of analysis: trees within species and species within vector. Some readers may note that the design of the study suggests random-effects models for both trees within species and species within vectors, i.e., the magnitude of variation among trees and among species is of interest rather than the particular values of dispersal parameters for each unit. However, when we fitted random-effects models, we found that because of small sample sizes (five trees per species and three species per vector), the model always converged on a solution that ascribed all variation to per-seed variation (i.e., more overdispersion/a smaller value of the negative binomial k) and none to differences among units. Our models successfully fit random among-unit variation for simulated data with larger numbers of units, so we concluded that we simply had too little data to estimate random-effects models in this case: we were essentially trying to estimate variances from at most five independent samples. (A Bayesian hierarchical model [Clark et al. 1999] would provide a technical solution to this estimation problem, but we would still harbor concerns about the appropriateness of estimating random effects with such sparse information.)

For each dispersal kernel and level of analysis (species and vector), we used a likelihood-ratio test to compare among the nested models. Having determined the best model for a dispersal kernel, we used the Akaike Information Criterion (AIC) to arbitrate among competing dispersal kernels. Like the likelihood-ratio test, the AIC (defined as twice the negative log-likelihood plus 2 times the number of parameters) weighs improvements in fit (likelihood) against increased model complexity (Hilborn and Mangel 1997). Unlike the likelihood-ratio test, the AIC does not provide a simple frequentist measure of statistical significance; models with lower AIC scores fit the data better, and a rule of thumb is that models within four AIC units of the best

model are considered plausible explanations for the data (Burnham and Anderson 1998).

We used multiple linear regression to determine whether tree characteristics explain variation in parameter estimates for mean dispersal distance, fecundity, and clumping. After examining plots of residuals, we used a logarithmic transformation on fecundity and crop size to satisfy the assumptions of normality and homoscedasticity. We then regressed height, crop size, and crown area against our estimates of average dispersal distance, fecundity, and clumping for each tree. All modeling and statistical procedures were performed using the R language (R Development Core Team 2004).

Effectiveness of dispersers

The models of seed shadow introduced above (*Modeling the seed shadow*) describe the distribution of seeds dispersed up to 60 m from the tree. In order to quantify the relative contribution of different vectors to dispersal at longer distances, we calculated the proportion of the entire seed crop falling below the canopy within 60 m of the parent, and beyond 60 m. Following Laman (1996), we calculated the proportion of the seed crop falling under the canopy by multiplying the mean density of conspecific seeds captured in traps by crown area and dividing by the crop size. The proportion of the seed crop recorded between the canopy edge and 60 m 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. We assumed that the proportion of the estimated seed crop not accounted for within 60 m of the parent canopy dispersed at distances >60 m. This assumption likely overestimates long-distance dispersal, because some seeds accounted for in crop size estimates were probably preyed upon before dispersal and 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 used supplementary seed trap data from a concurrent study to estimate long-distance dispersal (Clark et al. 2001, 2004). For each seed recorded in these traps, we measured the straight-line distance from the trap to the nearest fruiting conspecific. We identified the nearest fruiting conspecific by circling outward from the point of seed collection in a spiraling fashion until the nearest potential fruit source was discovered. Because we assumed that seeds originated from the nearest seed source, our estimates of dispersal >60 m are conservative.

RESULTS

Fitting dispersal functions to the data

At the species level, animal-dispersed species were generally best described by the inverse power and neg-

ative exponential functions, and wind-dispersed species were best described by the Gaussian, with the negative exponential and Student *t* function providing a plausible fit for all three species (Fig. 1, Table 2, Appendix B). When tree species were grouped by vector, the inverse power best described animal-dispersed species, while the Student *t* fit wind-dispersed species (with the Gaussian fitting almost exactly as well; Fig. 2, Table 2, Appendix C). Fits of models appear to be largely driven by the high densities of seeds near the source (the negative power parameter $a = -0.259$ for *T. superba*, which led to observed seed density falling off approximately as $r^{3/4}$, seemed to be determined by the under-canopy trap data; it could be made positive by dropping the under-canopy data or fitting it separately). The Gaussian and Student *t* functions described the convexity of wind-dispersed species at the source well, but described the highly leptokurtic distributions of animal-dispersed species less well. For wind-dispersed species, the Gaussian and Student *t* estimated similar dispersal distances, whereas the negative exponential underestimated dispersal distance for animal-dispersed species because its tail drops off more steeply than the inverse power function.

There were significant individual effects for six of nine species (Table 2, Appendix B), indicating high variation in dispersal scale, fecundity, or clumping among the seed shadows of conspecifics (Table 2). Taking the average of parameter estimates for dispersal, fecundity, and contagion across all best-fitting models for individuals within a species, seeds of monkey-dispersed species ($\bar{x} = 42.43$ m, SE = 4.17) were dispersed farther than bird-dispersed ($\bar{x} = 35.85$, SE = 9.96), or wind-dispersed ($\bar{x} = 32.97$ m, SE = 20.74) species. The bird- and monkey-dispersed species had similar standard deviations of dispersal (28.10 to 30.02 m, calculated from the best-fit estimated dispersal kernel), higher than wind-dispersed standard deviations (11.45 to 27.51 m); standard deviations of dispersal are correlated with leptokurtosis. Wind-dispersed species had the highest average fecundity ($\bar{x} = 251\,126$ seeds, SE = 199\,939), followed by monkey- ($\bar{x} = 44\,102$ seeds, SE = 31\,156) and bird-dispersed species ($\bar{x} = 37\,302$ seeds, SE = 24\,059). There was not a large difference in clumping of seeds (negative binomial *k* parameter) among species dispersed by different vectors (bird-dispersed, $\bar{x} = 2.23$, SE = 0.64; monkey-dispersed, $\bar{x} = 1.48$, SE = 0.58; wind-dispersed, $\bar{x} = 1.45$, SE = 0.46).

There was significant variation in the dispersal parameters of different species dispersed by the same vector (Table 2, Appendix C). Bird- and wind-dispersed species differed in both their dispersal scale *a* and fecundity *f*, indicating high variation in the distance and number of seeds dispersed. For monkey-dispersed species, there were significant differences in fecundity estimates. Consistent with the individual-level analysis, species dispersed by monkeys and birds had greater average dispersal distances than wind-dispersed spe-

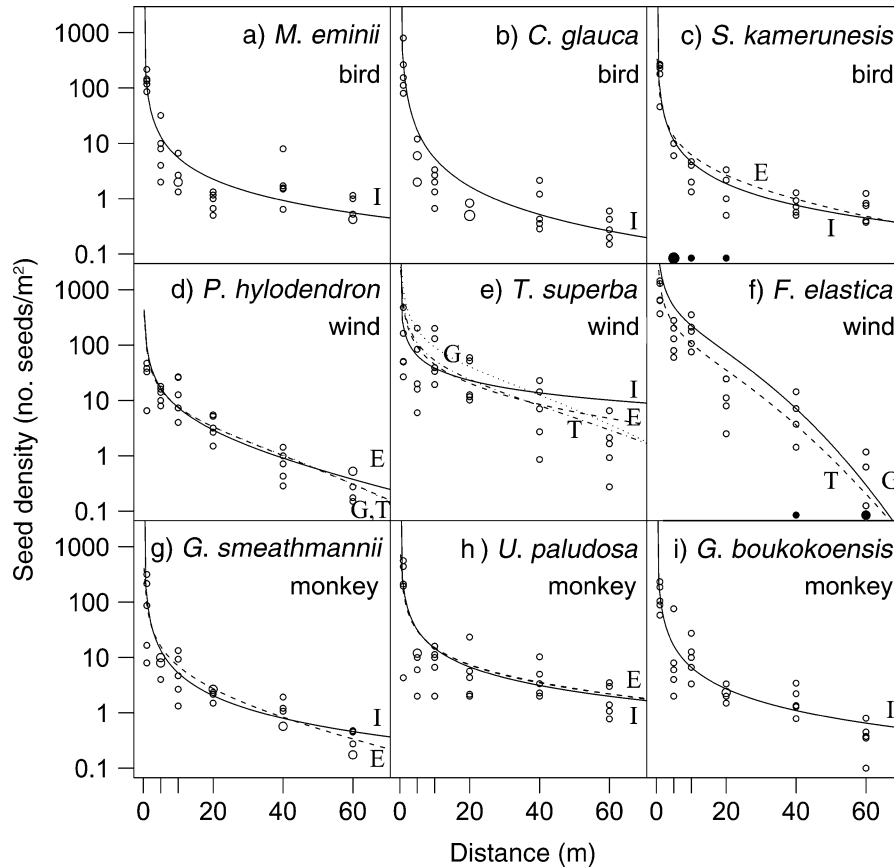


FIG. 1. Best-fitting dispersal function for each species: I, inverse power; G, Gaussian; E, negative exponential; T, Student *t*. Open circles show seed densities in traps (on a logarithmic scale) in relation to distance from tree, with circle areas proportional to the number of co-occurring points; black circles at the bottom of subplots show traps with zero density. Dispersal functions are depicted for bird-vectored species (a–c), for wind-vectored species (d–f), and for monkey-vectored species (g–i). See Table 3 for full species names.

cies. However, the differences in mean dispersal distances were small, with monkey-dispersed species being dispersed only 4.5 m farther than wind-dispersed species on average. (The high standard deviation of dispersal estimated for wind-dispersed species is probably driven by the variation among species.) Wind-dispersed species had higher fecundities than animal-dispersed species, and clumping was similar across vectors (Table 2).

Influence of tree characteristics on seed shadows

Fruit production, height, crown area, and dbh of trees ranged widely, both within and among species and among seed-dispersal agents (Table 3). Fecundity was poorly explained by tree characteristics ($F_{2,42} = 1.406$, $P = 0.256$, $R^2 = 0.063$). Because both average dispersal distance and clumping of seeds may be influenced by tree characteristics and dispersal vector, we included vector in the regression model. None of the variables contributed significantly to variation in clumping ($F_{4,40} = 1.11$, $P = 0.365$, $R^2 = 0.01$), nor average dispersal distance ($F_{2,40} = 0.606$, $P = 0.661$, $R^2 = 0.06$).

Deposition patterns of the seed crop

For all but one species (*G. smeathmannii*), >55% of the seed crop fell to the ground below the parent canopy. Higher percentages of the seed crop fell directly under bird-dispersed species than under monkey- or wind-dispersed species (Table 1). The proportion of the seed crop deposited beyond the parent canopy, but within 60 m of the parent crown, varied among species and vectors. At the vector level, higher proportions of wind-dispersed seeds ($\bar{x} = 38.48$, $SD = 14.25\%$) arrived in this area compared to monkey- ($\bar{x} = 29.23$, $SD = 23.94\%$) and bird-dispersed species ($\bar{x} = 9.9$, $SD = 8.1\%$). More than 85% of all seeds for all species (with the exception of *G. smeathmannii*, $\bar{x} = 39.11$, $SD = 24.26\%$) were deposited within 20 m of the parent tree. A larger proportion of the seed crops of monkey-dispersed species were dispersed beyond 60 m than for other dispersal agents (Table 1). The estimated proportion of seeds dispersed >60 m differed significantly among vectors (one-way ANOVA, $F_{2,6} = 5.362$, $P = 0.046$).

TABLE 2. Best-fit dispersal functions and estimated parameters.

Level	Dispersal function	Model	<4 AIC	Mean dispersal distance (m)
Species				
<i>M. eminii</i> (B)	inv	<i>k</i>		41.87
<i>C. glauca</i> (B)	inv	<i>a</i>		24.35
<i>S. kamerunensis</i> (B)	inv	<i>k</i>	NE <i>k</i>	41.32
<i>P. hylo dendron</i> (W)	Gaus	No	NE No	28.03
			<i>t</i> No	
<i>T. superba</i> (W)	inv	<i>af</i>	NE <i>f</i>	55.73
			Gaus <i>f</i>	
			<i>t f</i>	
<i>F. elastica</i> (W)	Gaus	<i>a</i>	<i>t a</i>	15.15
<i>G. smeathmannii</i> (M)	inv	No	NE No	38.96
			Gaus No	
<i>U. paludosa</i> (M)	inv	No	NE No	47.06
			Gaus No	
<i>G. boukokoensis</i> (M)	inv	<i>k</i>		41.27
Vector				
Bird	inv	<i>af</i>		39.40
Wind	<i>t</i>	<i>af</i>	Gaus <i>fk</i>	38.27
			NE <i>a</i>	
Monkey	inv	<i>f</i>	NE <i>f</i>	42.83
			Gaus <i>f</i>	

Notes: Mean dispersal distance and parameter values (mean with 95% confidence limits) of the best-fitting functions for species and vector. Models within four AIC values of the best-fitting model are also presented. Species are labeled as bird-dispersed (B), wind-dispersed (W), and monkey-dispersed (M). Dispersal function abbreviations are: inverse power (inv), negative exponential (NE), Gaussian (Gaus), and Student *t* (*t*). The model indicates the fixed-effect parameters for the best-fitting dispersal function: "No" means no-effect (identical parameters for all individuals). Student *t* shape parameter (*b*) for wind-dispersed seeds = 2.146 (95% CL = 0.003, 4.288). See Table 3 for full species names; see *Methods; Modeling the seed shadow* for definitions of models.

Dispersal beyond 60 m from the canopy edge

Maximum dispersal distances observed outside of the seed trap design ranged from 90 m to 473 m. The longest dispersal distances were recorded for bird-dispersed species (Table 1). Monkeys dispersed seeds up to 200 m. The maximum distance for wind-dispersed species was 158 m. To verify that our estimates of dispersal beyond 60 m do not simply reflect the density of trees in the forest, we correlated maximum dispersal distance against the density of each species. The dispersal distance and density of species were not significantly correlated ($t = -0.991$; $df = 7$; $P = 0.354$, $R = -0.35$; Table 1).

DISCUSSION

Seed shadows of animal-dispersed tree species differed from wind-dispersed species in several ways. First, they had different functional forms. Animal-dispersed species were better described by the inverse power function, whereas wind-dispersed species were better described by the Gaussian and Student *t* functions. Second, animal-dispersed species had lower fecundities than wind-dispersed species. Third, bird- and monkey-dispersed species exhibited greater mean dispersal distances than wind-dispersed species (although this difference was slight when examined at the vector level). However, fitting dispersal functions to trees of the same species and to species of the same vector demonstrated marked variability in seed shadows.

Thus, although we have identified dispersal vector as one of the determinants of the spatial distribution of seeds, many of the factors that contribute to the variation in patterns of seed dispersion are yet to be quantified. Finally, examination of the proportions of the seed crop dispersed near and far from the parent tree demonstrated that most seeds, regardless of vector, fell directly under the parent canopy or within 60 m of the parent. Long-distance dispersal events (>60 m) account for a relatively small proportion of the seed crop.

The different shapes of seed shadows

Our comparison of seed shadows of wind- vs. animal-dispersed species supports the conclusion that vertebrate dispersal may produce seed shadows with shapes different from those produced by wind (Willson 1993, Laman 1996). The Student *t* function, which has performed better than other dispersal functions in previous studies (Clark et al. 1999), and Gaussian distributions best described wind-dispersed species but not animal-dispersed species in our contest of functions. Seed shadows of wind-dispersed species appeared to be more convex at the source, whereas seed shadows for animal-dispersed species were highly leptokurtic. These results, when coupled with the high fecundity values of wind-dispersed species, as compared to animal-dispersed species, provide indirect evidence of a trade-off among dispersal syndromes. Though a large number of wind-dispersed seeds escaped the parent

TABLE 2. Extended.

Distance parameter a	SD dist	Fecundity f (no. seeds/m ²)	Clumping parameter k
0.279 (0.099, 0.460)	29.91	25 120 (17 314, 32 927)	2.73 (0.467, 15.79)
0.686 (0.432, 0.941)	28.10	21 771 (13 908, 29 633)	2.45 (1.31, 4.57)
0.296 (0.053, 0.538)	29.94	65 017 (33 376, 96 658)	1.50 (0.29, 7.81)
35.125 (25.905, 44.344)	21.174	21 823 (15 547, 28 098)	1.85 (1.12, 3.05)
-0.259 (-0.529, 0.011)	27.51	342 520 (85 912, 599 129)	1.54 (0.92, 2.59)
18.998 (13.636, 24.360)	11.45	389 036 (227 792, 550 280)	0.95 (0.54, 1.67)
0.362 (0.176, 0.549)	30.02	22 500 (15 941, 29 058)	2.12 (1.26, 3.59)
0.111 (-0.121, 0.343)	29.37	79 818 (45 142, 114 495)	0.99 (0.60, 1.68)
0.297 (0.154, 0.438)	29.94	29 989 (21 247, 38 732)	1.34 (1.17, 1.55)
0.35 (0.165, 0.539)	30.01	75 032 (34 151, 115 912)	1.34 (0.96, 1.87)
28.7 (15.6, 41.7)	103.08	122 408 (74 485, 170 331)	1.02 (0.77, 1.36)
0.251 (0.131, 0.370)	29.84	44 438 (30 860, 58 016)	1.61 (1.20, 2.16)

canopies, they did not disperse as far in terms of mean dispersal distance or long-distance dispersal (beyond 60 m of the canopy), and should thus experience fewer colonization opportunities and slower range expansion rates than those of animal-dispersed species. However, the strength of this trade-off may depend on fruit morphology. *Terminalia superba*, which produces winged fruits, was best fit by the inverse power function and had a mean dispersal distance nearly twice as far as *Pteleopsis hylodendron* (samara fruits) and three and a half times as far as *Funtumia elastica* (plumed fruits).

We did not find notable differences between bird- and monkey-dispersed tree species in their mean dispersal distances or the degree of clumping of their seed shadows. Previous studies of bird movement and seed dispersal by birds and monkeys (Holbrook and Smith 2000, Poulsen et al. 2001, Clark et al. 2004) demonstrated that birds dispersed seeds farther and in more contagious patterns than monkeys. We found that birds also disperse seeds to greater maximum distances than monkeys (see *Long-distance dispersal* below). However, because most seeds were deposited directly under parent or conspecific canopies, the mean dispersal distance was driven downward to be slightly less than that of monkeys.

Tree species and vectors demonstrated high variability in their seed shadows (significant fixed effects of a , f , b , and k parameters), indicating that other factors, in addition to dispersal vector, influence seed shadows. Remarkably, examination of tree characteristics (height and crown area) in relation to dispersal distance, fecundity, and clumping failed to explain this variability. We suggest that, in addition to modes of dispersal, seed shadow patterns may also be influenced by forest characteristics surrounding fruiting trees. For

animals, post-feeding patch selection, and the resulting spatial distribution of seeds, could depend on the proximity of a tree to other fruiting trees, nest cavities, sleeping trees, breeding display sites, or forest gaps (Julliot 1997, Kinnaird et al. 1998, Wenny and Levey 1998, Clark et al. 2004). Current research illustrates that patterns of contagious seed dispersal (higher seed densities deposited in areas frequently visited by frugivores) and directed dispersal (preferential dispersal to sites with high recruitment probabilities) are common and complicate conceptual models of seed shadows (Howe and Smallwood 1982, Wenny and Levey 1998, Schupp et al. 2002, Clark et al. 2004, Russo and Augspurger 2004). Great strides have been made in the development of mechanistic models to predict seedfall patterns for wind-dispersed species (Nathan et al. 2001). In theory, similar models can be developed for animal dispersal based on knowledge of animal behavior and characteristics of tree species. Because animal post-feeding behaviors may depend on characteristics of fruiting trees and on the habitat surrounding them, we suggest that mechanistic models for vertebrate seed dispersal should incorporate aspects of forest structure that may influence vertebrate post-feeding movements and, therefore, patterns of seed deposition.

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, seed dispersal processes are likely dispersal limited (Schupp et al. 2002). Disperser activity or the wind velocities necessary to transport most seeds away from the crown constrain the number of dispersed seeds. Greater proportions of seed crops were deposited below canopies of bird-dispersed species than under monkey- and wind-dispersed species. High density of

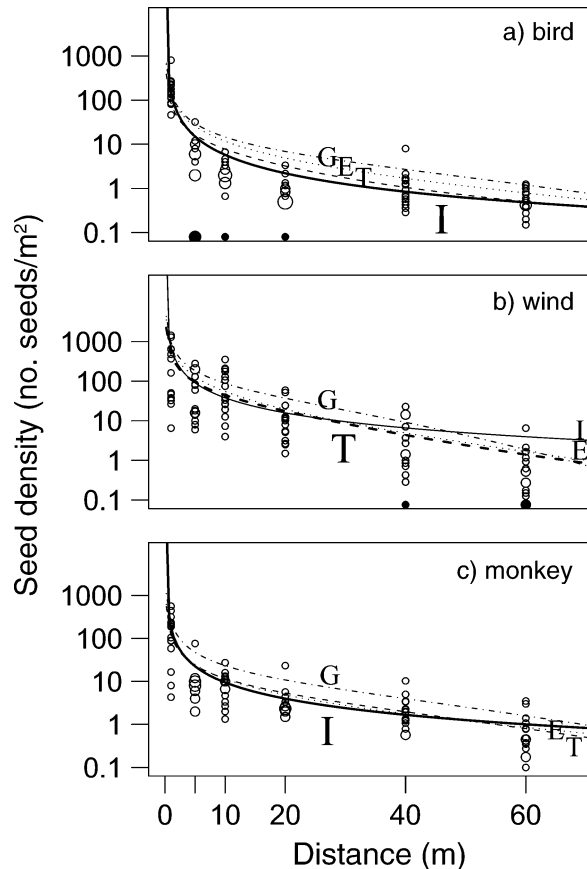


FIG. 2. Fit of dispersal functions for each vector. Data are shown by open circles (nonzero densities) and black circles (zero densities) as in Fig. 1. Thick lines show the best-fitting dispersal functions for each vector; thin lines show alternative fits. Fits are denoted by line type (solid, inverse power; dashed, Student t ; dotted, negative exponential; dot-dashed, Gaussian), and abbreviated (I, T, E, G) as in Fig. 1. The largest letter in each panel indicates the best fit: (a) bird, I; (b) wind, T; (c) monkey, I. Note log scales on y-axes.

seeds deposited under the canopy may influence the fate of 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 (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, Augspurger 1983, Howe et al. 1985). Alternatively, high seed densities near parent crowns could also satiate predators, resulting in greater seedling recruitment near parents than away (Augspurger and Kitajima 1992).

Long-distance dispersal

Much attention has been focused on the role of long-distance dispersal in structuring plant populations and communities (e.g., *Ecology* volume 84(8)). Our seed trap design focused on dispersal to 60 m, an intermediate distance that extends beyond the zone of intense intraspecific competition under the canopy, but does not quantify extremely long-distance dispersal or colonization. Most seeds are moved to intermediate distances, as evidenced by mean dispersal distances between 15 m and 25 m and the low proportion of seed crops moved beyond 60 m. However, because overall seed production is high (10 000–100 000 seeds), even a small percentage of dispersed seeds could translate into a high number of seeds in absolute terms. While we found maximum dispersal distances of 473 m and 100 m for birds and monkeys, these estimates of long-distance dispersal are conservative because they assume the nearest fruiting conspecific to be the source. Calculations of dispersal based on animal movement suggest that hornbills could move seeds as far as 6500 m and monkeys could disperse seeds up to 2000 m (Holbrook and Smith 2000, Poulsen et al. 2001). Both estimates demonstrate the potential for long-distance dispersal to play an important role in population advance and colonization in the tropics. Thus, our finding that a high proportion of seed crops fall directly around parent trees does not negate the potential importance of long-distance dispersal to plant populations. Rather, it underscores the need to develop a framework that examines the relative importance of local and long-distance dispersal in determining plant population structure and community dynamics.

TABLE 3. Characteristics of adult trees included in the study.

Species	Vector	Tree height (m)	dbh (m)	Crown area (m ²)	Estimated seed crop
<i>Maesopsis eminii</i>	bird	50.1 ± 2.9	0.96 ± 0.06	302.3 ± 44.7	48 200 ± 8558
<i>Cleistopholis glauca</i>	bird	41.9 ± 3.4	0.79 ± 0.08	188.3 ± 29.2	25 200 ± 2010
<i>Staudtia kamerunensis</i>	bird	36.0 ± 4.7	0.77 ± 0.14	173.7 ± 54.3	41 600 ± 16 872
<i>Pteleopsis hylodendron</i>	wind	45.7 ± 5.5	0.91 ± 0.05	237.4 ± 35.3	13 800 ± 7850
<i>Terminalia superba</i>	wind	43.1 ± 3.6	1.09 ± 0.22	268.1 ± 132.6	51 200 ± 11 465
<i>Funtumia elastica</i>	wind	33.1 ± 1.1	0.42 ± 0.04	49.5 ± 7.7	72 400 ± 15 661
<i>Garcinia smeathmannii</i>	monkey	22.2 ± 1.0	0.37 ± 0.02	22.0 ± 4.7	10 000 ± 2665
<i>Uapaca paludosa</i>	monkey	33.3 ± 1.8	0.60 ± 0.07	224.0 ± 26.8	70 300 ± 18 719
<i>Gambeya boukokoensis</i>	monkey	34.1 ± 2.8	0.78 ± 0.07	162.2 ± 24.2	29 400 ± 6961

Notes: Values for estimated crop size and tree sizes for the nine study species are mean ± SE ($N = 5$ for each species). Estimated crop size has been rounded to the nearest hundred seeds; dbh = diameter at breast height.

Future research

Quantification of seed shadows using a seed trap design centered on a focal tree has come under criticism because past studies have sampled isolated trees that may not reflect dispersal patterns of the population (Willson 1993). This has led to considerable advances in our ability to model dispersal within forest stands using traps situated randomly or along transects and inverse modeling techniques (Ribbens et al. 1994, Clark et al. 1998, 1999). However, in situations where trees are widely spaced, tree-centered seed trap designs are ideal to answer comparative questions that require replication of trees within a species or vector. The tree-centered approach may also be more tractable than stand-based sampling in the tropics, where many species are rare and adequate sample sizes for inverse modeling are difficult to achieve. Our study has demonstrated considerable variation in the seed shadows of individual trees within species and species within vectors. Future studies are necessary to examine variation in seed shadows in time and space. Do the patterns found here hold up across years? How are seed shadows influenced by phenological patterns, animal abundance, different magnitudes of pre-dispersal depredation and habitat? Finally, a similar approach could be used to link seed shadows with seedling shadows to determine the extent to which seedling emergence and survival mirrors dispersal patterns. In this way, we can begin to tease apart the role of dispersal for recruitment and the multifarious processes that influence forest structure and composition.

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APPENDIX A

A list of vertebrates observed eating fruits of study tree species is available in ESA's Electronic Data Archive: *Ecological Archives* E086-143-A1.

APPENDIX B

A comparison of seed shadow function fits by species is available in ESA's Electronic Data Archive: *Ecological Archives* E086-143-A2.

APPENDIX C

A comparison of seed shadow function fits by vector is available in ESA's Electronic Data Archive: *Ecological Archives* E086-143-A3.