



Community seed rain patterns and a comparison to adult community structure in a West African tropical forest

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Abstract

We examined the seed rain throughout a twelve month period in a lowland tropical forest in Cameroon, West Africa, 1996–97. Traps (0.5 m², n = 216) were erected throughout a 25 km² area in 24 randomly placed clusters of nine traps each. Fruits and seeds that landed in traps were collected every 7–10 days and classified by species and dispersal type. More than 32,000 seeds from approximately 200 species fell into the traps, an average of 297 seeds m⁻² yr⁻¹. Thirty species represent 82% of the total seed rain while an additional 175 species comprise the remaining 18%. When we compared the adult community to the seed rain community within the same plots, we found no apparent correlation between seed rain patterns and adult community structure for this year of study. Furthermore, only 49% of the adult tree community produced and dispersed seed into traps in this year. More than 100 species (52%) found in the seed rain represented long-distance immigrant seed rain. Seed rain was highly variable at several scales, both spatially and seasonally, although seeds arrived in traps during each collection period. Cluster analyses showed that traps within plots were seldom more similar to one another than traps between plots. While 82% of the tree species in the community are thought to be animal dispersed, only 28% of all seeds that fell into traps had been obviously “handled” (bitten, chewed, or passed) by animals. Tests for fruit and seed removal by predators or dispersers found 5% or less removal rate from traps.

Introduction

Seed rain is central to forest structure and regeneration and constrains dynamics by determining the demographic potential of future populations. The importance of seed dispersal has been increasingly recognized as an essential process that underlies forest community structure and dynamics (Clark et al. 1999; Hamilton 1999; Harms et al. 2000). For any site, the seed community reflects the input of seeds of local origin, as well as the movement into a unit area by long distance immigrants (Harper 1977; Martinez-Ramos and Soto-Castro 1993). For any particular plant species, ecologically seed dispersal is critical for both short-term local dynamics, and the immigration of seeds on a longer time or larger spatial scale (Pitelka 1997; Clark et al. 1998).

At the community level, predictions of expected seed dispersal patterns are difficult to accurately assess because individual and species patterns are highly variable in both space and time. Recent literature addresses the importance of the seed life history stage in understanding processes that structure forest composition and dynamics, though the relationship between seed rain and dispersal patterns is difficult to model, particularly in tropical forest systems (Houle 1992; Clark et al. 1999; Nathan and Muller-Landau 2000). In tropical forests, trees exhibit clumped distributions (Hubbell 1979; Howe 1989; Condit et al. 2000) and the high diversity is composed of mostly rare tree species, both characteristics that make it increasingly difficult to make accurate predictions about the seed rain. Adding to the complexity, reproduction often does not occur annually (Foster 1982; Tutin and

Fernandez 1993; van Schaik et al. 1993; Tutin et al. 1997).

While dispersal patterns can be fit to general patterns regardless of the dispersal agent (Willson 1993; Nathan and Muller-Landau 2000), temporally and spatially variable patterns of dispersal and associated seed shadows are observed among dispersal modes (e.g. wind, ballistic, gravity, and animal) and vectors (e.g. ants, birds, bats, primates, rodents and ungulates) (Murray 1988; Izhaki et al. 1991). For example, wind speeds may increase during a particular season, the location and size of treefall gaps may affect dispersal, and seed production itself may be triggered or limited by rainfall, temperature, and variability in the local light environment. In tropical forests, vertebrates disperse a large proportion of tree species and often exhibit large fluxes in seasonal abundance (Terborgh 1990; Gauthier-Hion et al. 1985; Schupp 1993; Compton et al. 1996; Holbrook and Smith 2000). Frugivore numbers change with fluctuations in fruit availability, and their diets change seasonally (Blake et al. 1990; Chapman et al. 1994; Whitney and Smith 1998).

Research addressing community-wide seed rain patterns in tropical forests is rare. Most approaches to understanding tropical seed dispersal and plant species availability have focused on patterns of specific animal dispersers (Estrada et al. (1984) and Byrne and Levey (1993), Kaplan and Moermond (1998) and others), specific plant species (Howe and Smallwood (1982) and Coates-Estrada and Estrada (1986), Alvarez-Buylla and Martinez-Barrios (1990) and others), or spatially distinct sites such as gaps/non-gaps and pastures/nearby forests (Levey (1988) and Denslow and Diaz (1990), Holl (1998) and others). In this study, we focus on the seed rain and dispersal patterns at the community level throughout a closed-canopy forest preserve in Cameroon, West Africa. We describe the seed abundance, dispersal mode, and seasonal patterns of seed rain in an intact and highly species-rich forest over one year. We used a randomly placed array of large seed traps to assess the net input of fruit and seed to the forest floor; at each random site we used a cluster of traps. The adult forest structure and composition was known at each site. Seed rain collected in this way permits us to investigate aspects of dispersal dynamics on both local and forest-wide scales.

Specifically, we were interested in assessing variance in seed shadows that is rarely addressed in descriptions of seed shadow patterns in both mechanis-

tic models and empirical studies of seed shadows. Studies indicate probabilistic patterns associated with individual source trees and seed shadows are often fit to curves (e.g. Willson (1993)). Tropical forests contain a large diversity of dispersal modes and tree species. Here, we examine seed rain at two scales, a local scale (clusters of seed traps within large plots) and a forest scale (among plot similarity). Based on descriptions and models of seed shadows, patterns in species richness within seed traps should parallel the patterns of adult abundance and reflect local dispersal events with most seed arrival falling beneath or near parent plants (Janzen 1970; Connell 1971; Clark et al. 1999; Nathan and Muller-Landau 2000). We were also interested in testing if nearby seed traps sample from overlapping seed shadows or if the high vector diversity and tree species diversity creates spatially dissimilar seed rain composition even at relatively local scales. While seed rain heterogeneity (i.e. spatial and temporal patchiness) is expected, the seed rain is still anticipated to reflect the adult community structure. Different modes of dispersal and variability in fruiting periods of plant species may result in annual, seasonal and local patch patterns of increasing uniqueness such that predictions of dynamics at any one site are difficult to make. We grouped wind dispersed and non-wind dispersed species and tested for differences between their spatial and temporal variability in the seed rain. Our site exhibits strong seasonal patterns of wet and dry seasons, but as fruiting continues through both season types, we predicted an essentially non-modal pattern of peak seed densities and species richness in individual traps for an annual period.

Methods

Study area

This study took place in the Dja Reserve in southern Cameroon (Figure 1). The area was designated an IUCN Biosphere Reserve in 1987. The 25 km² study site is located toward the middle of the 526,000 ha. reserve (central point 3°11'27" N, 12°48'41" E), and is protected from logging and extensive hunting practices (but see Muchaal and Ngandjui (1999)). In this semi-deciduous primary forest, canopy height averages ≥ 35 m, with variable understory and midstory density (Hardesty, unpublished data.). In addition to the dominant forest, wet swamp-like "marecage" areas and rocky inselberg outcroppings with reduced

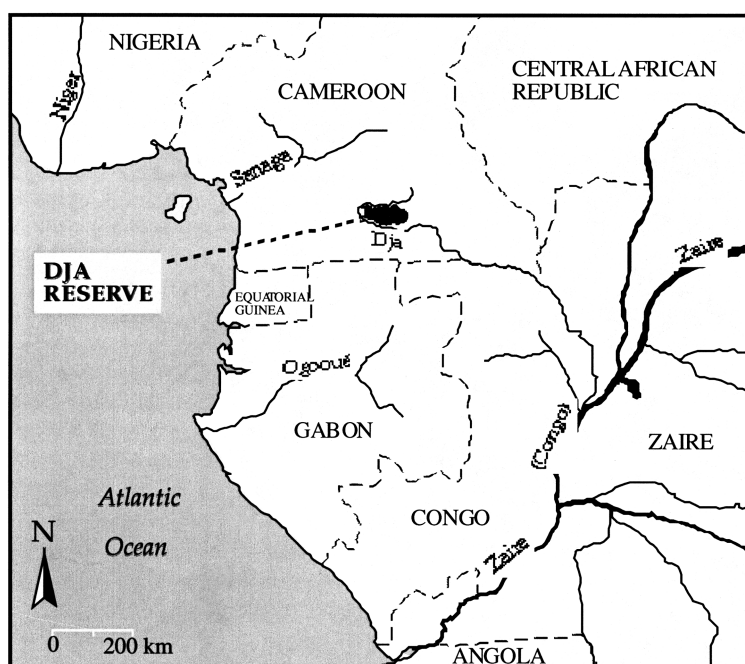


Figure 1. Location of Cameroon and the Dja Reserve in Western Africa.

canopy height (15–25 m) are present, comprising less than 12% of the forest area collectively. Rainfall averages 1600 mm annually (Laclavere 1980). The site is characterized by two wet and two dry seasons; the wet seasons (March–June and September–October) contribute 87% of the annual rainfall (average of 1300 mm from 1994–1998). The wet seasons correspond to sample periods 2–14 and 23–29, respectively. For a detailed description of site, see Whitney et al. (1998).

Estimating seed rain

To estimate seed rain, traps (surface area = 0.5 m² [80.5 cm × 62 cm] each, n = 216) were constructed and placed throughout the study site in 24 clusters of nine traps, each cluster located within randomly-selected permanent 40 m × 40 m plots established in 1994. Plot locations were chosen using a random number generator to select locations from a hypothetical grid laid over the entire study area. Within each of these 1600 m² plots, all adult trees, defined as diameter at breast height (dbh) of 10 cm or greater, were identified and mapped. Traps were constructed of rattan frames with a plastic woven catch area, positioned 70–90 cm above ground. The woven plastic mesh size was less than 0.50 mm, with a catch area

that regularly trapped seeds of ≤ 2 mm diameter (i.e. *Ficus* sp.), though smaller seeds could have been missed. Traps were located within the central 20 × 20 m of each plot, each trap spaced 10 meters apart in a 3 × 3 array.

Seed rain was collected throughout a 12-month period, February 1996–March 1997. The contents of all traps were collected every 7–10 days. Since collecting periods had unequal numbers of days, data were normalized using seeds per m² day⁻¹ for analyses. Fruits and seeds were identified to species when possible, otherwise to genus or family. All data presented refer to seed number, based upon either a count of actual seeds per fruit, or calculated based upon the mean number of seeds per fruit from field estimates. We verified taxa identity using specimens and literature from the National Herbarium in Yaounde, Cameroon. Taxa were categorized as WD (wind or ballistically dispersed) and NWD (non-wind, predominantly vertebrate dispersed), based on fruit and seed characteristics and >5000 hours of field observations over four years (1994–1998). NWD taxa generally produce arils, drupes, berries, or capsules.

Additionally, we determined whether seeds and fruits had been “handled,” (i.e. obvious evidence of being bitten, chewed, regurgitated or passed by animals). Handling by vertebrate dispersers or predators

is evident from marks on ends of seeds or fruits by mandibles of birds, and bite marks from primates or other mammals, or from fecal matter containing seeds which was observed in traps. Conservative decisions were made for this category, and any fruits or seeds where signs of handling were questionable were classified as not handled for all analyses. However, a taxa was classified as handled if any seed that arrived in a trap was observed to have signs of handling.

Fruit and seed loss from traps

To determine if seeds were removed from traps by predators or dispersers, we placed marked seeds and fruits in traps throughout the year. Then, each subsequent 7–10 day sample period, we counted the number of marked items lost from traps. Between one and five mature fruits or seeds were placed in a single trap during a given sample period. Traps used each period were chosen at random, within multiple plots. The number of traps used for each sampling interval was determined by availability of ripe fruits or seeds. Plant species chosen ($n = 25$) generally reflected dietary preferences of frugivores/granivores within the study site.

Statistical analyses

We used cluster analysis to reveal spatial aggregation patterns of seed rain at both the single trap and plot scales. Cluster analyses were run on a matrix of seed traps \times plant taxa using annual totals. All species with five seeds or less were removed from the data matrix, as was the one seed trap that collected no seeds during the study year (215 traps \times 120 taxa). Several similarity indices were used (Sorenson's, Euclidean, and TWINSpan) to test both presence/absence and seed quantity data. Group average and Ward's linkage methods were used for cluster analyses. (Gauch 1982). We report on the Sorenson's similarity index dendrograms that produced the least chaining using Group average and Ward's linkage (PCORD version 3.15, McCune and Mefford (1993)).

Because tree abundance, size, and frequency vary considerably among species in the adult vegetation we used a generalized linear model to examine the contribution of relative importance (IV) of each tree species (the sum of relative frequency, relative basal area, and relative density) to explain abundance in the numbers of seeds of a particular species in the seed rain. Generalized linear models are an extension of

traditional linear models to situations where the response variable follows any member of the exponential family of probability distributions. Because data represent counts of seeds from a series of samples and fit a Poisson distribution, models were built assuming the response variables followed a Poisson distribution, using a log link function and accounting for over-dispersion (McCullagh and Nelder 1989; Agresti 1996; Connor et al. 1997). Generalized linear models were constructed using importance value as the explanatory component and seed rain as the dependent response variable (S-Plus 1997).

Seasonal variability in seed rain density by dispersal mode was tested using analysis of variance (ANOVA) on Box-Cox transformed data. Box-Cox transformation provides a continuous definition to transform the response fit to the model by raising it some power to find a "best" fit (JMP version 3.1). Seasons were based upon observed rainfall patterns averaged over five years (wet season rainfall average exceeds 160 mm per month, while dry season rainfall averages <30 mm monthly). Seed numbers were relativized by number of days per sample period and proportion of periods in each season (wet/dry). We used a nested ANOVA approach with number of seeds by dispersal type nested within season (by rainfall) to compare seasonal differences in WD and NWD seed rain and data reflect mean seasonal differences (JMP 3.1).

Results

Species composition of the seed rain

Seed rain in this forest totaled 297 seeds/m² during the twelve month period (total trap area = 108 m²). Over 180 identified taxa were represented in the 32,054 total seeds analyzed from the traps (93% identified at least to family, 90% of these identified to genus or species). The unidentified 7% of seeds comprise a minimum estimate of 24 additional species, based upon morphological differences. A list of identified taxa with dispersal mode, handling status, and total number found in the seed rain is found in Appendix 1.

Approximately 280 adult (≥ 10 cm dbh) tree species have been identified within the 25 km² study area (M. Fogiel, unpublished data). One hundred eighty four of those tree species were found in the 24 sample plots used for this study. The rank order of these spe-

Table 1. The 30 most important¹ tree species in the adult community, in rank order.

Family	Species	Rel. IV ¹	% plots ²	Disp. Mode
Apocynaceae	<i>Tabernaemontana crassa</i>	6.30	87.50	NWD
Euphorbiaceae	<i>Uapaca acuminata</i>	5.97	66.67	NWD
Irvingiaceae	<i>Irvingia gabonensis</i>	5.09	70.83	NWD
Olacaceae	<i>Strombosiopsis tetranda</i>	3.54	87.50	NWD
Mimosoideae	<i>Pentaclethra macrophylla</i>	3.02	45.83	WD
Apocynaceae	<i>Alstonia boonei</i>	2.78	45.83	NWD
Combretaceae	<i>Terminalia superba</i>	2.51	33.33	WD
Lecythidaceae	<i>Petersianthus macrocarpus</i>	2.19	41.67	NWD
Caesalpinioideae	<i>Anthonothea sp.</i>	2.17	75.00	NWD
Annonaceae	<i>Polyathia suaveolens</i>	2.14	66.67	NWD
Olacaceae	<i>Strombosia pustulata</i>	1.99	54.17	NWD
Rubiaceae	<i>Rubiaceae spp.</i>	1.93	66.67	NWD
Olacaceae	<i>Strombosia grandiflora</i>	1.81	54.17	NWD
Euphorbiaceae	<i>Drypetes sp.</i>	1.65	54.17	NWD
Annonaceae	<i>Enantia chlorantha</i>	1.65	66.67	NWD
Sapindaceae	<i>Eriocoelum macrocarpum</i>	1.61	66.67	NWD
Euphorbiaceae	<i>Antidesma sp.</i>	1.58	66.67	NWD
Sapotaceae	<i>Gambeya sp.</i>	1.43	75.00	NWD
Burseraceae	<i>Santiria trimera</i>	1.35	54.17	NWD
Tiliaceae	<i>Duboscia macrocarpa</i>	1.32	20.83	NWD
Euphorbiaceae	<i>Plagiostylus africanus</i>	1.25	58.33	NWD
Moraceae	<i>Myrianthus arboreus</i>	1.24	50.00	NWD
Tiliaceae	<i>Desplatsia sp.</i>	1.24	50.00	NWD
Caesalpinioideae	<i>Hylodendron gabonense</i>	1.20	20.83	NWD
Faboideae	<i>Pterocarpus soyaxii</i>	1.13	37.50	NWD
Rubiaceae	<i>Naclea diderrichii</i>	1.08	33.33	NWD
Ulmaceae	<i>Celtis mildraedii</i>	0.99	25.00	NWD
Meliaceae	<i>Trichelia rubescens</i>	0.96	45.83	NWD
Mimosoideae	<i>Piptadeniastrum africanum</i>	0.94	8.33	WD
Caesalpinioideae	<i>Dialium sp.</i>	0.91	54.17	NWD
Total		62.9%	$\bar{x} = 52.8\%$	

¹ IV = Importance values are based upon relative density, relative basal area, and relative frequency.

² % plots indicates percent of plots (n = 24) with at least one adult individual of this species.

cies by IV showed a steep negative exponential distribution with a large proportion of rare species. The top-ranking thirty species by IV comprise 63% of the adult forest community (Table 1), while the 20 top ranked families included 130 species and represent 91% of the forest structure (Table 2). For a comparison with the seed rain, the 30 most abundant species comprise 81% of the total seed fall (Table 3), and the 20 most abundant families contained 90% of the seed rain (Table 4).

Overall, poor correspondence was found between the total species composition of the seed rain and the adult forest community. Ninety species were shared between the adult and seed rain communities, and 94

of the 184 adult species (52%) present in the 40 × 40 m sample plots were not represented in the seed rain during the year studied. At least an additional 110 taxa recorded in the seed rain were not found in the adult community (approximately 36% of these are lianas, shrubs, or tree species which may fruit at <10 cm dbh). Results of the Poisson generalized linear model found no relationship between abundance of species in the adult vegetation and the abundance of seeds of that species arriving in seed traps. The model was corrected for over-dispersion and produced a regression coefficient of 0.007 (SE ± 0.015), and a t-value of 0.46 (DF=285, p ≥ 0.65). Abundance in the

Table 2. The 20 most important families¹ in the adult tree community, in rank order.

Family	#species	Rel. IV ¹	% plots ²
Euphorbiaceae	18	12.71	100
Apocynaceae	5	9.65	95.8
Olacaceae	6	8.60	95.8
Annonaceae	15	7.93	100
Irvingiaceae	4	6.41	91.7
Caesalpinoideae	9	5.56	91.7
Mimosoideae	6	5.37	75.0
Rubiaceae	9	4.34	95.8
Meliaceae	12	4.16	100
Tiliaceae	6	3.27	58.3
Sapindaceae	5	3.22	95.8
Combretaceae	2	3.21	45.8
Moraceae	6	3.16	70.8
Burseraceae	3	2.68	83.3
Lecythidaceae	1	2.18	41.7
Sapotaceae	8	2.11	66.7
Violaceae	3	1.94	66.7
Anacardiaceae	4	1.67	58.3
Ulmaceae	2	1.55	45.8
Flacourtiaceae	6	1.54	66.7
Total	130	91.3%	$\bar{x} = 77.3$

¹ Rel. IV is based upon relative density, relative basal area, and relative frequency.

² % plots indicates percent of plots (n = 24) with at least one adult individual in this family.

adult vegetation does not predict presence or relative abundance in the seed rain in this forest.

Dispersal mode and seasonality

Eighty-three percent of the total number of seeds that arrived in traps fell from more than 171 NWD taxa (n = 26,739 seeds). The twenty-nine WD taxa comprise the remaining 17% (n = 5315 seeds) of the total seed rain (Table 3, Appendix 1). The proportion of seeds arriving in traps was equivalent for NWD and WD species in proportion to their respective abundances in the adult community.

Total seed rain varied considerably through time (Figure 2). While the seed arrival in traps varied seasonally, particularly at the individual trap scale, the overall spatial structure of seed rain was fairly consistent. Seeds were found in an average of $38 \pm 11\%$ (SE) of all traps for each census period (range 21–62%).

Seasonal seed abundance was significantly associated with rainfall for total number of seeds (ANOVA, $F = 38.16$, $DF = 3$, $P < 0.0001$) and for the number of taxa present in the seed rain (ANOVA, $F = 38.16$, $DF = 3$, $P < 0.0001$). NWD seed dispersal in seed traps generally declined during 1996, though this trend was non-significant ($P = 0.43$). There overall slight decline in total seed rain during 1996 was consistent with the pattern of fruit availability between 1995–1997 using alternative census methods (Hardesty unpublished data): total fruit production was higher in 1995 and lower in 1997 when assessed using twice monthly raked-trail surveys over the three year period.

Spatial patterns in the seed rain

The number of seeds per trap and the seed rain taxa distribution patterns were widely variable among the study plots. Annual seed rain totals for individual traps ranged from zero to 2156 seeds ($\bar{x} = 148.6 \pm 226.4$). The rank order distribution for traps was strongly negatively exponential, and only 58 of the 216 traps (27%) exceeded the average annual seed total per trap. Summarizing traps within plots and comparing between plots, we found high variability at both scales. For example, two traps within the same plot differed by 2140 seeds ($4280 \text{ seeds m}^{-2} \text{ yr}^{-1}$). Among plots, (9 traps summed), annual seed rain ranged from $87.6 \text{ seeds m}^{-2}$ to $915.6 \text{ seeds m}^{-2}$ ($\bar{x} = 297.2 \pm 205.9 \text{ seeds m}^{-2}$). No trap caught more than 10 taxa ($\bar{x} = 2.65$) during a given sample period (Figure 3).

Seed rain indicated that local processes were influencing dispersal events. Fifty-two taxa (24% of the total) were rarely found in traps ($N \leq 5$ seeds for the year), and an additional 114 taxa arrived in five or fewer different traps during the year. As a result of the large number of rare taxa that landed in traps, cluster analyses generally suggested spatial aggregation is occurring at the individual trap level. We used several different similarity measures, and all yielded essentially similar results (not illustrated). For the cluster analysis using Sorensen's similarity index and group average linkage, only one of the 24 plots placed all nine traps within a single unique cluster (minimum chaining = 9.91). Two additional plots had all nine traps clustered together, though other traps were present in the same cluster. For the remaining 21 plots, traps clustered in two to six different clusters along with traps from other plots. TWINSpan clus-

Table 3. The 30 most numerous species in the seed traps, in rank order.

Family	Species	# seeds	% total	Disp. Mode*
Euphorbiaceae	<i>Uapaca cf. paludosa</i>	4572	14.30	NWD
Dilleniaceae	<i>Tetracera podotricha</i>	2734	8.53	NWD*
Moraceae	<i>Ficus sp. Unk.</i>	2176	6.98	NWD*
Combretaceae	<i>Terminalia superba</i>	2078	6.48	WD
Rubiaceae	<i>Porterandia cladantha</i>	1240	3.87	NWD
Combretaceae	<i>Combretum cf. clemeusei</i>	1235	3.85	WD*
Euphorbiaceae	<i>Macaranga barteri</i>	1164	3.63	NWD
Moraceae	<i>Treculia sp.</i>	1083	3.38	WD
Rubiaceae	<i>Naclea diderichii</i>	1071	3.34	NWD
Mimosoideae	<i>Piptadeniastrum africanum</i>	943	2.94	WD
Euphorbiaceae	<i>Alchornia floribunda</i>	841	2.62	NWD*
Annonaceae	<i>Xylopia hypolampra</i>	811	2.53	NWD
Annonaceae	<i>Pachypodanthium staudtii</i>	775	2.42	NWD
Passifloraceae	<i>Ademia gracilis</i>	622	1.94	NWD*
Violaceae	<i>Rinorea sp.</i>	534	1.67	NWD
Ixocanthaceae	<i>Octhocosmos africanus</i>	477	1.49	NWD*
Euphorbiaceae	<i>Unknown</i>	390	1.22	NWD
Olacaceae	<i>Strombosia pustulata</i>	385	1.20	NWD
Euphorbiaceae	<i>Discoglyprena caloneura</i>	327	1.02	NWD
Olacaceae	<i>Heisteria zimmereri</i>	283	0.88	NWD
Rubiaceae	<i>Cephaelis mannii</i>	275	0.86	NWD*
Erythroxylaceae	<i>Erythroxylum emarginatum</i>	263	0.82	NWD
Rubiaceae	<i>Canthium sp.</i>	242	0.75	NWD
Euphorbiaceae	<i>Antidesma sp.</i>	230	0.72	NWD
Verbenaceae	<i>Vitex ferrugineae</i>	222	0.69	NWD
Rubiaceae	<i>Pausynstalia brachythyrsa</i>	218	0.68	NWD
Tiliaceae	<i>Grewia coreacea</i>	198	0.62	NWD
Sapotaceae	<i>Synsepalum sp.</i>	192	0.60	NWD
Olacaceae	<i>Strombosia grandifolia</i>	191	0.60	NWD
Euphorbiaceae	<i>Macaranga schweinfurtherii</i>	188	0.59	NWD
Total		26,020	81.2%	

* Indicates liana or species in which fruiting may occur at <10 cm dbh.

tering was similar as well. No strong, consistent spatial correlation was found among traps within a plot, as might have been predicted given the short distances between traps in a particular plot.

Animal handling and removal rates

Of the 32,054 seeds that landed in traps, 28% (9003) had been clearly handled by animals (birds, mammals, or insects). The proportion of seeds handled in a given census period, however, varied from 2–78% ($\bar{x} = 33\%$, Figure 3). More than half of the total taxa represented in the seed rain exhibited some handling (110 species from 36 families). However, animal handling was most frequent in those taxa that regularly arrived in traps. In the seed rain, the twenty species

handled most frequently comprised 86% of the total amount of handling (Table 5). Of those frequently handled taxa, handling occurred in 1–29% of the total seed rain crop for a particular taxa. An additional seventeen of 52 taxa rarely found in the seed rain ($N \leq 5$ total seeds) were also handled, which may reflect rare long-distance dispersal events. The *Uapaca* species complex, a widespread, abundant tree that is primarily primate dispersed, comprised 29% of the total seeds handled (Table 5).

Results from the fruit and seed loss experiments indicated that loss due to wind, rain, predation or removal was minimal. Five percent of the 285 experimental items (9 fruits, 4 seeds) were not recovered from the seed traps throughout the five-month experimental period. Loss was restricted to four of the 25

Table 4. The 20 most abundant families in the seed rain, in rank order.

Family	# species	# seeds	% tot. rain
Euphorbiaceae	35+	8221	25.6
Combretaceae	3	3313	10.3
Rubiaceae	20	3296	10.3
Dilleniaceae	2	2740	8.5
Moraceae	6	2302	7.2
Annonaceae	12	1878	5.9
Meliaceae	6	1186	3.7
Olacaceae	6	1063	3.3
Mimosoideae	6	1027	3.2
Passifloraceae	2	703	2.2
Violaceae	1	531	1.7
Ixocanthaceae	1	477	1.5
Sapotaceae	7	433	1.3
Tiliaceae	5	333	1.0
Erythroxylaceae	1	263	0.8
Caesalpinoideae	8	256	0.8
Verbenaceae	2	246	0.8
Sapindaceae	4	205	0.6
Lecythidaceae	1	169	0.5
Apocynaceae	5	150	0.5
Total	133	28,792	89.7%

species placed in traps (*Cleistopholis glauca*, *Maesopsis eminnii*, *Xylopia staudtia*, and *Lannea welwitschii*). Each of these large-fruit species is bird and/or primate dispersed.

Discussion

The seed rain of the equatorial Dja forest was highly variable and diverse, but continuous throughout the year. The seed rain averaged 297 seeds m² yr⁻¹, with a wide range in seedfall for any particular location. The proportion of traps that captured seeds remained constant throughout the year, though considerable spatial and temporal patchiness was found among traps and among plots. More than 200 taxa were represented in the seed rain, which was dominated by a small number of these species producing a large seed crop, with most species represented by few seeds during the year studied. A poor match was found between the resident source of seeds (adults) and the seed rain community, partly because less than half of the adult species in the plots were found in the seed rain as measured using seed traps. The high proportion of seeds from outside the plots also contributed to gen-

erally low similarity among traps within plots. Total seed rain from wind-dispersed versus animal-dispersed tree species matched their relative summed proportions in the adult forest. Additionally, no previous studies have assessed the proportion of seeds in the total seed rain actually handled by animals, which in this study was 38% of the total seed rain (see also Clark et al. (2001)).

For the year investigated, the species composition and dominance within the seed rain community differed substantially from that of forest adults. In our study, the source of this dissimilarity was from the failure of resident species to produce fruit, as well as from substantial long-distance dispersal. These results parallel findings in a number of vegetation types, although there are studies in which high similarity was found between seed rain and vegetation. For example, Jensen (1998) observed high (>90%) similarity between seed rain and adults in a community-level study, with cluster analyses matching by plot. In contrast, Drake (1998) found a lack of congruence between adults and seed rain in a Hawaiian forest. Campbell and Peart (2001) also found 46% of seedlings in plots in a Borneo tropical forest were from species not found locally. Hubbell et al. (1999) report that in a ten year seed rain study, 54 of 260 adult census species (21%) still failed to deposit seeds in any trap.

The failure of seeds to arrive in traps for more than half of the adult species that occurred in the plots suggests that most species or individuals are not reproducing annually. Studies in other tropical forests have indicated that many species reproduce only every other year or every few years (Foster 1982; Tutin and Fernandez 1993; van Schaik et al. 1993; Tutin et al. 1997). On Barro Colorado Island, for example, seed rain arriving in more than 200 traps in a 50 ha. plot over ten years reflected that only 18% of the adult tree species reproduce in a given year (Hubbell et al. 1999). While a number of hypotheses might be suggested to explain patterns for a particular taxa, for our site and year, reproductive failure cannot be explained by anomalous weather patterns, low rainfall or generally low fruit productivity (Hardesty 1999). In fact, fruit production in this year of study was well above average for a seven-year period (1993–1999): we base this upon assessment of phenology studies, raked-trail surveys, and the presence of breeding *Ceratogymna* hornbills (which nest only with adequate fruit production) (unpublished data). The lack of similarity between adults and the seed rain does not re-

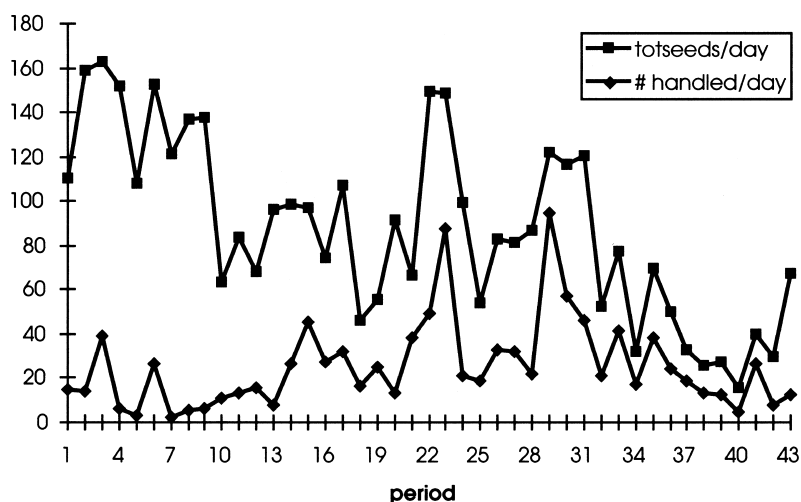


Figure 2. Total number of seeds per day in all traps combined for each sample period, and the total number of those seeds that were handled. Data are combined for all traps in each sample period. Open symbols represent wet season, filled symbols indicate dry season sample periods.

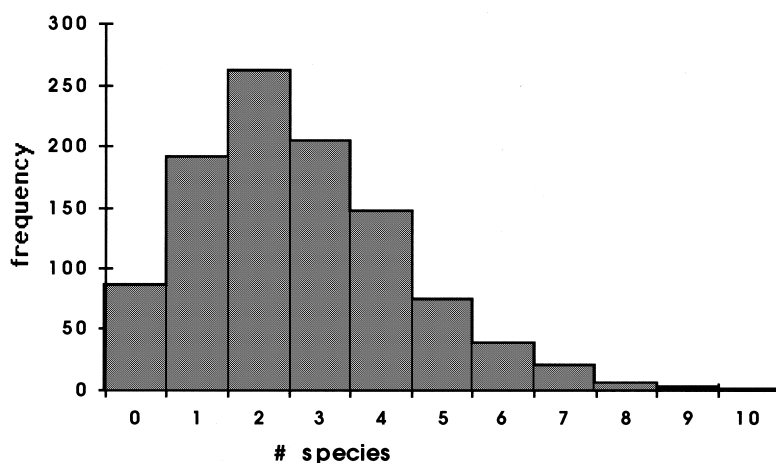


Figure 3. Frequency of seed rain by number of species arriving in seed traps. Data are combined for all plots and periods.

flect a low fruiting year in this forest, but instead reflects the diversity of tropical ecosystems. The large proportion of non-reproductive adults during this study period suggests that perhaps some of these species produce persistent seed or seedling banks (Garwood 1989; Parker et al. 1989). Finally, effective reproduction may occur on a longer temporal scale, with periodic (or mast) fruiting for several of the taxa. However, these patterns have not yet been identified in this forest.

Differences in this forest between adults and seed rain also may be partly explained by lianas and other individuals with a <10 cm dbh that may have fruited and deposited seed into traps. Neither lianas nor small trees (shrubs) were included in the adult forest struc-

ture assessment. While their overall density was relatively small for most plots, differential input from these species might affect our results. When seeds from lianas and small trees (<10 cm dbh) were excluded from analyses, however, a pattern of high immigration was still statistically indicated by the data.

The high proportion of seeds immigrating by long-distance dispersal indicates the relative importance of the tail of seed shadows (Willson 1993; Martinez-Ramos and Soto-Castro 1993; Clark et al. 1999; Nathan and Muller-Landau 2000). Half of the taxa in the seed rain were not found within the study plots, and several others have not been detected within the 25 km² study area. The seed shadows of tropical trees in this forest regularly can exceed the 20-m buffer area

Table 5. Top 20 species handled by animals, from seed rain in all plots throughout study year, in rank order.

family	Genus	# seeds handled	% tot. ¹	Mode*
Euphorbiaceae	<i>Uapaca sp.</i>	2615	29.1	NWD
Moraceae	<i>Ficus sp.</i>	1309	14.5	NWD*
Dilleniaceae	<i>Tetracera podotrichia</i>	927	10.3	NWD*
Euphorbiaceae	<i>Alchornea floribunda</i>	533	5.9	NWD*
Annonaceae	<i>Xylopia hypolampra</i>	474	5.3	NWD
Rubiaceae	<i>Porterandia cladantha</i>	352	3.9	NWD
Combretaceae	<i>Terminalia superba</i>	341	3.8	WD
Passifloraceae	<i>Ademia gracilis</i>	205	2.3	NWD*
Rubiaceae	<i>Cephaelis mannii</i>	183	2.0	NWD*
Combretaceae	<i>Combretum sp.</i>	121	1.3	WD
Tiliaceae	<i>Grewia caloneura</i>	121	1.3	NWD
Rubiaceae	<i>Canthium sp.</i>	80	0.9	NWD
Olacaceae	<i>Heisteria zimmereri</i>	79	0.9	NWD
Violaceae	<i>Rinorea sp.</i>	73	0.8	NWD
Annonaceae	<i>Enantia chlorantha</i>	72	0.8	NWD
Mimosoideae	<i>Piptadeniastrum africanum</i>	69	0.8	WD
Verbenaceae	<i>Vitex ferruginea</i>	60	0.7	NWD
Olacaceae	<i>Strombosia pustulata</i>	59	0.7	NWD
Chrysobalanaceae	<i>Parinari congensis</i>	58	0.6	NWD
Olacaceae	<i>Strombosia scheffleri</i>	58	0.6	NWD
Total		7789	85.9%	

¹ % tot. represents total percent of each species listed for all handled seeds (not total seed rain).

* Indicates liana or species in which fruiting may occur at <10 cm dbh.

around the seed trap clusters in each plot (Clark et al. 2001), but the high proportion of immigrant seed rain remains remarkable. Other studies in this forest indicate a strong potential for long distance dispersal for at least a small proportion of any individual's fruit production (Holbrook and Smith 2000; Clark 2001).

The high proportion of immigrant seed rain may also reflect the large number of potentially vertebrate dispersed tree species in this forest. We estimate the proportion of woody species dispersed by vertebrates here at approximately 82%, based upon field observations and previously published information (M. Fogiel, pers. comm., Whitney et al. (1998)). This falls well within published estimates of 62–93% for the proportion of vertebrate dispersed woody plant species in tropical forests (Jordano 1992). Principal vertebrate dispersers in this forest include large birds such as hornbills, turacos and parrots, seven primate species, and arboreal rodents and squirrels (Whitney et al. 1998; Holbrook and Smith 2000; Poulsen et al. 2001). We found that 28% of the total seed rain and approximately half of the total taxa occurring in the seed rain were handled in some manner by vertebrates (Appendix 1). Most taxa are represented by only a

few seeds or have a small percent of their seed crop actually dispersed by vertebrates. Fluxes in numbers of vertebrate-handled seeds generally paralleled seed rain trends, though the percent of seeds handled during a particular sample period varied. Of handled taxa, the few taxa that were frequently handled represent predominantly primate and bird dispersed taxa. In addition, WD taxa (n = 12) that are not typically expected to be vertebrate dispersed, comprised 6% of the total seeds handled. The local “over-representation” of immigrant seeds compared with local forest sources has been attributed to frugivores in Los Tuxtlas, Mexico (Martinez-Ramos and Soto-Castro 1993), and Levey (1988) has suggested disproportionate seed input into gaps by avian dispersers.

Studies of seed dispersal in tropical forests have generally emphasized the role of particular vertebrate dispersers or whether the seed shadow of particular plants has sufficient long distance dispersal to escape density dependent mortality associated with the parent. We sampled the seed rain randomly to examine assumptions of a number of these types of studies. For example, seed shadow studies generally hypothesize a probability distribution that would suggest rel-

atively similar seed rain in adjacent seed traps sampling overlapping seed shadows. While this was generally true for some of our plots (especially if dominated by a large wind dispersed species such as *Terminalia superba*), the majority of traps were no more similar to those within plots as among plots. In spite of the dominance of this forest by trees that produce vertebrate dispersed fruit, only 28% of the seed-fall showed evidence of vertebrate handling. The variability of seed rain composition in any particular trap and the range of actual seedfall into a trap indicate considerably greater patchiness in seed rain than might be appreciated from either focused studies or modeling. The role of such spatial patchiness or aggregation has been hypothesized to be critical for plants in stressful habitats as well as in maintaining tropical diversity (Jordano and Schupp (2000, 2000)). We conclude that processes principally influencing seed rain in this study vary stochastically and include reproductive failure of over half the adults, overlapping tails of seed shadows from individuals over a range of distances, and significant input from long distance dispersal.

Appendix 1

Table A1. All taxa present in the seed rain, March 1996–February 1997. Family, name, dispersal mode, total number of seeds, and percent each species represents of total seed rain included.

Family	Genus	Disp. Mode*	Total #	%Total
Anacardiaceae	<i>Lansea nigritiana</i>	NWD*	55	0.17
Anisophyllaceae	<i>Anopyxis klaineana</i>	NWD	24	0.07
Annonaceae	<i>Cleistopholis glauca</i>	NWD*	45	0.14
Annonaceae	<i>Cleistopholis patens</i>	NWD	6	0.02
Annonaceae	<i>Enantia chlorantha</i>	NWD*	124	0.38
Annonaceae	<i>Greenwayodendron suaveolens</i>	NWD*	35	0.11
Annonaceae	<i>Monodora tenuifolia</i>	NWD*	13	0.04
Annonaceae	<i>Pachypodanthium staudtii</i>	NWD*	775	2.37
Annonaceae	<i>Strombosia scheffleri</i>	NWD	1	0
Annonaceae	<i>Uvriastrum pierreanum</i>	NWD*	21	0.06
Annonaceae	<i>Xylopa hypolampra</i>	NWD*	811	2.48
Annonaceae	<i>Xylopa rubescens</i>	NWD*	28	0.09
Annonaceae	<i>Xylopa staudtii</i>	NWD*	19	0.06
Apocynaceae	<i>Futumia elastica</i>	WD*	80	0.25
Apocynaceae	<i>Laudolfia hirsula</i>	NWD*	36	0.11
Apocynaceae	<i>Rauwolfia macrophylla</i>	NWD*	2	0.01
Apocynaceae	<i>Tabernaemontana crassa</i>	NWD	30	0.09
Apocynaceae	<i>Tabernaemontana penduliflora</i>	NWD*	2	0.01
Arecaceae	<i>Eremospatha macrocarpa</i>	NWD	10	0.03
Arecaceae	<i>Lacospermum secundiflorum</i>	NWD*	23	0.07
Arecaceae	<i>Raffia sp.</i>	NWD*	1	0
Bursleraceae	<i>Canarium schweinfurthii</i>	NWD*	30	0.09

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Table A1. continued.

Family	Genus	Disp. Mode*	Total #	%Total
Burseraceae	<i>Santiria trimera</i>	NWD	1	0
Caesalpinoideae	<i>Anthonotha macrophylla</i>	NWD	1	0
Caesalpinoideae	<i>Anthonotha sp.</i>	NWD	167	0.51
Caesalpinoideae	<i>Berlinia grandifolia</i>	NWD	2	0.01
Caesalpinoideae	<i>Dialium africanum</i>	NWD	1	0
Caesalpinoideae	<i>Dialium sp. #3</i>	NWD*	1	0
Caesalpinoideae	<i>Distemonanthus benthamianus</i>	NWD*	36	0.11
Caesalpinoideae	<i>Tessmannia africanum/anomola</i>	NWD*	45	0.14
Caesalpinoideae	<i>unknown</i>	WD	5	0.02
Chrysobalanaceae	<i>Parinari congensis</i>	NWD*	58	0.18
Clusiaceae	<i>Allenblackia floribunda</i>	NWD*	20	0.06
Clusiaceae	<i>Garcinia sp.</i>	NWD*	10	0.03
Clusiaceae	<i>Mammea africana</i>	NWD*	7	0.02
Clusiaceae	<i>Pentadesma butyracea</i>	NWD*	6	0.02
Combretaceae	<i>Combretum cf. clemeusei</i>	WD*	1235	3.79
Combretaceae	<i>Terminalia superba</i>	WD*	2078	6.37
Connaraceae	<i>Aegelea pseudobliqua</i>	NWD	2	0.01
Connaraceae	<i>Rouzeopsis obliquifoliolata</i>	NWD	1	0
Dichapetalaceae	<i>Dichapetalum cf. mombuttense</i>	NWD*	18	0.06
Dichapetalaceae	<i>Lenga2</i>	NWD	3	0.01
Dichapetalaceae	<i>Uunknown</i>	NWD*	37	0.11
Dilleniaceae	<i>Tetracera cf. alnifolia</i>	NWD*	6	0.02
Dilleniaceae	<i>Tetracera podotrichia</i>	NWD*	2734	8.37
Dioscoriaceae	<i>Dioscoria sp.</i>	WD*	75	0.23
Ebenaceae	<i>Diosporos conocarpa</i>	NWD	10	0.03
Erythroxylaceae	<i>Erythroxylum emarginatum</i>	NWD	263	0.81
Euphorbiaceae	<i>Alcornia floribunda</i>	NWD*	841	2.58
Euphorbiaceae	<i>Antidesma laciniatum</i>	NWD	20	0.06
Euphorbiaceae	<i>Antidesma membranaceum</i>	NWD*	30	0.09
Euphorbiaceae	<i>Antidesma sp.</i>	NWD	230	0.7
Euphorbiaceae	<i>Bridelia atrovirides</i>	NWD	31	0.09
Euphorbiaceae	<i>Dichostemma glaucescense</i>	NWD*	42	0.13
Euphorbiaceae	<i>Discoglyprema caloneura</i>	NWD	327	1
Euphorbiaceae	<i>Drypetes cf. aframensis</i>	NWD	2	0.01
Euphorbiaceae	<i>Drypetes chevalieri</i>	NWD*	12	0.04
Euphorbiaceae	<i>Drypetes gilgiana</i>	NWD	3	0.01
Euphorbiaceae	<i>Drypetes ivorensis</i>	NWD	14	0.04
Euphorbiaceae	<i>Drypetes sp.1</i>	NWD	6	0.02
Euphorbiaceae	<i>Drypetes sp.2</i>	NWD	24	0.07
Euphorbiaceae	<i>Drypetes sp.3</i>	NWD	13	0.04
Euphorbiaceae	<i>Macaranga barteri</i>	NWD*	1164	3.57
Euphorbiaceae	<i>Macaranga schweinfurthii</i>	NWD*	188	0.58
Euphorbiaceae	<i>Macaranga sp.</i>	NWD	51	0.16
Euphorbiaceae	<i>Manniophyton fulvum</i>	WD*	140	0.43
Euphorbiaceae	<i>Margaritoria discoidea</i>	NWD	9	0.03
Euphorbiaceae	<i>Microdesmis puberula</i>	NWD	1	0
Euphorbiaceae	<i>Plagiostylus africana2</i>	NWD	3	0.01
Euphorbiaceae	<i>Ricinodendron heudelotii</i>	NWD*	24	0.07
Euphorbiaceae	<i>Uapaca sp.</i>	NWD*	4572	14

Table A1. continued.

Family	Genus	Disp. Mode*	Total #	%Total
Euphorbiaceae	<i>Unknown 1</i>	NWD	2	0.01
Euphorbiaceae	<i>Unknown 2</i>	NWD	390	1.19
Euphorbiaceae	<i>Unknown 3</i>	NWD	85	0.26
Euphorbiaceae	<i>Unknown 4</i>	NWD	15	0.05
Euphorbiaceae	<i>Unknown 5</i>	NWD*	3	0.01
Euphorbiaceae	<i>Unknown 6</i>	NWD	3	0.01
Euphorbiaceae	<i>Unknown 7</i>	NWD	3	0.01
Euphorbiaceae	<i>Unknown 8</i>	NWD*	1	0
Euphorbiaceae	<i>Unknown 9</i>	NWD	1	0
Faboideae	<i>Amphimas pterocarpus</i>	WD*	57	0.17
Flacourtiaceae	<i>Caloncoba glauca</i>	NWD	2	0.01
Flacourtiaceae	<i>Lindackeria dentata</i>	NWD	34	0.1
Flacourtiaceae	<i>cf.L. dentata or C. glauca</i>	NWD	103	0.32
Hippocrataceae	<i>Hippocratea myriantha</i>	WD*	13	0.04
Hugoniaceae	<i>Hugonia spicata</i>	NWD*	57	0.17
Irvingiaceae	<i>Desbordesia glaucescens</i>	NWD*	3	0.01
Ixocanthaceae	<i>Othocosmos africanus</i>	NWD	477	1.46
Lecythidaceae	<i>Petersianthus macrocarpus</i>	WD*	169	0.52
Lepidobotryaceae	<i>Lepidobotrys staudii</i>	NWD*	12	0.04
Loganiaceae	<i>Strychnos longicaudata</i>	NWD*	28	0.09
Marantaceae	<i>Unknown</i>	NWD	4	0.01
Meliaceae	<i>Carapa procera</i>	NWD*	4	0.01
Meliaceae	<i>Entadophragma cylindricum</i>	WD	73	0.22
Meliaceae	<i>Guarea cedrata</i>	NWD*	1	0
Meliaceae	<i>Trichelia zenkeri</i>	NWD	7	0.02
Meliaceae	<i>Trichilia welwitschii</i>	NWD	1	0
Mimosoideae	<i>Albizia glaberrima</i>	NWD	2	0.01
Mimosoideae	<i>Albizia ferruginea</i>	NWD	1	0
Mimosoideae	<i>Pentaclethra macrocarpa</i>	WD*	77	0.24
Mimosoideae	<i>Piptadeniastum africanum</i>	WD*	943	2.89
Mimosoideae	<i>Unknown</i>	WD*	7	0.02
Moraceae	<i>Antiaris africana</i>	NWD*	9	0.03
Moraceae	<i>Chlorophora excelsa</i>	NWD*	30	0.09
Moraceae	<i>Ficus sp.</i>	NWD*	2236	6.98
Moraceae	<i>Milicia excelsa</i>	NWD*	4	0.01
Moraceae	<i>Myrianthus arboreus</i>	NWD*	2	0.01
Moraceae	<i>Treculia africana</i>	NWD*	21	0.06
Moraceae	<i>Treculia sp.</i>	NWD*	1083	3.32
Myristicaceae	<i>Coelocaryon preussii</i>	NWD*	10	0.03
Myristicaceae	<i>Pycnanthus angolensis</i>	NWD*	3	0.01
Myristicaceae	<i>Staudtia stipitata</i>	NWD*	130	0.4
Ochnaceae	<i>Ouratea elongata</i>	NWD	10	0.03
Olacaceae	<i>Heisteria zimmereri</i>	NWD*	283	0.87
Olacaceae	<i>Strombosia grandifolia</i>	NWD*	197	0.61
Olacaceae	<i>Strombosia pustulata</i>	NWD*	385	1.18
Olacaceae	<i>Strombosia scheffleri</i>	NWD*	56	0.17
Olacaceae	<i>Strombosia sp.</i>	NWD*	16	0.05
Olacaceae	<i>Strombiopsis tetandra</i>	NWD*	126	0.39
Pandaceae	<i>Panda oleosa</i>	NWD*	1	0

Table A1. continued.

Family	Genus	Disp. Mode*	Total #	%Total
Papilionidae	<i>Mucuna flagellipes</i>	NWD	2	0.01
Passifloraceae	<i>Ademia gracilis</i>	NWD*	622	1.91
Passifloraceae	<i>Deidamia clematoideia</i>	NWD*	81	0.25
Rhamnaceae	<i>Lasiodiscus manii</i>	NWD	1	0
Rhamnaceae	<i>Maesopsis eminii</i>	NWD*	26	0.08
Rubiaceae	<i>Aidia sp.</i>	NWD	2	0.01
Rubiaceae	<i>Belonophora coriacea</i>	NWD*	6	0.02
Rubiaceae	<i>Bertiera aethiopiaca</i>	NWD	4	0.01
Rubiaceae	<i>Canthium sp.</i>	NWD*	242	0.74
Rubiaceae	<i>Cephaelis mannii</i>	NWD*	275	0.84
Rubiaceae	<i>Hensia crinata</i>	NWD*	4	0.01
Rubiaceae	<i>Massularia acuminata</i>	NWD	2	0.01
Rubiaceae	<i>Nauclea diderichii</i>	NWD*	1071	3.28
Rubiaceae	<i>Oxyanthus sp.</i>	NWD	1	0
Rubiaceae	<i>Pausynstalia brachythyrso</i>	NWD*	218	0.67
Rubiaceae	<i>Porterandia cladantha</i>	NWD*	1240	3.8
Rubiaceae	<i>Rothmannia lateriflora</i>	NWD*	84	0.26
Rubiaceae	<i>Rothmannia talbotii</i>	NWD	4	0.01
Rubiaceae	<i>Rub sp. #2</i>	NWD*	58	0.18
Rubiaceae	<i>Rub sp. #8</i>	NWD	13	0.04
Rubiaceae	<i>Tricalysia ferovum</i>	NWD	1	0
Rubiaceae	Unknown	NWD*	46	0.14
Rutaceae	<i>Vepris lousiii</i>	NWD*	10	0.03
Sapindaceae	<i>Blighia welwitschii</i>	NWD*	5	0.02
Sapindaceae	<i>Chytranthus sp.</i>	NWD	6	0.02
Sapindaceae	<i>Eriocoelem macrocarpum</i>	NWD*	83	0.25
Sapindaceae	<i>Lecaniodiscus cupaniodes</i>	NWD*	111	0.34
Sapotaceae	<i>Brevia cf. siricea</i>	NWD*	105	0.32
Sapotaceae	<i>Gambeya lacourtiana</i>	NWD*	53	0.16
Sapotaceae	<i>Gambeya perpulchra</i>	NWD*	74	0.23
Sapotaceae	<i>Manilkara letouzei</i>	NWD	1	0
Sapotaceae	<i>Synsepalum sp.</i>	NWD	192	0.59
Sapotaceae	Unknown	NWD*	8	0.02
Sterculiaceae	<i>Cola sp.</i>	NWD	3	0.01
Sterculiaceae	<i>Nesgordonia papaverifera</i>	NWD*	4	0.01
Sterculiaceae	<i>Sterculia tragacantha</i>	NWD*	39	0.12
Sterculiaceae	Unknown	NWD*	3	0.01
Tiliaceae	<i>Desplatsia dewevrei</i>	NWD*	1	0
Tiliaceae	<i>Duboscia macrocarpa</i>	NWD*	56	0.17
Tiliaceae	<i>Grewia caloneura</i>	NWD*	60	0.18
Tiliaceae	<i>Grewia coreacea</i>	NWD*	198	0.61
Tiliaceae	<i>Grewia oligoneura</i>	NWD	18	0.06
Ulmaceae	<i>Celtis adolfia</i>	NWD	10	0.03
Ulmaceae	<i>Celtis milbraedii</i>	NWD*	34	0.1
Ulmaceae	<i>Celtis tessmanii</i>	NWD	4	0.01
Verbenaceae	<i>Vitex doniana</i>	NWD	24	0.07
Verbenaceae	<i>Vitex ferrugineae</i>	NWD*	222	0.68
Violaceae	<i>Rinorea sp.</i>	NWD*	534	1.64
Vitaceae	<i>Cissus dinklagei</i>	NWD*	66	0.2
Zingiberaceae	<i>Reinealmia africana/macrocolea</i>	NWD*	15	0.05
Total # seeds			30,855	95%

* indicates handling occurred in this taxa.

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