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The Role of Arboreal Seed Dispersal Groups on the Seed Rain of a Lowland Tropical Forest[1]

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ABSTRACT

Most tropical plants produce fleshy fruits that are dispersed primarily by vertebrate frugivores. Behavioral disparities among vertebrate seed dispersers could influence patterns of seed distribution and thus forest structure. This study investigated the relative importance of arboreal seed dispersers and seed predators on the initial stage of forest organization—seed deposition. We asked the following questions: (1) To what degree do arboreal seed dispersers influence the species richness and abundance of the seed rain? and (2) Based on the plant species and strata of the forest for which they provide dispersal services, do arboreal seed dispersers represent similar or distinct functional groups? To answer these questions, seed rain was sampled for 12 months in the Dja Reserve, Cameroon. Seed traps representing five percent of the crown area were erected below the canopies of 90 trees belonging to nine focal tree species: 3 dispersed by monkeys, 3 dispersed by large frugivorous birds, and 3 wind-dispersed species. Seeds disseminated by arboreal seed dispersers accounted for *ca* 12 percent of the seeds and 68 percent of the seed species identified in seed traps. Monkeys dispersed more than twice the number of seed species than large frugivorous birds, but birds dispersed more individual seeds. We identified two distinct functional dispersal groups, one composed of large frugivorous birds and one composed of monkeys, drop dispersers, and seed predators. These groups dispersed plants found in different canopy strata and exhibited low overlap in the seed species they disseminated. We conclude it is unlikely that seed dispersal services provided by monkeys could be compensated for by frugivorous birds in the event of their extirpation from Afrotropical forests.

Key words: *Cameroon; frugivory; lowland tropical forest; seed dispersal; seed rain.*

PATTERNS OF SEED RAIN REPRESENT THE INITIAL PHASE of tropical forest organization and structure. Because few tropical trees produce seeds with long dormancy mechanisms (Garwood 1983, Baskin & Baskin 1998), advanced forest regeneration results from relatively recent input of seeds from the seed rain. Although a variety of dispersal mechanisms are found within tropical forests, most plants produce fleshy fruits, and vertebrate frugivores act as the primary seed dispersers (Jordano 1992). Behavioral disparities among seed dispersers could influence patterns of seed distribution (Howe 1990); consequently, the abundance, diversity, and feeding preferences of the frugivore community may influence forest structure.

Although numerous studies have confirmed the involvement of many frugivores in seed dispersal (Fleming & Heithaus 1981, Julliot 1997, Whitney *et al.* 1998, Voysey *et al.* 1999), the extent to which frugivory influences seed rain patterns is unclear (Martinez-Ramos & Soto-Castro 1993, Loiselle 1996); considerable impact, however, has always been assumed. Seed rain studies that examine vertebrate dispersal generally estimate seed shadows of individual trees as seeds are removed from a parent plant (Howe *et al.* 1985, Laman 1996) or measure dispersal into deforested habitats (Gorchov *et al.* 1993, Guevera & Laborde 1993, Duncan & Chapman 1999) or forest gaps (Martinez-Ramos & Soto-Castro 1993, Loiselle 1996, Wenny & Levey 1998). Yet, our understanding of vertebrate seed dispersal patterns in closed canopy forests remains limited.

Community-level studies that compare seed deposition patterns among different seed dispersers are rare, with the exception of comparisons between limited subsets of taxa such as birds and bats (Charles-Dominique 1991, Da Silva *et al.* 1996, Duncan & Chapman 1999) or birds and monkeys (Howe 1990). Instead, community-level studies generally focus on vertebrate feeding behaviors, cre-

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ate diet species lists, and describe ecological similarities between species based on these data (Fleming 1979, Gautier-Hion *et al.* 1985). Thus, they only can speculate on overall seed dissemination patterns resulting from dietary preferences. Seed rain studies reflect dispersal patterns as affected by the consumer community and are therefore a more direct measure of a seed disperser's contribution to dispersal processes.

Our study investigated the importance of various disperser groups on seed rain patterns. Specifically, we asked: (1) To what degree do arboreal seed dispersers influence the species richness and abundance of the seed rain? and (2) Do arboreal seed dispersers represent similar or distinct functional groups? We classified functional groups based on the following criteria: (a) They differentially disseminate the seeds of lianas, upper, middle, and lower canopy plant species; and (b) They express limited overlap in the seed species they disperse. We are aware of no other studies that have directly compared community-level seed rain patterns generated by diverse arboreal dispersal groups in a closed canopy forest.

MATERIALS AND METHODS

STUDY SITE.—Our study took place from May 1998 to May 1999 at the Bouamir Research Station (BRS) in the Dja Reserve, south–central Cameroon. The Dja Reserve, an IUCN Biosphere Reserve (526 km^2), is the largest protected area in Cameroon. Our study area was a 25 km^2 site located roughly at the center of the reserve (3°11′27″N, 12°48′41″E). The vegetation is semideciduous tropical rain forest (Letouzey 1970) and has never been logged. The climate is characterized by two wet and two dry seasons, with major and minor rainfall peaks in September and May, respectively (Whitney *et al.* 1998). Average annual rainfall is *ca* 1600 mm (Laclavère 1980).

The arboreal seed dispersers investigated in this study included 23 species belonging to three taxonomic groups (Appendix 1): 6 species of large frugivorous birds (hornbills and turacos), 7 species of monkeys, and at least 12 species of squirrels (Colyn & Perpete 1995). Bats, gorillas, and chimpanzees also occur on our study site. However, very few seeds recorded in seed traps showed evidence of dispersal by these animals, and they were excluded from analysis.

TREE SPECIES SELECTION AND SEED TRAP PLACEMENT.—Based on prior research at the BRS indicating that *ca* 85–90 percent of the known tree species on the study site are dispersed by monkeys, large frugivorous birds, or wind (Fogiel, pers. comm.), we sampled seed rain under the canopies of trees falling into these dispersal categories. Within each dispersal category, tree species were randomly selected from a list (produced from observations made by researchers at the BRS from 1994 to 1997 and the knowledge of local Baka guides; Whitney *et al.* 1998, Clark 2001, Poulsen *et al.* in press [b]) of all possible trees for that category.

Seed rain was sampled below the canopies of nine focal tree species, three dispersed predominately by monkeys: *Gambeya boukokoensis* (Sapotaceae), *Garcinia smeathmannii* (Clusiaceae), and *Uapaca paludosa* (Euphorbiaceae); three dispersed mainly by large frugivorous birds: *Cleistopholis glauca* (Annonaceae), *Maesopsis eminii* (Rhamnaceae), and *Staudtia kamerunensis* (Myristicaceae); and three wind-dispersed species: *Terminalia superba* (Combretaceae), *Pteleopsis hylodendron* (Combretaceae), and *Funtumia elastica* (Apocynaceae; nomenclature follows Hutchinson *et al.* 1963, Letouzey 1970, Tailfer 1989). To verify our tree classification, bird-dispersed and monkey-dispersed tree species were observed for a total of over 1500 hours to determine the animals that fed on them. Over 90 percent of all observed fruit removal was by the seed disperser to which a tree species was assigned (Clark 2001).

We selected 10 adults of each species, totaling 90 trees. The height of each tree was measured with a clinometer. All trees, lianas, and understory shrubs with vegetative structures hanging within 5 m of the canopy were identified and recorded. At each tree, we calculated the crown area using the average of ten canopy radius measurements. Then, seed traps representing five percent of the crown area were placed randomly under the canopy. Traps ranged in size (0.25 −1.25 m^2) and number (2–25 traps) to reflect differences among crown areas of individual trees (24.09–366.25 m^2). Combined sampling area under all trees totaled 779 m^2. Traps were constructed of durable plastic mesh stapled to frames constructed of rattan. Mesh was loosely attached to frames, allowing enough slack to prevent seeds from bouncing out of the traps on impact or from being removed by wind and rain. Seed traps were elevated 1.0–1.5 m from the ground to discourage seed removal by animals; however, nearly ten percent of 896 seeds marked and placed into traps were either removed or chewed by vertebrates within ten days of placement.

While a completely random seed trap design

TABLE 1. *Species averages of tree characteristics from focal tree (*N *= 10 for each species). CLGL =* Cleistopholis glauca*; MAEM =* Maesopsis eminii*; STKA =* Staudtia kamerunensis*; UAPA =* Uapaca paludosa*; GASM =* Garcinia smeathmannii*; GABO =* Gambeya boukokoensis*; PTHY =* Pteleopsis hylodendron*; FUEL =* Funtumia elastica*; and TESU =* Terminalia superba.

Species	Vector	Tree height (m) ±SE	DBH (m) ±SE	Crown area (m^2) ±SE
CLGL	Bird	40.64 ± 2.13	0.87 ± 0.07	169.44 ± 28.86
MAEM	Bird	48.44 ± 2.15	0.97 ± 0.07	305.54 ± 34.87
STKA	Bird	34.99 ± 2.99	0.77 ± 0.19	167.20 ± 34.07
UAPA	Monkey	33.29 ± 1.90	0.71 ± 0.09	160.31 ± 23.91
GASM	Monkey	22.34 ± 2.05	0.32 ± 0.02	24.77 ± 2.18
GABO	Monkey	30.49 ± 1.93	0.80 ± 0.06	94.09 ± 13.08
PTHY	Wind	47.79 ± 3.55	0.96 ± 0.08	223.64 ± 32.94
FUEL	Wind	34.17 ± 1.63	0.44 ± 0.06	47.38 ± 5.73
TESU	Wind	40.29 ± 2.04	1.05 ± 0.19	240.54 ± 32.94

might have better described patterns of seed deposition associated with the range of dispersal mechanisms in this paper (birds, monkeys, manual dispersers, seed predators, and wind), we selected an alternative design, randomizing our selection of tree species within the most prevalent dispersal categories to facilitate further comparisons among dispersal vectors (Clark 2001). We recognized that the placement of seed traps under canopies of bird-, monkey-, and wind-dispersed trees could overrepresent the number of seeds and seed species contributed to the seed rain by these dispersal mechanisms during the fruiting period of a tree; however, the random selection of tree species within vector categories encompassed tree species with a wide range of characteristics (Table 1) and variation among tree species reduced bias that may have been introduced by the fixed factor of vector categories during fruiting periods (Clark 2001). The 12-month sampling period, which offered continued data collection during non-fruiting periods, and the influence of other vegetation (dispersed by various vectors) overlapping with the canopies of our focal trees further diluted potential over representation of bird-, monkey-, and wind-dispersed seeds and seed species in the seed rain. However, to test that the trees under which we sampled did not significantly bias our results, we compared cumulative seed density, species richness, density of vertebrate-dispersed seeds, and the density of wind-dispersed seeds among tree dispersal categories using analysis of variance. Data were normalized with log transformation. We found no significant difference among tree vector categories in the seed density (seeds/m^2/yr: df = 2, 87, $F = 2.571$, $P = 0.082$), species richness (seed species/m^2/yr: df = 2, 87, $F = 2.176$, $P = 0.119$), density of vertebrate-dispersed seeds (vertebrate-deposited seeds/m^2/yr: df = 2, 87, $F = 0.882$, $P = 0.417$), or density of wind-dispersed seeds (wind-dispersed seeds/m^2/yr: df = 2, 87, $F = 1.834$, $P = 0.165$) collected from traps below tree canopies. We assume that the lack of significant differences among trees within different dispersal categories indicates that our choice of tree species did not bias the data to exaggerate or de-emphasize the actual role of vertebrate seed dispersers in the forest.

SEED TRAP MONITORING AND SEED PROCESSING.—All fruits, seeds, and fruit or seed pieces were collected from traps at ten-day intervals for 12 months. The contents of seed traps were placed in plastic bags and returned to the field station for processing. Fecal clumps in traps were also collected to ensure all seeds within clumps were classified as dispersed by the appropriate vector. When fecal clumps contained more than one seed, each seed was catalogued independently. *Ficus* seeds represented a particular case because a single defecation can contain thousands of seeds resulting in over representation of this species in the seed rain. During our study, however, only one fecal clump was recorded that contained more than 20 *Ficus* seeds. Given the bias that could be introduced by counting each seed independently, we estimated this single fecal clump to contain 50 seeds. The average number of seeds defecated per fecal clump was low (1.76 seeds/clump; range: 1–50 seeds).

To determine the degree to which vertebrate seed dispersers influenced the overall species richness and density of the seed rain, we recorded fruit and seed number, condition (mature, immature, rotten, chewed, defecated, or germinated), species, and dispersal mechanism for all propagules collected from seed traps. Each seed or fruit was placed into one of the following dispersal categories: bird-dispersed (determined by the presence of white uric acid or evidence of regurgitation); monkey-defecated (identified by presence of monkey scat); drop-dispersed (intact seeds or fruits that have visible teeth, claw, or bill marks, indicating they had been carried in the mouth or hands of a vertebrate seed disperser); preyed upon prior to dispersal by vertebrates (severely damaged or chewed seeds with visible teeth, claw, or bill marks); and wind or ballistic dispersal category. Seeds were cautiously placed into the vertebrate-handled categories; any fruits or seeds that did not obviously fit were classified as not handled, likely resulting in a conservative estimate of vertebrate seed dispersal. Although admittedly not all-inclusive, the dispersal categories were chosen because each could have different consequences for seed fate. For example, seeds defecated by large birds and monkeys may represent long-distance dispersal (Sun *et al.* 1997, Holbrook & Smith 2000, Poulsen *et al.* in press[a]) whereas seeds drop-dispersed by monkeys and squirrels frequently result in short-distance dispersal (Rowell & Mitchell 1991, Lambert 1999, Poulsen *et al.* in press[a]). Therefore, this paper broadly defines frugivore dispersal groups based on treatment of seeds and fruits, which may largely determine their ecological function.

To determine if the seed dispersers and predators described above differentially disperse seeds from different canopy strata, all seed species were categorized as produced by upper canopy tree species (adult heights >35 m), middle canopy tree species (adult heights between 15 and 35 m), lower canopy species (adult heights <15 m), or lianas. Lianas were treated as a separate category because the canopy level at which they are found varies within species. Decisions regarding appropriate canopy level categories were made using knowledge of existing flora (Hutchinson *et al.* 1963, Letouzey 1970, Tailfer 1989).

Seed rain description and data analysis.—Seeds collected from all traps were combined for analysis. We describe seed rain in terms of density (seeds/m^2) and species richness (species/sampling period). Tests for comparing two proportions employing a normal approximation of the chi-square test were used to determine if the total number of seeds and seed species collected from traps differed between pairs of disperser categories (Zar 1999). We examined if disperser groups represent distinct or similar functional groups by calculating dispersal overlap using the coefficient of community, a similarity index where $C = 2W/(A + B)$ (Snow & Snow 1971, Fleming 1979). For this equation, C = coefficient of community, W = number of shared species, A = number of fruit species in the diet of one disperser group, and B = number of fruit species in the diet of the second disperser group. Chi-square analysis tested if the number of seed species dispersed from different canopy levels was significantly different among disperser groups. We used the number of seed species rather than number of seeds for these comparisons to facilitate comparison with other studies. When multiple comparisons were made, we report significance with Bonferroni corrections (Sokal & Rohlf 1995).

RESULTS

A total of 159,696 seeds from 371 species were recorded in seed traps. Total seed density was 204.9 seeds/m^2/yr. When data analyses required knowledge of canopy level, all unidentified seeds (52 of 371 species) were eliminated.

Influence of vertebrate dispersal on species richness and seed density.—The vast majority of all seeds recorded from seed traps (66.5%) were deposited directly under a conspecific canopy, with no evidence of vertebrate handling or dispersal by wind. Vertebrate handling was recorded for 17.1 percent of all collected seeds whereas vertebrates did not noticeably influence the remaining 82.9 percent of seed deposition. Vertebrate seed dispersal (defined here as seeds deposited by vertebrate vectors more than 5 m from a conspecific canopy) contributed minimally to the total number of seeds recorded in traps (12.4%; Fig. 1; Table 2). Seed predators contributed significantly greater numbers of seeds to the seed rain than all other disperser categories (Tables 2 and 3). Significantly greater numbers of bird- and drop-dispersed seeds were collected from traps than monkey-defecated seeds (Table 3). Wind and ballistic dispersal contributed significantly greater seed numbers to seed traps (16.3%) than vertebrate dispersal (12.4%; Table 3). Thus, despite the common conception that trees in tropical forests depend largely on vertebrate seed dispersers, wind and ballistic mechanisms may disperse greater total seed numbers beyond conspecific canopies.

Of the 371 species recorded in seed traps, 81.1 percent showed evidence of dispersal or predation by vertebrates. Vertebrates dispersed 254 species (68.4%) at least 5 m beyond a conspecific canopy, of which 132 species (35.5%) showed evidence of occasional pre-dispersal predation. Large birds,

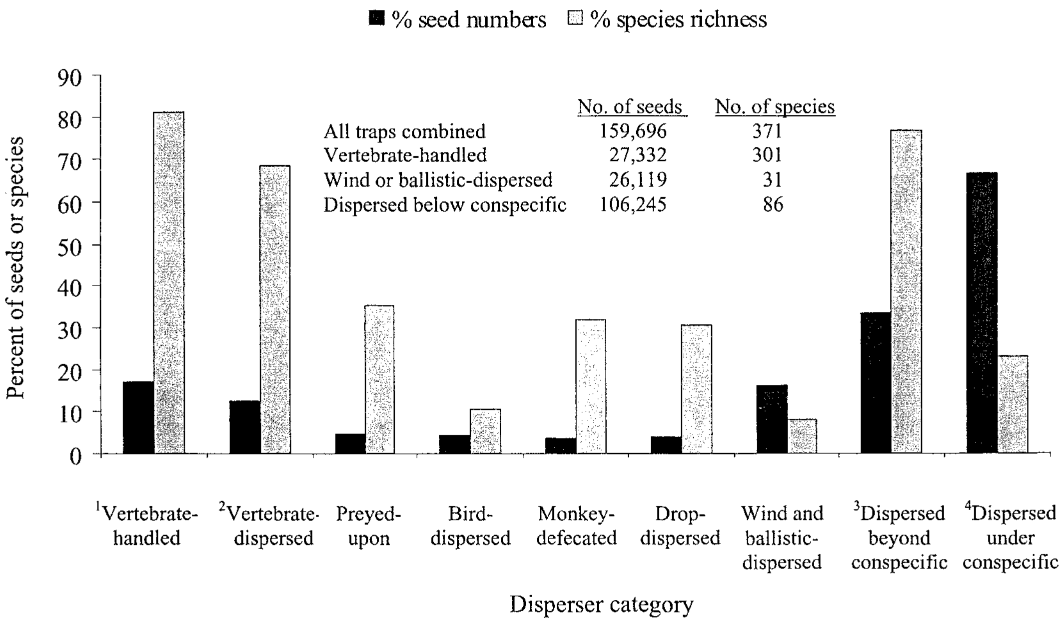

FIGURE 1. Percent of seed numbers and seed species recorded in each seed dispersal category. Because many seeds and seed species were classified in multiple categories, data do not sum to 100 percent. [1]Vertebrate-handled = vertebrate dispersal + pre-dispersal predation. [2]Vertebrate-dispersed = bird-dispersed + monkey-defecated + drop-dispersed seeds taken farther than 5 m from conspecific canopy. [3]Dispersal beyond conspecific canopy = wind + ballistic + bird + monkey + drop dispersal beyond conspecific canopy. [4]Dispersed under canopy = preyed upon + seeds dispersed by any mechanism below a conspecific canopy. Vertebrates preyed upon many wind- and ballistic-dispersed seeds. These seeds have been excluded from the wind-and ballistic-dispersed categories and included in the pre-dispersal predation category. Percentages are calculated with all seed traps combined (sampling area = 779 m^2; N = 159,696 seeds, 371 species).

monkeys, drop dispersers, and seed predators, respectively, deposited 34 (10.6%), 102 (31.9%), 98 (26.4%), and 132 species (41.3%; Fig. 1; Appendix 2), with large birds disseminating significantly fewer seed species into seed traps than monkeys, drop-dispersers, and seed predators (Table 3). Wind and ballistic dispersal mechanisms contributed significantly fewer seed species to seed traps than vertebrate dispersers (Fig. 1; Table 3).

Dispersal of seeds from different canopy levels, dispersal overlap, and functional groups.—Upper and middle canopy species constituted the majority of bird-dispersed seeds. Large frugivorous birds disseminated no lower canopy species and few liana species. Seed species dispersed by large birds differed significantly in life-form from those defecated by monkeys and drop-dispersed (Fig. 2).

Monkeys disseminated seed species from the middle and lower canopy of the forest and many monkey-defecated seed species were lianas. Only one percent of the seed species defecated by monkeys was from the upper canopy. Monkeys defecated seed species of plants located at significantly

TABLE 2. *Densities and species richness of frugivore-handled seeds deposited more than 5 m from a conspecific canopy; 52 unidentified species (*N *= 319 seeds) were excluded from these data.*

Disperser category	Total seeds	Seeds/m^2/yr	Percent of all seeds	No. of species	Percent of all species
Large bird-dispersed	7071	8.9	4.3	34	10.6
Monkey-defecated	6061	7.8	3.7	102	31.9
Unknown vector	221	0.3	0.1	34	10.6
Drop-dispersed	6486	8.3	4.1	98	30.7
Preyed upon	7421	9.5	4.6	132	41.3

TABLE 3. *Results of tests comparing two proportions that employ a normal approximation of the chi-square test (Zar 1999), which examined differences among disperser categories in the number of seeds and the number of seed species deposited into seed traps. Asterisks represent significance with Bonferroni corrections (Sokal & Rohlf 1995).*

	Number of seeds			Number of species		
Disperser groups compared	*z*	df	Sig.	*z*	df	Sig.
Bird-dispersed vs. Monkey-dispersed	8.9917	1	*	6.3572	1	*
Bird-dispersed vs. Drop-dispersed	5.1257	1	*	6.0477	1	*
Bird-dispersed vs. Preyed upon	2.9671	1	*	8.5449	1	*
Monkey-dispersed vs. Drop-dispersed	3.8619	1	*	0.2482	1	
Monkey-dispersed vs. Preyed upon	11.9593	1	*	2.2911	1	
Drop-dispersed vs. Preyed upon	8.0983	1	*	2.6195	1	
Wind/ballistic-dispersed vs. Vertebrate-dispersed	5.4066	1	*	16.751	1	*

different canopy levels than those dispersed by large birds, but similar to those species drop-dispersed or preyed upon (Fig. 2).

Drop-dispersed seed species represented plants from all canopy levels, with similar proportions of the seed species dispersed from the middle canopy, lower canopy, and liana species. Patterns of predispersal predation mimicked those of drop dispersal. Seeds from all canopy levels were preyed upon but seed predators more frequently consumed seeds from the lower canopy, with middle canopy and liana seed species being equally represented in preyed upon seed species.

Coefficients of community identified dispersal overlap to be greatest between drop dispersers (predominantly squirrels and monkeys) and seed predators (squirrels, other arboreal rodents, and some monkeys), followed by monkeys (defecated seeds) and seed predators, and, lastly, monkeys (defecated seeds) and drop dispersers (Fig. 3). Dispersal overlap between large birds and all other disperser cat-

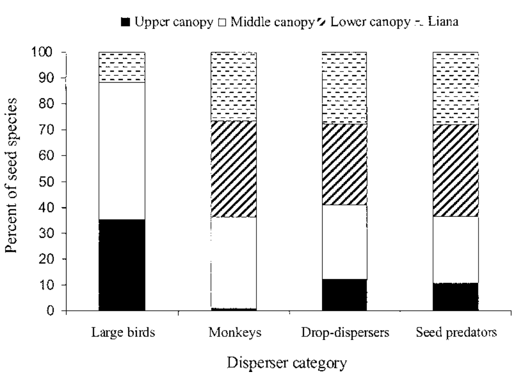

FIGURE 2. Percent of seed species dispersed by each vertebrate seed disperser category from different canopy strata. Canopy strata are defined as upper canopy species (N = 22), mid-canopy species (N = 75), lower canopy species (N = 155), and liana species (N = 67). The number of species dispersed or preyed upon by each dispersal category are as follows: large birds = 34 species, monkeys = 102 species, drop dispersers = 98 species, and seed predators = 132 species. Percentages were calculated as the number of species collected in traps from each canopy strata dispersed by each disperser group divided by the total number of species consumed by each disperser group. We used chi-square analysis to test if disperser groups disseminated seeds from different canopy strata. Only birds versus monkeys (χ^2 = 48.49, P < 0.001), birds versus drop dispersers (χ^2 = 25.11, P < 0.001), and birds versus seed predators (χ^2 = 10.94, P = 0.012) were significantly different from one another after Bonferroni corrections for multiple tests. Among monkeys, drop dispersers, and seed predators, seed species were not selected from significantly different canopy strata.

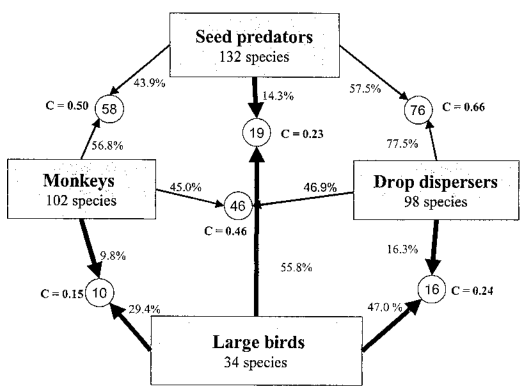

FIGURE 3. Dispersal overlap of arboreal frugivores as expressed in seed rain. Boxes represent disperser category and indicate the number of plant species consumed. Numbers in circles represent the number of species shared between two groups. Percentages were calculated as percent of diet species shared. C = coefficient of community, a similarity index where C = 2W/(A + B); W = number of shared species; A = number of fruit species in the diet of one taxa; and B = number of fruit species in the diet of the second taxa. Heavy arrows indicate that disperser groups differ significantly (χ^2 < 0.05) in the number of seed species dispersed from different canopy levels.

egories was low. Because monkeys were responsible for some drop dispersal, our monkey-defecated and drop-dispersal categories are not independent of each other. We examined to what degree this lack of independence impacted our results by recalculating overlap values after monkey-defecated seeds and drop-dispersed seeds were pooled into a single group. The resulting values were similar to the ungrouped values. For example, dispersal overlap between birds and monkeys/drop dispersers was still low (C = 0.20), compared to ungrouped overlap between birds and drop dispersers and birds and monkeys of C = 0.23 and C = 0.15, respectively. Therefore, we report ungrouped community coefficient values.

DISCUSSION

Two important points emerge from this study. First, arboreal seed dispersers and seed predators (vertebrate-handled seeds) contributed minimally to the total number of seeds that fell into seed traps (17.1%) but greatly contributed to the number of seed species recorded in traps (81.1%). Second, we identified two distinct vertebrate groups that provide different dispersal services, one composed of large frugivorous birds and one composed of monkeys, drop dispersers, and seed predators. These groups disseminated plants located in different canopy strata and exhibited low overlap in dispersed seed species.

Influence of vertebrate dispersal on species richness and seed density.—Between 62 and 93 percent of all tropical plant species depend on animal dispersal for dissemination of their seeds (Jordano 1992), implying that vertebrate seed dispersal is disproportionately important to the maintenance and structure of tropical forests. The proportion of the total seed rain actually dispersed by vertebrate seed dispersers, however, is rarely calculated. In this study, we found that the total number of seeds dispersed away from conspecific canopies by vertebrates (12.4%) was not greater than the number of seeds dispersed from conspecific adults by other dispersal mechanisms (wind and ballistic dispersal: 16.3%). In fact, vertebrates did not influence the deposition of 82.9 percent of all seeds recorded in seed traps; however, consistent with other studies, 81 percent of all seed species recorded in traps were either dispersed or preyed upon by vertebrate seed dispersers, although only 68 percent were disseminated away from a conspecific canopy.

The importance of vertebrate seed dispersal in this system depends on the spatial scale at which vertebrate dispersal services are examined. At a small spatial scale, within 5 m of the parent tree, the vertebrate community rarely depleted seed crops, and high seed densities, untouched by vertebrates, fell below conspecific canopies. We would expect this to result in little or no recruitment under parent trees (Janzen 1970, Clark & Clark 1984, Howe *et al.* 1985) or high densities of seedling recruitment near parent canopies, where densities of seed deposition are high (Harms *et al.* 2000). At a larger spatial scale, however, less frequent dispersal of a greater number of plant species could be disproportionately important in survival and plant recruitment (Janzen 1970, Connell 1971), genetic structure (Cain *et al.* 2000), and range expansion rates (Clark *et al.* 1998) of plant populations. Thus, although arboreal vertebrate vectors may not deplete seed crops or disseminate large numbers of seeds away from parent trees, they may be important in dispersing seeds of a great number of species and could therefore be critical to the maintenance of plant species richness in tropical forests.

As mentioned above, the majority of fruits and seeds collected from seed traps fell below the crown of a conspecific adult and were not handled by vertebrates. Many studies have offered theories to explain patterns of tropical fruit abundance that, from a vertebrate perspective, indicate excessive fruit production by the plant community. Large fruit crops may increase a plant's visibility, and therefore the chance that an individual will be visited by a greater number of frugivores (Howe & DeSteven 1979, Denslow *et al.* 1986). On the other hand, high risk of pre- and post-dispersal predation and the vagaries of seedling establishment would also select for high fruit production by plants. The high proportion of seeds that fell into seed traps below conspecific canopies suggests that post-dispersal predation (Schupp & Frost 1989, Hulme 1998) and secondary dispersal by forest ruminant species (Dubost 1984), ants (Levey & Byrne 1993, Kalisz *et al.* 1999), or rodents (Horvitz & Le Corff 1993) could also be important dispersal processes in this forest.

Large birds contributed greater numbers of seeds to the seed rain than any other single disperser category; however, they disseminated the fewest seed species. In contrast, monkeys dispersed more seed species than any other group. The specialized diets of large frugivorous birds compared to monkeys and squirrels may limit the number of fruit species they disperse (Poulsen *et al.* in press[b]). Results from two vertebrate-centered studies in the Dja Reserve also suggest that monkeys disseminate more species of plants than hornbills, the most common large frugivorous birds (Whitney *et al.* 1998, Poulsen *et al.* in press[a]). Drop dispersal contributed to the dissemination of a greater number of seed species than monkey defecation, indicating that drop dispersal may be an under appreciated dispersal mechanism for Afrotropical forest plant species.

Despite differences in the number of seeds and species disseminated among vertebrate seed dispersers, more information is required to determine which one contributes most importantly to forest dynamics. Because it only takes a single well placed seed for successful establishment, a seed disperser that effectively distributes only a few seeds or seed species to safe sites (Schupp 1993) may have a greater impact on forest organization than a disperser that disseminates a greater number of seeds or seed species to sites at which seeds cannot germinate or seedlings establish.

Dispersal of seeds from different canopy levels, dispersal overlap, and functional groups.—We identified two groups of arboreal seed dispersers that disseminate the seeds of plants found at different canopy levels and that have low overlap in the species they disperse: large frugivorous birds (hornbills and touracos) and frugivorous monkeys, drop dispersers (normally monkeys and squirrels), and seed predators (some monkeys and squirrels [and other rodents]).

Fruit and tree characteristics including color (Gautier-Hion *et al.* 1985), seed size and number (McKey 1975, Levey 1987a), nutrient content (Herrera 1982, Levey 1987b), fruit arrangement (Denslow & Moermond 1982, Levey *et al.* 1984), and fruiting phenology (Herrera 1981) may determine fruit selection by vertebrates. Our data suggest that the canopy level at which fruits are produced may also influence consumer selection. Specifically, monkeys, drop dispersers, and seed predators disseminated greater numbers of seed species from liana and lower to middle canopy levels, while large frugivorous birds dispersed seed species produced in middle to upper canopy strata (dispersing no lower canopy species and few liana species). This is consistent with findings in the Dja Reserve that hornbill feeding heights were significantly higher than those of monkeys (Poulsen *et al.* in press[b]). By avoiding the upper canopy and feeding primarily on species of the lower to middle canopy, where vegetation is often more dense, monkeys and squirrels may reduce the risk of predation. Monkeys and large squirrels are often targeted as prey by Crowned Hawk-eagles (*Stephanoaettus coronatus*) in the Dja Reserve (Clark, pers. obs.) as well as in other areas of central Africa (Gautier-Hion & Tutin 1988). The ability of monkeys and squirrels to forage through dense foliage also increases their ability to locate and recover fruit of lower canopy and liana species, giving them a distinct foraging advantage over large birds for fruits at these canopy levels.

Low dispersal overlap between large frugivorous birds and monkeys, drop dispersers, and seed predators supports our findings that these groups select fruit species from different canopy levels. Because these overlap values represent seed dispersal rather than fruit consumption and are therefore a direct measure of frugivore contribution to seed dispersal processes, we conclude that large frugivorous birds play a different functional role than do other arboreal vertebrates in the Dja Reserve.

High overlap between monkeys, drop dispersers, and seed predators in the species they dispersed to traps led us to place them in a single functional group, despite the fact that seed fate may depend on the handling technique used to originally place them in separate categories. High overlap between these groups may be explained by the fact that many vertebrate species both prey upon and disperse the same seed species, blurring the distinction between groups. Monkeys, for example, may (1) swallow and defecate seeds; or (2) similar to squirrels and other rodents, may damage seeds while attempting to consume the fruit pulp; or (3) may drop seeds undamaged when manipulating fruit (Kaplin & Moermond 1998). Thus, the same vertebrate species can regularly act as both seed disperser and seed predator, and seed predation may simply be one cost of reliable dispersal (Janzen 1971). Plant species eaten by both monkeys and squirrels, or that are both defecated and dropped by monkeys, may benefit from dispersal at different distances from the parent plant. Such differential treatment of seeds of the same species may increase the probability that a seed reaches a safe site (Wheelwright & Orians 1982).

Our dispersal overlap results differ from a study in Gabon where researchers concluded that plant species have a large set of alternative consumers that can functionally replace one another in seed dispersal (Gautier-Hion *et al.* 1985, Gautier-Hion 1990). These studies also found that the frugivore community consisted of two large guilds; however, the first was comprised of large birds and monkeys and the second consisted of rodents and ruminants. We did not examine seed dispersal by ruminant species, and rodents were only indirectly incorporated in our study as drop dispersers and seed predators. Seed trap sampling in the Dja Reserve, however, strongly indicated that large birds and monkeys play very different seed dispersal roles and should not be considered part of a common disperser guild.

IMPLICATIONS.—Two important lessons emerge from our study. First, using seed traps to measure seed rain and quantify dispersal by vertebrates has advantages over traditional vertebrate-centered studies. It allows one to determine not only the number of species dispersed but also the proportion of the seed rain disseminated by vertebrates. In addition, seed rain studies provide a community perspective (although detailed information on any single species may be lost). While it is understood that vertebrates provide seed dispersal services for a large proportion of forest plant species, it is less clear if the relatively small percentage of seeds removed and their distribution results in successful recruitment.

Second, the fact that different disperser groups take seeds from different canopy levels suggests that forest structure could be important for maintaining the species assemblages and diversity of the frugivore community. Few studies have demonstrated the importance of lower and middle canopy strata to large-bodied frugivores, specifically monkeys. Thus, selective logging practices that cause considerable damage to lower canopy fruit resources, although not impacting many upper canopy species, may fall short of maintaining important resources for monkey populations. Alternatively, because birds and monkeys represent different functional groups, they probably cannot replace one another as seed dispersers. Therefore, slight changes in the vertebrate composition within a forest, for example due to hunting pressures, could leave some plant species without vertebrate dispersers and potentially alter forest structure.

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APPENDIX 1. *List of arboreal frugivore species present at BMS, Dja Reserve, Cameroon.*

Birds:	BUCEROTIDAE	*Ceratogymna atrata*
		C. cylindricus
		C. fistulator
	MUSOPHAGIDAE	*Corythaeola cristata*
		Tauraco macrorhynchus
		T. persa
Primates:	CERCOPITHECIDAE	*Cercocebus albigena*
		Cercopithecus cephus
		C. nictitans
		C. pogonias
	COLOBIDAE	*Colobus guereza*
	STREPSIRHINI	*Galago alleni*
		G. demidovii
Squirrels:	SCIURIDAE	*Atherurus africanus*
		Cricetomys emini
		Deomys ferrugineus
		Funisciurus lemniscatus
		Heliosciurius rufobrachium
		Hybomys univittatus
		Hylomyscus sp.
		Lophuromys nudicaudus
		Oenomys hypoxanthus
		Paraxerus poensis
		Praomys sp.
		Protoxerus stangeri
		Stochomys longicaudatus
		Tattus sp.

APPENDIX 2. *Species list of fruit and seed species handled by the arboreal frugivore community. CS = canopy strata; MON = monkey-dispersed; BRD = bird-dispersed; DD = drop-dispersed; and PREY = preyed upon. Canopy strata are defined as UC = upper canopy species (adult heights >35 m); MC = mid-canopy species (adult heights 15–35 m); LC = lower canopy species (adult height <15 m); and LI = liana species.*

Species	Family	CS	MON	BRD	DD	PREY
Antrocaryon klaineanum	ANACARDIACEAE	MC	x			
Lannea welwitschii	ANACARDIACEAE	MC	x	x		
Pseudospondias microcarpa	ANACARDIACEAE	MC	x			
Sorindeia grandifolia	ANACARDIACEAE	LC	x		x	x
Trichoscypha acuminata	ANACARDIACEAE	MC			x	
Annonidium mannii	ANNONACEAE	LC			x	x
Artabotrys rufus	ANNONACEAE	LI	x		x	x
Cleistopholis glauca	ANNONACEAE	MC		x		
C. patens	ANNONACEAE	MC		x		x
Enantia chlorantha	ANNONACEAE	MC		x	x	x
Hexalobus crispiflorus	ANNONACEAE	LC			x	x
Monanthotaxis sp.	ANNONACEAE	LI	x		x	x
Monodora tenuifolia	ANNONACEAE	LC			x	x
Pachypodanthium staudtii	ANNONACEAE	MC	x	x	x	
Polyalthia suaveolens	ANNONACEAE	UC		x	x	x
Uvaria muricata	ANNONACEAE	LI	x		x	x
Uvaria sp.	ANNONACEAE	LI	x		x	x
Uvaria sp.	ANNONACEAE	LI	x			x
Uvariastrum pierreanum	ANNONACEAE	LC			x	x
Uvariopsis sp.	ANNONACEAE	LC			x	x
Xylopia aethiopica	ANNONACEAE	MC		x		
X. hypolampra	ANNONACEAE	UC		x	x	x
X. parviflora	ANNONACEAE	MC	x		x	x
X. quintasii	ANNONACEAE	MC	x			
X. rubescens	ANNONACEAE	MC		x	x	
X. staudtii	ANNONACEAE	MC		x	x	
Funtumia elastica	APOCYNACEAE	MC				x
Landolphia owariensis	APOCYNACEAE	LI			x	x
Landolphia sp.	APOCYNACEAE	LI			x	x
Landolphia sp.	APOCYNACEAE	LI			x	x
Landolphia sp.	APOCYNACEAE	LI			x	x
Landolphia sp.	APOCYNACEAE	LI			x	x
Rauvolfia macrophylla	APOCYNACEAE	MC	x	x		
R. vomitoria	APOCYNACEAE	LC	x			x
Tabernaemontana crassa	APOCYNACEAE	LC				x
Anchomanes difformis	ARACEAE	LC				x
Calamus deërratus	ARECACEAE	LI		x		x
Elaeis guineensis	ARACACEAE	LC				x
Eremospatha macrocarpa	ARECACEAE	LC				x
Laccosperma secundiflorum	ARECACEAE	LI		x	x	x
Raphia monbuttorum	ARECACEAE	LC				x
Canarium schweinfurthii	BURSERACEAE	UC		x	x	
Dacryodes edulis	BURSERACEAE	LC	x			x
Dacryodes sp.	BURSERACEAE	LC			x	x
Santiria trimera	BURSERACEAE	MC	x	x	x	x
Anthonotha macrophylla	CAESALPINIOIDEAE	LC				x
Berlinia bracteosa	CAESALPINIOIDEAE	LC				x
Dialium dinklagei	CAESALPINIOIDEAE	MC	x		x	x
D. guineense	CAESALPINIOIDEAE	MC	x		x	x
Distemonanthus benthamianus	CAESALPINIOIDEAE	UC				x
Erythrophoem suaveolens	CAESALPINIOIDEAE	UC			x	x
Helictonema velutinum	CELASTRACEAE	LI			x	x
Salacia sp.	CELASTRACEAE	LC	x		x	
Salicia sp.	CELASTRACEAE	LI	x		x	x
Salicia sp.	CELASTRACEAE	LI	x			
Allanblackia floribunda	CLUSIACEAE	MC				x
Garcinia cf. *mannii*	CLUSIACEAE	LC			x	x

APPENDIX 2. *Continued.*

Species	Family	CS	MON	BRD	DD	PREY
G. cf. *ovalifolia*	CLUSIACEAE	LC	x			x
G. cf. *smeathmannii*	CLUSIACEAE	LC	x		x	x
Pentadesma butyracea	CLUSIACEAE	MC	x		x	
Symphonia globulifera	CLUSIACEAE	MC	x			
Pteleopsis hylodendron	COMBRETACEAE	UC				x
Agelaea sp.	CONNARACEAE	LI	x			x
Cnestis sp.	CONNARACEAE	LI	x			x
Roureopsis obliquifoliolata	CONNARACEAE	LI		x		x
Dichapetalum heudlotii	DICHAPETALACEAE	LI	x		x	
D. mombuttense	DICHAPETALACEAE	LI	x			
Tapura africana	DICHAPETALACEAE	LI	x		x	
Tetracera podotricha	DILLENIACEAE	LI	x			x
T. potatoria	DILLENIACEAE	LI	x			x
Diospyros cf. *conocarpa*	EBENACEAE	LC	x			x
Alchornea cordifolia	EUPHORBIACEAE	LC				x
Antidesma laciniatum	EUPHORBIACEAE	LC	x			
Antidesma sp.	EUPHORBIACEAE	LC	x			x
Discoglypremna caloneura	EUPHORBIACEAE	MC	x			x
Drypetes capillipes	EUPHORBIACEAE	LC	x		x	
D. chevalieri	EUPHORBIACEAE	LC	x		x	
D. gossweileri	EUPHORBIACEAE	LC	x		x	x
Drypetes sp.	EUPHORBIACEAE	LC			x	x
Keayodendron bridelioides	EUPHORBIACEAE	LC	x		x	
Macaranga gabunica	EUPHORBIACEAE	LI	x			x
M. spinosa	EUPHORBIACEAE	MC	x	x		
Manniophyto fulvum	EUPHORBIACEAE	LI			x	x
Margaritaria discoidea	EUPHORBIACEAE	LC	x			x
Microdesmis puberula	EUPHORBIACEAE	LC	x			
Plagiostyles africana	EUPHORBIACEAE	LC	x			x
Uapaca acuminata	EUPHORBIACEAE	MC	x		x	x
U. cf. *guineensis*	EUPHORBIACEAE	MC	x			x
U. cf. *paludosa*	EUPHORBIACEAE	MC	x		x	x
U. vanhouttei	EUPHORBIACEAE	MC	x			
Caloncoba glauca	FLACOURTIACEAE	MC	x		x	x
Casearia barteri	FLACOURTIACEAE	MC	x		x	x
Lindackeria dentata	FLACOURTIACEAE	LC	x			
Scottellia mimfiensis	FLACOURTIACEAE	MC	x			
Hippocratea myrioneura	HIPPOCRATOIDEAE	LI				x
Klainedoxa gabonensis	IRVINGIACEAE	UC			x	x
Beilschmeidia sp.	LAURACEAE	LC	x			x
Petersianthus macrocarpus	LECYTHIDACEAE	UC				x
Lepidobotrys staudtii	LEPIDOBOTRYACEA	LC			x	x
Hugonia platysepala	LINACEAE	LI	x		x	x
Strychnos camptoneura	LOGANIACEAE	LI			x	x
Strychnos sp.	LOGANIACEAE	LI	x		x	x
Haumania danckelmaniana	MARANTACEAE	LI			x	x
H. liebrechtsiana	MARANTACEAE	LI			x	x
Hypselodelphis scandens	MARANTACEAE	LI			x	
Megaphrynium macrostachyum	MARANTACEAE	LC	x		x	
Sarcophrynium brachystachyum	MARANTACEAE	LC	x		x	
Guarea cedrata	MELIACEAE	UC		x	x	x
G. thompsonii	MELIACEAE	UC		x	x	x
Trichilia rubescens	MELIACEAE	MC		x		x
T. welwitschii	MELIACEAE	MC	x	x	x	x
Turreanthus africanus	MELIACEAE	MC	x		x	x
Acacia pennata	MIMOSOIDEAE	LI				x
Albizia adianthifolia	MIMOSOIDEAE	UC				x
Calpocalyx cf. *dinklagei*	MIMOSOIDEAE	LC				x
Entada gigas	MIMOSOIDEAE	LI				x
Entada sp.	MIMOSOIDEAE	LI			x	x
Pentaclethra macrophylla	MIMOSOIDEAE	MC				x

APPENDIX 2. *Continued.*

Species	Family	CS	MON	BRD	DD	PREY
Piptadeniastrum africanum	MIMOSOIDEAE	UC			x	x
Ficus jansii	MORACEAE	LC	x			
F. variifolia	MORACEAE	MC	x	x		
Ficus sp. 1	MORACEAE	LI	x	x		
Ficus sp. 2	MORACEAE	LI	x			
Ficus sp. 3	MORACEAE	LI	x			
Musanga cecropiodes	MORACEAE	LC	x		x	x
Myrianthus arboreus	MORACEAE	LC	x		x	
Treculia africana cf. var. *mollis*	MORACEAE	LC			x	x
Trilepisium madagascariense	MORACEAE	MC		x	x	x
Coelocaryon preussi	MYRISTICACEAE	UC		x	x	
Pycnanthus angolensis	MYRISTICACEAE	UC		x	x	
Staudtia kamerunensis	MYRISTICACEAE	UC		x		
Syzgium rowlandii	MYRTACEAE	UC		x	x	x
Heisteria zimmereri	OLACACEAE	MC	x	x		x
Ongokea gore	OLACACEAE	MC			x	x
Strombosia grandifolia	OLACACEAE	MC	x		x	x
S. pustulata	OLACACEAE	MC			x	x
S. scheffleri	OLACACEAE	MC	x		x	x
Strombosiopsis tetrandra	OLACACEAE	MC				x
Panda oleosa	PANDACEAE	LC				x
Dalbergia cf. *rufa*	PAPILIONOIDEAE	LI				x
Dalbergia sp.	PAPILIONOIDEAE	LI			x	x
Millettia drastica	PAPILIONOIDEAE	LI			x	x
M. duchesnei	PAPILIONOIDEAE	LI			x	x
Physostigma venenosum	PAPILIONOIDEAE	LI			x	x
Lasiodiscus mannii	RHAMNACEAE	LC				x
Maesopsis eminii	RHAMNACEAE	UC		x		x
Adia micrantha	RUBIACEAE	LC	x		x	x
Bertiera sp.	RUBIACEAE	LC	x		x	
Canthium sp.	RUBIACEAE	LC			x	x
Cephaelis densinervia	RUBIACEAE	LC	x			
C. mannii	RUBIACEAE	LC	x			
Coffea sp.	RUBIACEAE	LC			x	x
Heinsia crinita	RUBIACEAE	LC			x	x
Psychotria vogeliana	RUBIACEAE	LC	x		x	x
Fagara macrophylla	RUTACEAE	LC	x			x
F. poggei	RUTACEAE	LI	x			x
F. viridis	RUTACEAE	LI	x			x
Blighia welwitschii	SAPINDACEAE	MC		x		x
Chytranthus angustifolius	SAPINDACEAE	LC	x			x
C. cf. *gilletii*	SAPINDACEAE	LC	x			x
Eriocoelum macrocarpum	SAPINDACEAE	MC		x		x
Afrosersalisia sp.	SAPOTACEAE	MC	x			x
Aningeria robusta	SAPOTACEAE	MC	x		x	x
Donella ubanguiensis	SAPOTACEAE	MC	x			
Gambeya boukokoensis	SAPOTACEAE	MC	x		x	x
G. perpulchra	SAPOTACEAE	MC	x		x	x
Manilkara aff. *multinervis*	SAPOTACEAE	MC	x		x	x
Manilkara sp.	SAPOTACEAE	MC	x		x	x
Synsepalum cf. *longecuneatum*	SAPOTACEAE	MC	x		x	x
S. stipulatum	SAPOTACEAE	LC	x		x	x
Eribroma oblongum	STERCULIACEAE	UC		x		x
Sterculia tragacantha	STERCULIACEAE	LC			x	x
Desplatsia chrysochlamys	TILIACEAE	LC			x	x
D. dewevrei	TILIACEAE	LC			x	x
Duboscia macrocarpa	TILIACEAE	MC	x		x	x
Grewia coriacea	TILIACEAE	LC	x			

APPENDIX 2. *Continued.*

Species	Family	CS	MON	BRD	DD	PREY
G. hookerana	TILIACEAE	LI	x			
G. pubescens	TILIACEAE	LC	x			x
Celtis adolfi-friderici	ULMACEAE	MC	x			
C. mildraedii	ULMACEAE	UC	x	x		
Vitex ferruginea	VERBENACEAE	LC	x		x	
V. grandifolia	VERBENACEAE	LC	x			
V. thyrsiflora	VERBENACEAE	LI	x			
Cissus densiflora	VITACEAE	LI	x			
C. dinklagei	VITACEAE	LI	x			
C. producta	VITACEAE	LI	x			
Afromomum dalzielii	ZINGIBERACEAE	LC	x			x