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Seed rain beneath remnant trees in a slash-and-burn agricultural system in southern Cameroon

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ABSTRACT. On clearing fields, Ntumu farmers in southern Cameroon leave some large trees. The seed rain beneath 30 such remnant trees (12 species) was compared with that 10 m away from the edges of their crowns. Of a total of 39 765 seeds recorded in 90 seed traps over 2 y, 73.6% were of species different from the tree associated with each set of traps ('foreign seed rain'). Seed rain included 100 morphospecies, two-thirds of which possessed endozoochorous seeds. Seeds of the pioneer tree *Musanga cecropioides* accounted for 71.4% of total foreign seed rain; seeds of this and other animal-dispersed species accounted for 94.5% of the total. Seed rain was 25 times higher beneath remnant trees than 10 m away. Mean species richness of monthly seed rain was three times higher beneath remnant trees than 10 m away. Both fleshy-fruited and wind-dispersed species of remnant trees attracted seed-dispersing animals which greatly enhanced the seed rain; attraction thus did not depend solely on presence of fleshy fruits. Seed rain was lower when human activity in fields was intense and increased during the period of growth of the last crops, which were not usually weeded. Heavy seed rain just before fallow may contribute significantly to regeneration, as does the presence of remnant trees.

KEY WORDS: regeneration, remnant trees, seed dispersal, slash-and-burn agriculture, succession, tropical forest

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INTRODUCTION

Remnant trees in fields are seen as 'recruitment foci' by tropical forest farmers (Carrière 1999, Warner 1995) as well as by researchers (McDonnell & Stiles 1983, Slocum 1997). In particular, the transition from fallow field to regenerating forest in slash-and-burn farming systems may be especially dependent upon the arrival of fresh seed rain, because burning after the clearing of a field could destroy most of the seeds stored in the soil, as well as root and stump sprouts and seedlings that appeared after clearing (Nepstad *et al.* 1991, Whitmore 1990). In tropical forest systems, in general, regeneration from soil seed banks after a disturbance, such as slash-and-burn cultivation, is often dominated by pioneer species (Ashton 1978, Guevara & Gomez-Pompa 1972, Hall & Swaine 1980, Keay 1960, Vasquez-Yanes 1976), while regeneration of mature forest species is dependent upon fresh seed rain (Garwood 1989). Many studies in neotropical and temperate ecosystems have shown that remnant or planted trees and other perches, in active or fallow fields and in regenerating pastures, attract seed dispersers which enhance the seed rain beneath their crowns and thus speed forest regeneration (Cardoso *et al.* 1996, Guevara *et al.* 1986, 1992; Guevara & Laborde 1993, Holl 1998, Janzen 1988, McClanahan & Wolfe 1987, 1993; McDonnell & Stiles 1983, Nepstad *et al.* 1996; Parrotta 1995, Vieira *et al.* 1994, Wegner & Merriam 1979). In addition to this effect, the shaded conditions and the higher availability of soil nutrients and moisture under remnant trees (Belsky & Canham 1994, Buschbacher *et al.* 1988, Nepstad *et al.* 1991, Parrotta 1992, Sirois *et al.* 1998, Vieira *et al.* 1994) make such sites favourable for establishment of forest species. These 'foci of regeneration' of persistent species may eventually coalesce with others, according to the 'nucleation model of succession' developed by Yarranton & Morrison (1974), and thus speed up the transition towards mature forest. African studies of the role of remnant trees in forest regeneration have been conducted primarily in savanna and dry forest ecosystems. Moreover, little is known, for any part of the tropics, about the key characteristics of sites chosen as perches by seed-dispersing frugivores (Guevara *et al.* 1986, Janzen 1988).

The aim of this study was to compare the seed rain (composition and quantity) beneath the crowns of remnant trees and away from their crowns in clearings created by slash-and-burn agriculture. By comparing seed rain beneath species with different dispersal modes, we determined whether fleshy fruits were essential to attracting seed dispersers. A companion study (Carrière *et al.* 2002) examined the effects of remnant trees on regeneration, which may be influenced not only by seed rain but also by specific effects of remnant trees on conditions for establishment.

STUDY SITE

The study was conducted at the village of Nkongmeyos (2°27′N, 10°27′E) in southwestern Cameroon, on the north bank of the Ntem river, near the border with Gabon and Equatorial Guinea. This Ntumu village, at the edge of the Ntem valley, is on a plateau *c.* 500 m asl (IRD 1990). The mean annual temperature is *c.* 25 °C and the site receives *c.* 1497 mm of rainfall annually (Nyabessan, 2°24′N – 10°24′E; 1976–1980) (IRD 1990). There are two rainy seasons and two dry seasons per year. A short rainy season (March–May) is followed by a long dry season (June–August), then a long rainy season (September–November) and a short dry season (December to February) (Table 1). Ferralitic yellow soils characterize the region; they are acidic and poor in nutrients (Letouzey 1985). Predominant original vegetation is classified as transitional (Letouzey 1985) between semi-deciduous forest of areas to the north and the evergreen Congolean rain forest found to the south and east, with many tree species typical of old secondary forests (no agricultural disturbance for about 100–150 y), such as *Ceiba pentandra* (L.) Gaertn. (Bombacaceae), *Terminalia superba* Engl. & Diels (Combretaceae), *Pycnanthus angolensis* (Welw.) Warb. (Myristicaceae), *Triplochiton scleroxylon* K. Schum. (Sterculiaceae), and *Lophira alata* Banks ex Gaertn. f. (Ochnaceae) (Letouzey 1985). Young secondary forests are dominated by a few abundant pioneer species such as *Musanga cecropioides* R. Br. (Moraceae), *Trema guineensis* (Schum. & Thonn.) Ficalho (Ulmaceae), *Alchornea floribunda* Müll. Arg. (Euphorbiaceae) and many species of large herbaceous monocots (Zingiberaceae, Marantaceae and Commelinaceae) which compose the dense undergrowth of secondary forests.

Table 1. Correspondences between sample number, date of collecting, and period sampled for seed rain in the Ntem Valley, southern Cameroon, 1996–1998. Period and season codes used in the text and figures.

Date number		Period sampled for seed rain		Season code
1	1996	15 April – 15 May	(sr)	Short Rainy
2		15 May – 15 June	(tld)	Transition to Long Dry
3		15 June – 15 July	(ld)	Long Dry
4		15 July – 15 August	(ld)	Long Dry
5		15 August – 15 September	(tlr)	Transition to Long Rainy
6		15 September – 15 October	(lr)	Long Rainy
7		15 October – 15 November	(lr)	Long Rainy
8		15 November – 15 December	(tsd)	Transition to Short Dry
9	1997	15 December – 15 January	(sd)	Short Dry
10		15 January – 15 February	(sd)	Short Dry
11		15 February – 15 March	(tsr)	Transition to Short Rainy
12		15 March – 15 April	(sr)	Short Rainy
13		15 April 96 – 15 May 96	(sr)	Short Rainy
14		15 May – 15 June	(tld)	Transition to Long Dry
15		15 June – 15 July	(ld)	Long Dry
16		15 July – 15 August	(ld)	Long Dry
17		15 August – 15 September	(tlr)	Transition to Long Rainy
18		15 September – 15 October	(lr)	Long Rainy
19		15 October – 15 November	(lr)	Long Rainy
20		15 November – 15 December	(tsd)	Transition to Short Dry
21	1998	15 December – 15 January	(sd)	Short Dry
22		15 January – 15 February	(sd)	Short Dry
23		15 February – 15 March	(tsr)	Transition to Short Rainy
24		15 March – 15 April	(sr)	Short Rainy
25		15 April – 15 May	(sr)	Short Rainy

The whole area is surrounded by old secondary forest, and many patches of this kind of forest are found throughout the village's territory. These areas serve as the sources of seed of forest species that colonize the regenerating fields.

METHODS

Selection of study fields and trees

Field work was carried out over 2 y (April 1996 – May 1998). Trees were all selected within an area of *c.* 3 km^2 belonging to one village, and all had similar climate and soils. The 17 chosen fields were in their first crop in the current cycle of cultivation (planted primarily with peanut, *Arachis hypogea* L., Fabaceae) at the beginning of the study. This uniformity allowed a comparison of levels of intensity of human presence in the fields throughout a large part of the cycle. After sowing and harvesting (*c.* 6 mo) of the crop of peanuts, human presence, especially that of women, decreases during growth of the next crop (cassava, banana, yams or others) and decreases even more during the fallow period, 1 y later (Carrière 1999). Twelve species of remnant trees were chosen based on two characteristics. First, all 12 species belong to the group of high-frequency species preferentially left by cultivators during clearing (Carrière 1999). Second, we chose species to include six with fleshy fruits and animal-dispersed seeds, and six with dry fruits and primarily wind-dispersed seeds. Species with fleshy fruits were hypothesized to be more attractive to frugivorous animals and thereby to have higher rates of seed deposition beneath them (Cardoso *et al.* 1996, Guevara *et al.* 1986, Guevara & Laborde 1993, Holl 1998, Janzen 1988, McClanahan & Wolfe 1987, McDonnell & Stiles 1983, Vieira *et al.* 1994, Wegner & Merriam 1979). The six species with fleshy fruits (or with arils or other rewards for frugivores) were (16 trees in all): *Duboscia macrocarpa* Bocq. (Tiliaceae, n = 3), *Eribroma oblongum* (Mast.) Bod. (Sterculiaceae, n = 3), *Uapaca heudelotii* Müll. Arg. (Euphorbiaceae, n = 1), *Ficus vogeliana* (Moraceae, n = 3), *Musanga cecropioides* (n = 3) and *Pycnanthus angolensis* (n = 3). The *Uapaca*, *Musanga* and *Pycnanthus* spp. are dioecious. Only female trees (known from interviews to have borne fruits in the past) were selected. A total of 14 individuals of six dry-fruited species were selected: *Ceiba pentandra* (n = 3), *Triplochiton scleroxylon* (n = 3), *Desbordesia glaucescens* (Engl.) v. T. (Irvingiaceae, n = 2), *Lovoa trichilioides* Harms (Meliaceae, n = 1), *Terminalia superba* (n = 3) and *Erythrophleum ivorense* A. Chev. (Caesalpinioideae, n = 2). Distance from forest edges and size and shape of fields have been shown to be important in determining seed rain in some other systems (Cardoso *et al.* 1996, McDonnell & Stiles 1983) but in the Ntumu system the range of distances between remnant trees in the fields and forest edges is not large enough to test for such variation. Remnant tree mean density was 15.4 tree ha^{-1}, area of most of the fields was between 0.5 and 1 ha, and fields were almost always surrounded by old or mature secondary rain forest (Carrière 1999). Thus the greatest distance between remnant trees in the fields and forest edges and other remnant trees was 30–50 m (Carrière 1999). Initially only 11 individual trees were included in the sample. After 10 mo of study, the number of sampled trees was increased to 30. Thus the period in which all 30 trees were sampled was from mo 11 to 25 of the study. Also, mo 1–6 and 13–18 were characterized by a relatively high frequency of human occurrence (peanut fields, which require a daily human presence) in half of our fields and mo 7–12 and 19–25 were characterized by lower intensity of human presence in the fields.

Seed collection in traps

To compare seed rain beneath and away from the crowns of remnant trees, for each of the 30 trees selected we placed a set of three seed traps at varying distance from the trunk. Trap 1 was near the trunk and trap 2 also beneath the tree's crown but at least 2 m from the trunk. Trap 3 was placed in the open field 10 m from the edge of the crown. Traps were constructed of nylon mesh (*c.* 0.5 mm) sewn around a circular bamboo frame, and were 50 cm in diameter and 1 m deep. All of the three traps around a focal tree were located on a single line originating from the trunk. For each tree sampled this direction was selected at random. Contents of each trap were collected monthly, dried, packed into paper bags and later sorted and analysed in the laboratory. A total of 25 monthly samples (May 1996 – May 1998) were thus collected (Table 1). Seeds were counted and identified. We tabulated separately seeds of the focal tree species, since these could have been produced by the focal individual. We thus distinguished between total (including conspecific) and 'foreign' seed rain. Seeds arriving from other individuals of the focal tree species are thus not counted in 'foreign' seed rain. We classified seeds by their dispersal mode (anemochorous, autochorous, ectozoochorous, endozoochorous). One-third of the species collected have not been determined to the family level and are distinguished as morphospecies; many others have not been determined to the species level. We thus used certain characteristics, based on our experience, to categorize the dispersal syndrome. For the analysis, two categories of seeds were distinguished, wind- and explosively dispersed seeds, and those dispersed by animals. Light seeds with hairs or wings on the seed or on the fruit were classified as wind-dispersed. All Leguminosae were determined at least to the family level and those with seeds borne in explosively dehiscent pods, in wind-dispersed fruits (e.g. *Pterocarpus* sp.) or with the seed itself bearing a wing (e.g. *Piptadeniastrum africanum*) could be distinguished from others. Small seeds or fruits of two species with apparent adaptations for ectozoochory (spines, needles or hooks) were found in the traps. Since such seeds can also be dispersed by wind, they were classified as wind-dispersed seeds. Other seeds, without any of the characteristics of wind- or explosively dispersed seeds, were classified as endozoochorous and thus animal-dispersed. In our experience, this classificatory decision is fully justified, as the great majority of plant species in the site possessed animal-dispersed seeds (cf. White & Abernethy 1996). Species richness was tabulated for each sample and cumulative species richness for seeds associated with each focal tree.

Data analysis

The sampling plan corresponded to a 'split-plot' design because the three positions were nested within trees. As the design was unbalanced over time (n = 11 for the first 10 mo and n = 30 for the last 15 mo) and the effect of seed trap position was generally strong, the data were analysed for two time periods. First we used mixed linear models (Proc mixed, routine in SAS 1996) and Student's t-tests to compare means and to test effects on seed rain of the position of the seed trap and dispersal mode of the focal tree. This first analysis was done only on the last 15 mo where all 30 trees were sampled, to avoid a complex analysis. Then, the analysis was performed by position, and the correlations between the dates were found by a first-order auto-regressive process with heterogeneous covariance structure. For that, linear mixed models (Proc mixed, routine in SAS 1996) and Student's t-tests were used to compare means and to test effects on seed rain of the following predictor variables: (1) position of the seed trap (1, 2 or 3); (2) dispersal mode of the focal tree, anemochorous or zoochorous; (3) season (with eight seasons including periods of transition between rainy and dry seasons; Table 1); (4) the year effect to compare the two years of study; and finally (5) human presence. Each tree unit was not sampled at all the dates, and the linear mixed model analyses more exactly the covariance structure between the dates. The different sources of variation are presented in Table 2. Dates are repeated measurements on the same units (trees). Because data were counts (close to a Poisson distribution), before calculation of means, values for each of the quantitative variables were normalized (Sokal & Rohlf 1969) by the following transformation: $Y' = \sqrt{(Y'+0.5)}$.

RESULTS

General description of seed rain

A total of 39 765 seeds were found in seed traps during the 25 mo of seed collection. Of this total, 29 250 seeds were of species different from the focal

Table 2. Structure of the analysis with the different sources of variation and the degree of freedom (df).

Source of variation	df
Dispersal mode	1
Season	7
Year	1
Season × year (interaction)	7
Date within (season × year)	9
Dispersal × season × year × date (interaction)	24
HP (human presence)	3
Date within (HP)	21
Dispersal × HP × date	24

tree (Table 3). 'Foreign seed rain' thus accounted for at least 73.6% of the total seed rain. Foreign seed rain included a taxonomically and morphologically diverse assemblage (seeds of 68 species were determined at least to the family level; 32 other morphospecies were distinguished) of 100 morphospecies (Appendix 1), 33 of which had wind- or explosively dispersed or ectozoochorous seeds and 67 of which had endozoochorous seeds. For the whole period, the number of traps × mo sampled was 1680 (Table 3). The total and thus the average density varied greatly among trap positions (Table 3). Seeds of wind- and explosively dispersed species represented only 5.5% of the total foreign seed rain, including such pioneer species as *Chromolaena odorata* (L.) R. M. King & H. Robinson (Asteraceae) and semi-deciduous mature forest tree species such as *Ceiba pentandra*, *Terminalia superba* and *Erythrophleum ivorense*. Animal-dispersed species accounted for 94.5% of the total. A very large proportion of the foreign seed rain was accounted for by seeds of *Musanga cecropioides*: 71.4% of the foreign seed rain and 75.5% of the animal-dispersed foreign seed rain. Animal-dispersed species other than *Musanga cecropioides* accounted for 6705 seeds, 22.3% of the total animal-dispersed foreign seed rain. These seeds belonged to a great diversity of forest tree species (Appendix 1), such as *Ficus* spp., *Pycnanthus angolensis*, *Polyalthia* spp., *Xylopia* spp., and pioneer species such as *Trema guineensis*, *Solanum* spp. and others.

Foreign seed rain overall

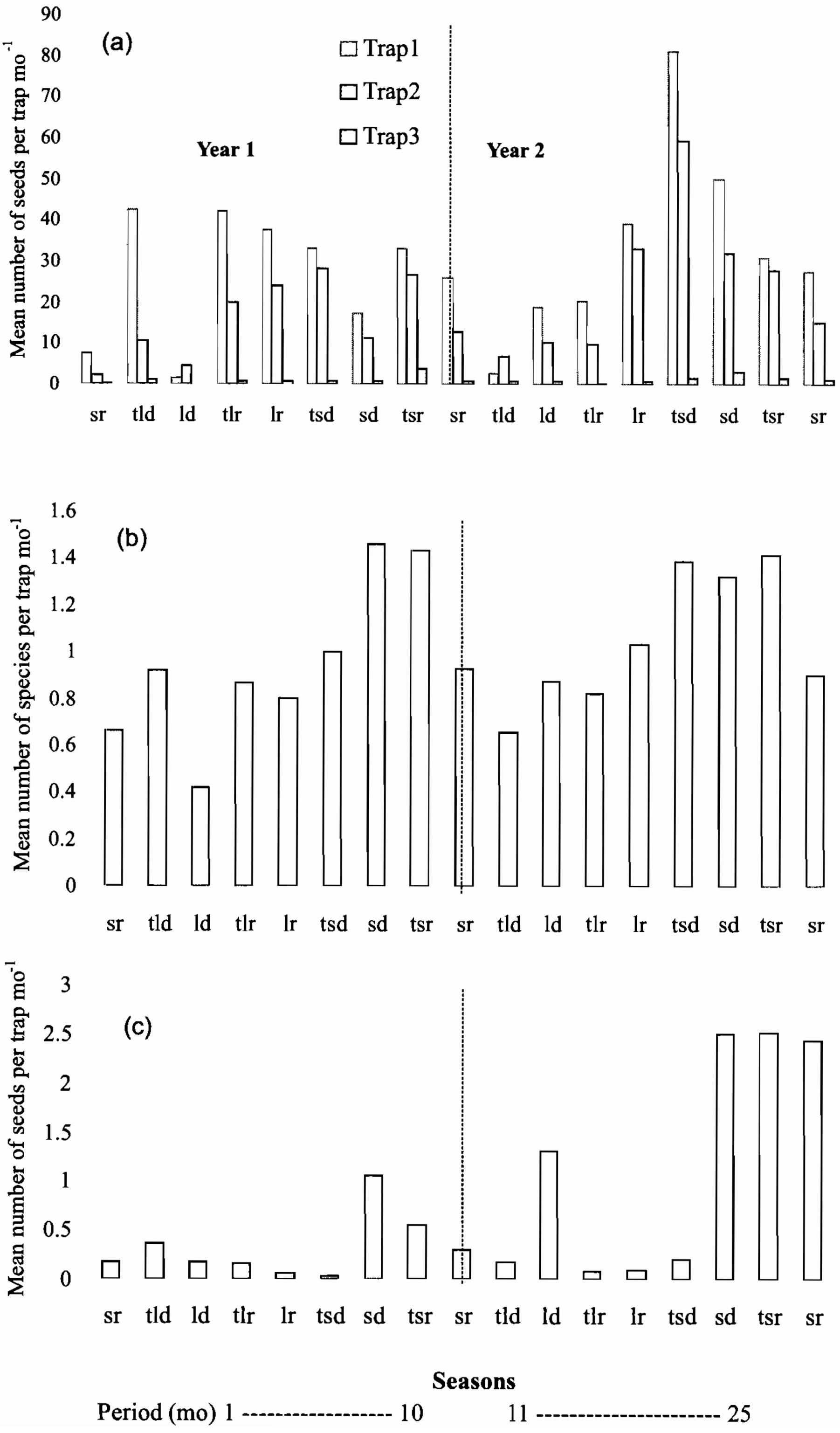
A strong position effect was found ($F = 28.3$, df = 2,28, $P < 0.0001$). Number of foreign seeds rained into traps at position 1 (30.2 seeds per trap mo^{-1}) was greater ($t = 1.79$, df = 28, $P < 0.02$) than that into traps at position 2 (20.9 seeds per trap mo^{-1}), which was in turn greater ($t = 7.63$, df = 28, $P < 0.0001$) than that into traps at position 3 (1.2 seeds per trap mo^{-1}). The analysis by position showed a season and date (within season × year) effect for the three positions (Table 4). A season × year interaction was observed for positions 1 and 3 (Table 4). Despite substantial variation between the two years of seed collection, some patterns were observed in both years (Figure 1a). Comparisons between the same season in the first and the second year are not significantly different (Student's t-test; $P > 0.05$). At position 1, seed rain during the long dry season and the transition to the long dry season was significantly different from that during the transition to the short dry season of the first year and the second year (for the three comparisons: $P < 0.03$). At position 2 (and to a lesser degree at position 1) for the two years, number of foreign seeds was significantly ($P < 0.05$) higher during the short dry season and the preceding transition to short dry season than during the long dry season (Figure 1a). The foreign seed rain was significantly ($P < 0.05$) lower during the short rainy season than the long rainy season and the following transition to short dry season. The number of foreign seeds was significantly higher during the transition between the long rainy season of the year 2 and the short dry season than the following short dry season (Figure 1a).

Table 3. Principal results (including mean number of seeds, seeds / trap mo^{-1} ± standard deviation) on seed rain beneath and away from the crowns of remnant trees in fields in the Ntem Valley, southern Cameroon, 1996–1998.

		Foreign seed rain			
		Trap position			
	n focal trees	1 (beneath the tree)	2 (2 m from the trunk)	3 (away from the crown)	Total
Study period					
10 mo	11 trees	110 traps	110 traps	110 traps	330 traps
15 mo	30 trees	450 traps	450 traps	450 traps	1350 traps
n seeds (out of a total of 39 765)		16 911	11 681	658	29 250
Average density (seeds m^{-2} mo^{-1})		152.9	105.6	5.9	88.1
Mean number of foreign seed		30.2 ± 31.4	20.9 ± 20.5	1.2 ± 1.4	17.4
Mean number of animal-dispersed seeds		28.6 ± 30.3	20.1 ± 20.4	0.7 ± 1.2	16.5
Mean number of *M. cecropioides* seeds		20.9 ± 23.3	16.0 ± 17.4	0.8 ± 0.7	12.6

Table 4. Results (only those that were significant [P < 0.05] are presented) of statistical analysis using a linear mixed model (SAS 1996) by position (degrees of freedom, F, and probability values). '-' indicates that the test was not possible due to small sample size for these variables or trap positions.

Dependent variables	Predictor variables	Beneath remnant trees						Away from remnant trees		
		Position 1			Position 2			Position 3		
		df	F	P	df	F	P	df	F	P
Foreign seed rain	Dispersal	1	3.2	0.08			ns			ns
	Season	7	4.8	0.0001	7	4.5	0.0001	7	7.1	0.0001
	Year			ns			ns			ns
	Season × Year	7	3.6	0.0018			ns	7	5	0.0001
	Date (Season × Year)	9	2.5	0.0109	9	2.2	0.024	9	4.1	0.0001
	Dispersal × Season × Year × Date			ns			ns			ns
Diversity of foreign seeds	Dispersal			ns			ns			ns
	Season	7	6.2	0.0001	7	3.2	0.029	7	6.7	0.0001
	Year			ns			ns			ns
	Season × Year	7	3.8	0.0013			ns	7	3	0.007
	Date (Season × Year)	9	4.5	0.0001	9	2.8	0.004	9	6.5	0.0001
	Dispersal × Season × Year × Date			ns			ns			ns
Animal-dispersed seed rain	Dispersal	1	3.3	0.08			ns	–	–	–
	Season	7	5.6	0.001	7	4.1	0.0003	–	–	–
	Year			ns			ns	–	–	–
	Season × Year	7	3.7	0.0015			ns	–	–	–
	Date (Season × Year)	9	2.7	0.006	9	2.3	0.02	–	–	–
	Dispersal × Season × Year × Date			ns			ns	–	–	–
M. cecropioides seed rain	Dispersal	1	8.6	0.0065			ns	–	–	–
	Season	7	7.1	0.0001	7	5.3	0.0001	–	–	–
	Year			ns			ns	–	–	–
	Season × Year	7	5.1	0.0001	7	2.3	0.03	–	–	–
	Date (Season × Year)	9	5.6	0.0001	9	2.0	0.04	–	–	–
	Dispersal × Season × Year × Date	24	2.5	0.0003			ns	–	–	–
Animal-dispersed seed rain: human presence model	Dispersal	1	3.3	0.08			ns	–	–	–
	HP	3	4.4	0.007	3	3.9	0.01	–	–	–
	Date within (HP)	21	4.01	0.0001	21	2.2	0.0015	–	–	–
	Dispersal × HP × Date			ns			ns	–	–	–
Animal-dispersed seed rain excluding *M. cecropioides* seeds	Dispersal			ns			ns	–	–	–
	Season			ns			ns	–	–	–
	Year			ns			ns	–	–	–
	Season × Year			ns			ns	–	–	–
	Date (Season × Year)			ns			ns	–	–	–
	Dispersal × Season × Year × Date			ns			ns	–	–	–


(a)
Mean number of seeds per trap mo-1
90
80
70
60
50
40
30
20
10
0
☐ Trap1
☐ Trap2
☐ Trap3
Year 1
Year 2
sr tld ld tlr lr tsd sd tsr sr tld ld tlr lr tsd sd tsr sr
(b)
Mean number of species per trap mo-1
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
sr tld ld tlr lr tsd sd tsr sr tld ld tlr lr tsd sd tsr sr
(c)
Mean number of seeds per trap mo-1
3
2.5
2
1.5
1
0.5
0
sr tld ld tlr lr tsd sd tsr sr tld ld tlr lr tsd sd tsr sr
Seasons
Period (mo) 1 ------------------ 10
11 --------------------- 25

Diversity of foreign seed rain

A strong position effect was found (F = 75.9, df = 2,28, $P < 0.0001$). Number of species found in seed rain in traps at position 1 (1.38 species per trap mo^{-1}) was not significantly different ($P > 0.05$) from that in traps at position 2 (1.25 species per trap mo^{-1}), but numbers of species at these two positions were both higher than that at position 3 (0.42 species per trap mo^{-1}): between positions 1 and 3, t = 11.0 (df = 28, $P < 0.0001$) and between positions 2 and 3, t = 10.9 (df = 28, $P < 0.0001$). The analysis by position showed a season and date (within season × year) effect for the three positions (Table 4). A season × year interaction was observed for positions 1 and 3 (Table 4). There was great seasonal variation, which was consistent for the two years, at position 2 (no interaction season × year). For the two years of study, diversity was significantly ($P < 0.05$) lower for the transition to long dry and the long dry season than the short dry season and the transition following the long dry season (tlr, Table 1). Species richness was significantly higher during the short dry season of the two years and during the periods of transition preceding and following the short dry season of the second year (Figure 1b).

Rain of animal-dispersed foreign seeds

A strong position effect was found (F = 30.5, df = 2,28, $P < 0.0001$). The number of animal-dispersed foreign seeds in traps at position 1 (28.6 seeds per trap mo^{-1}) was significantly greater (t = 2.53, df = 28, $P < 0.02$) than at position 2 (20.1 seeds per trap mo^{-1}), which was in turn greater than at position 3 (0.7 seeds per trap mo^{-1}; t = 7.79, df = 28, $P < 0.0001$ between position 1 and 3; t = 6.94, df = 28, $P < 0.0001$ between positions 2 and 3) (Figure 2a). The analysis by position showed a season and date (within season × year) effect for positions 1 and 2. A season × year interaction was also observed for position 1 (Table 4). Sample size at position 3 was too small to allow analysis. Seed rain was enhanced beneath both anemochorous and zoochorous tree species compared to the open-field site. The average number of seeds found under anemochorous trees was 17.2 seeds per trap mo^{-1}, compared to 15.5 seeds per trap mo^{-1} beneath zoochorous trees (ns; $P = 0.08$ at position 1). If a separate analysis at position 1 is conducted for seeds of *M. cecropioides* only (Table 4), a significant effect (F = 8.63, df = 1,28, $P < 0.007$) of dispersal mode in favour of the anemochorous trees is shown (14.8 seeds per trap mo^{-1}, compared to 10.1 seeds per trap mo^{-1} beneath zoochorous trees). Finally, there was a significant (Table 4) increase in the rain of animal-dispersed seeds per trap mo^{-1} at positions

Figure 1. (a) Mean number of foreign seeds rained per trap mo^{-1} into traps at positions 1 to 3 for each season of data collection and for the two years; (b) Mean number of species per trap mo^{-1} for each season of data collection and for the two years; (c) Mean number of foreign wind-dispersed seeds rained per trap mo^{-1} for each season over the two years of study (n = 11 traps at each position for the period 1 to 10, and n = 30 traps at each position for the period 11 to 25, season codes as in Table 1). For one season there are two periods of data collection (Table 1), thus there were 8 points on the curve for year (1) and 9 for year (2).

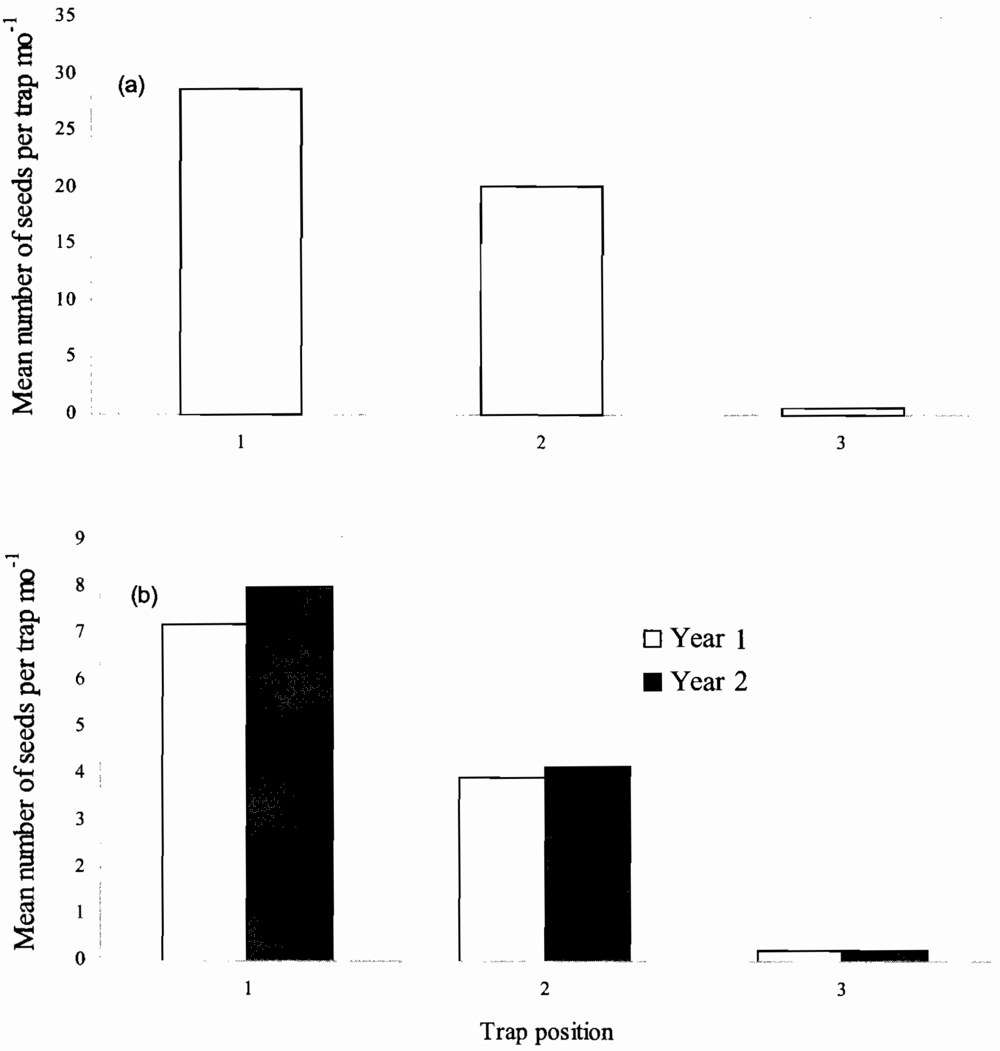


Figure 2. Mean number of foreign animal-dispersed seeds rained per trap mo^{-1} into traps at position 1 to 3; (a) all animal-dispersed seeds (year 1 and year 2) and (b) all animal-dispersed seeds excluding those of *Musanga cecropioides* for the two years of study.

1 and 2 during periods of low frequency (LF) of human presence in fields (Figure 3). At position 1 there was a significant difference between: (1) mo 1–6 characterized by high frequency of human presence (HF) and mo 18–25 (LF: $t = -1.99$, $df = 65$, $P < 0.05$) and (2) between mo 13–18 (HF) and mo 18–25 (LF: $t = -3.44$, $df = 65$, $P < 0.001$). At position 2, there was a tendency in the same direction between (1) mo 1–6 (HF) and mo 18–25 (LF: $t = -1.91$, $df = 65$, $P = 0.06$) and (2) between mo 7–12 (LF) and mo 13–18 (HF: $t = 1.84$, $df = 65$, $P < 0.07$), and a significant difference between mo 13–18 (HF) and mo 18–25 (LF: $t = -2.85$, $df = 65$, $P < 0.006$).

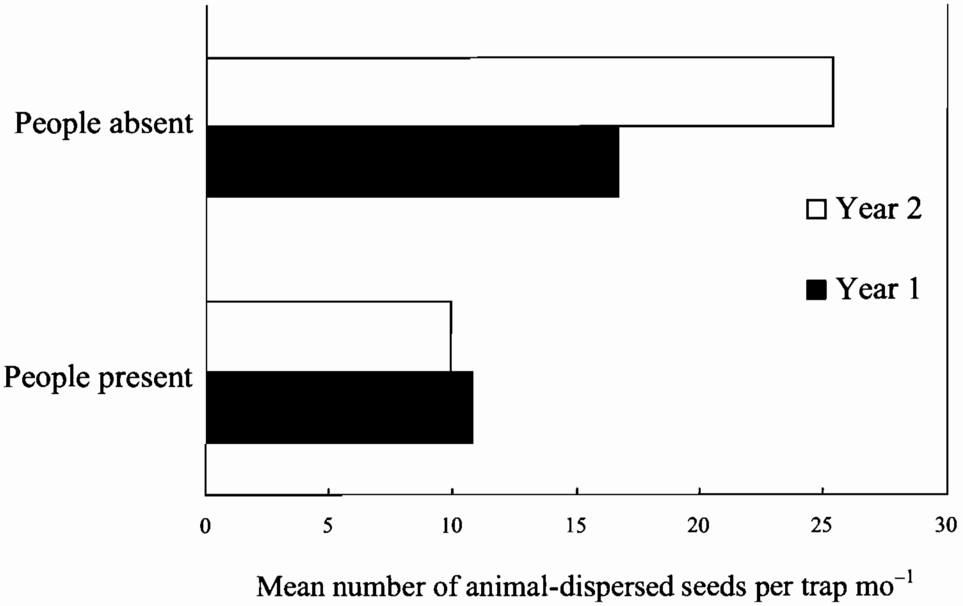


Figure 3. Mean number of foreign animal-dispersed seeds rained per trap mo^{-1} over the two years of study as a function of the frequency of human presence in the fields. Human presence period corresponds to mo 1–6 (first year) and 13–18 (second year); human absence period corresponds to mo 7–12 (first year) and 19–25 (second year).

Animal-dispersed foreign seed rain, excluding seeds of Musanga cecropioides

The pioneer species *Musanga cecropioides*, abundant in secondary forest, has fruits containing a large number of small seeds. These are eaten by a great diversity of animals, and their droppings often contain large numbers of seeds of this species. The high and continuous frequency of seeds of this species is the principal feature of seed rain into fields. However, pioneer species are not competitive in shaded conditions (Swaine & Whitmore 1988) and do not contribute to later stages of regeneration. In order to analyse patterns in the rain of other seeds, we excluded seeds of *M. cecropioides*. In this analysis, a position effect was found ($F = 9.16$, $df = 2,28$, $P < 0.001$) with no significant interactions (Figure 2b). Number of seeds averaged 7.7 seeds per trap mo^{-1} for position 1, 4.1 seeds per trap mo^{-1} for position 2 and 0.2 seeds per trap mo^{-1} for position 3 (position 1 compared to position 3: $t = 4.27$, $df = 28$, $P = 0.0002$ and position 2 compared to position 3: $t = 3.10$, $df = 28$, $P = 0.005$). The number of seeds tended to be lower (ns) beneath anemochorous trees (2.34 seeds per trap mo^{-1}) than beneath fleshy-fruited trees (5.48 seeds per trap mo^{-1}). Analysis by position revealed no significant effects of the predictor variables at position 1 and position 2 (Table 4).

DISCUSSION

Comparison of seed deposition beneath and away from remnant trees in the fields

Many frugivorous animals, such as birds, bats and monkeys, are reluctant to venture directly into open areas (Cardoso *et al.* 1996, Terborgh & Weske 1969, Wegner & Merriam 1979), but will use trees as perches when crossing agricultural lands (Guevara & Laborde 1993, Janzen *et al.* 1976). The frequent use of remnant trees as perches by animals is reflected by the fact that they are favoured as hunting sites by African rain-forest farmers (Carrière 1999, Dounias 1993). By frequenting these trees, frugivorous animals enhance seed deposition beneath them, dramatically increasing the abundance and/or diversity of seed rain beneath their crowns (Cardoso da Silva *et al.* 1996, Debussche *et al.* 1982, Debussche & Isenmann 1994, Guevara *et al.* 1986, 1992; Guevara & Laborde 1993, Holl 1998, Hooper & Bullington 1972, Janzen 1988, McClanahan & Wolfe 1987, McDonnell & Stiles 1983, Nepstad *et al.* 1996, Vieira *et al.* 1994). Season effects were very marked but quite unpredictable in their timing, especially during the transition phase between two seasons.

Rain of wind- and explosively dispersed seeds

As previously noted, 33 species had non-fleshy fruits. Seeds of this dispersal type do not depend on remnant trees to colonize fields. Without remnant trees in the fields, forest regenerating in fallows of Ntumu farms would likely have a higher proportion of wind-dispersed species. Predominance of wind-dispersed species can arrest succession. Wind-dispersed species include many herbaceous graminoids, Asteraceae, and ferns (Carrière 1999). Colonization of fallows by such plants results in conditions rendering difficult the establishment of seedlings of forest trees. The ease with which anemochorous herbaceous plants such as *Chromolaena odorata* and graminoids can colonize older fields and fallows in this kind of crop succession (S. Carrière, pers. obs.) points to the crucial role of remnant trees in enhancing animal-dispersed seed rain into some parts of the fields. We observed a peak in the rain of wind-dispersed seeds at the end of the short dry season and at the beginning of the short rainy season (Figure 1c) (February–March), when storms are frequent here (S. Carrière, pers. obs.) as elsewhere in African forests (Jackson 1981, Swaine & Hall 1983). There is thus reason to think that storms are a significant force in the dispersal of seeds of large pioneer trees, enabling them to disperse seeds over a large area during a period of high probability of gap formation (Swaine & Hall 1983).

Musanga cecropioides *seed rain*

One of the main results of this study is that seeds of *Musanga cecropioides* accounted for three-quarters of the total seed rain. This pioneer species, widespread in disturbed areas (road borders, fallows and gaps) throughout the African humid tropics, is dispersed by many birds and mammals, including bats, squirrels, large rodents, ruminants, and humans and other primates (Gautier-Hion *et al.* 1985, White & Abernethy 1996). Seeds of pioneer species are capable of dormancy and are well represented in the forest soil seed bank (Swaine & Whitmore 1988). Like many other pioneer species, *M. cecropioides* reaches sexual maturity very quickly and produces, more or less continuously, a very large number of small seeds (Swaine & Whitmore 1988). In this study, the mean number of seeds of *M. cecropioides* was 20.9 seeds per trap mo^{-1} for position 1 and 16.0 seeds per trap mo^{-1} for position 2 (i.e. 104.5 seeds m^{-2} mo^{-1} for position 1 and 80.0 seeds m^{-2} mo^{-1} for position 2). If we consider the total crown area of a common large tree such as *Ceiba pentandra* (15 m in diameter and 177 m^2), seed rain of *M. cecropioides* would range between 18 507 seeds per crown mo^{-1} (calculated with the mean number of seeds rained in traps at position 1) and 14 128 seeds per crown mo^{-1} (calculated with the mean number of seeds rained in traps at position 2). This result confirms the important cacacity of the dispersal of pioneer species (Richards 1952). Seeds of this species were similarly dominant among seeds germinating in soil in different forest communities in Ghana, with up to 116 seedlings in a 2-m^2 quadrat (Hall & Swaine 1980). With high light requirements, short maximum life span and high mortality due to competition, density of *M. cecropioides* sharply declines in older secondary forest (Swaine & Hall 1983).

Animal-dispersed foreign seed rain overall

Three-quarters of the foreign seed rain comprised seeds of animal-dispersed species. Remnant trees in fields are probably visited mainly by birds and bats, and much less often by monkeys. Most species of forest monkeys usually do not cross fields (A. Hladik, pers. comm.). Many frugivorous birds have been observed at remnant trees (Table 5). All of the species listed in Table 5 inhabit both mature and secondary forest, so that all should transport seeds of forest plants into farms and fallows (Mackworth-Praed & Grant 1973, Urban *et al.* 1986). Based on our observations, hornbills probably account for a large share of seeds dispersed in Ntumu farms and fallows. Three species of hornbill are

Table 5. List (not exhaustive) of frugivorous birds observed in fields and fallows in the study site in the Ntem Valley, southern Cameroon, 1996–1998 (S. M. Carrière & M. Raymond, *pers. obs.*). Food habits from Mackworth-Praed & Grant (1973) and Urban *et al.* (1986).

Family	Species	Feeding habits
Accipitridae	*Gypohierax angolensis*	Frugivorous and carnivorous
Columbidae	*Treron australis*	Frugivorous and granivorous
Psittacidae	*Poicephalus gulielmi*	Frugivorous
	Psittacus erythacus	Granivorous
Musophagidae	*Touraco macrorynchus*	Frugivorous
	Corythaeola cristata	Frugivorous
Bucerotidae	*Tockus fasciatus*	Frugivorous and insectivorous
	Tropicanus albocristatus	Frugivorous and insectivorous
	Ceratogymna atrata	Frugivorous
	Bycanistes cylindricus	Frugivorous
Pycnonotidae	*Andropadus virens*	Frugivorous
	Stegidocichla latorostris	Frugivorous and insectivorous
	Ixonotus guttatus	Frugivorous and insectivorous

frequent in the interface between fields, secondary regrowth, mature forest and remnant trees in the site (Carrière 1999, S. Carrière & M. Raymond, pers. obs.) and they dispersed seeds of 22% of the tree species in a site in the Dja Reserve in south-eastern Cameroon (Whitney *et al.* 1998). About half of the plant species (14 species) with animal-dispersed seeds are included among those that Whitney *et al.* (1998) observed to be ingested by *Ceratogymna* hornbills in southeastern Cameroon. Information on the length and frequency of visits by hornbills, combined with that on seed passage time in their guts, indicates that most seeds ingested are deposited away from the parent trees (Whitney *et al.* 1998). Seeds of forest species are thus likely to be deposited in large numbers beneath remnant trees in the fields. The total diversity of seed rain emphasizes this point, because the 100 species (trees, shrubs, lianas and herbaceous plants) found in the seed traps in this study is higher than numbers that have been found in other studies. Slocum (1997), for example, found seeds of 25 species of trees and shrubs in trays placed under remnant trees in Costa Rican pastures. A systematic study of bird movement between forest edges and remnant trees in fields, such as that conducted by Cardoso *et al.* (1996), could provide quantitative information on which bird species visit these sites, why they visit them, and what seeds they deposit in them.

Effect of human activity on rain of animal-dispersed seeds

Some studies have found that many bird species visit abandoned pastures in the neotropics and that fewer species go into active pastures (Cardoso *et al.* 1996). Our results show an increase in mean number of animal-dispersed seeds per trap mo^{-1} during periods of low frequency of human presence in the fields (Figure 3). High human presence corresponds to the period of sowing, weeding and harvesting peanuts in the fields. These operations require daily presence of women in the field, allowing them also to protect peanuts from granivorous birds. Seed dispersers generally avoid fields when humans are present. After harvesting of peanuts, other crops requiring less intensive care (cassava, bananas and yams) were planted. Regeneration in farms began during this last phase of the cultivation cycle characterized by lower intensity of human presence. This period is crucial, because after the last weeding, mature forest seeds that arrive have an opportunity to germinate and establish in the partial shade cast by these crops as well as beneath remnant trees. The augmentation of animal-dispersed seed rain at this time should provide improved conditions for colonization of the young secondary regrowth by mature-forest species.

Effect of dispersal mode of remnant trees

Our results indicated that animal-dispersed foreign seed rain was little influenced by dispersal mode of the focal tree. Animal-dispersed foreign seed rain tended to be slightly higher beneath trees without fleshy fruits. However, if the seeds of *M. cecropioides* are excluded, animal-dispersed seed rain showed a non-significant trend to be higher beneath trees with fleshy fruits. Part of the explanation for the absence of a significant increase in seed rain beneath trees without fleshy fruits may be that it is an artefact of our definition of 'foreign' seed rain. Seeds of a fleshy-fruited species deposited beneath a focal tree of that species were all counted as non-'foreign', although an unknown proportion could have come from individuals other than the focal tree. This would artificially lower the animal-dispersed foreign seed rain beneath fleshy-fruited focal trees, and not affect the animal-dispersed foreign seed rain beneath dry-fruited focal trees. The most likely source of such an artefact was seeds of *Musanga cecropioides* (which accounted for 3 of the 16 focal trees with fleshy fruits).

All focal trees, even those without fleshy fruits (Figure 4), greatly enhanced seed rain beneath them relative to that into open parts of the fields away from trees. Despite the fact that mechanisms relevant for animal attraction are poorly understood, previous studies have shown that plants with fleshy fruits are attractive to seed dispersers (Guevara & Laborde 1993, Nepstad *et al.* 1996). Vieira *et al.* (1994) emphasized the role of fleshy fruits of *Cordia multispicata* as a magnet for seed-dispersing frugivores. *Ficus* spp. have been observed to attract a large number of frugivorous animals (August 1981, Bronstein & Hoffman 1987, Coates-Estrada & Estrada 1986, Fleming & Heithaus 1981, Gautier-Hion *et al.* 1985, Janzen 1979, Jordano 1983, White & Abernethy 1996), and the same is true of many other fleshy-fruited species in African rain forests (Gautier-Hion *et al.* 1985, White & Abernethy 1996), including those we chose for our study. Many studies, however, have shown that higher seed rain occurs beneath remnant trees than elsewhere even when these trees are not fruiting

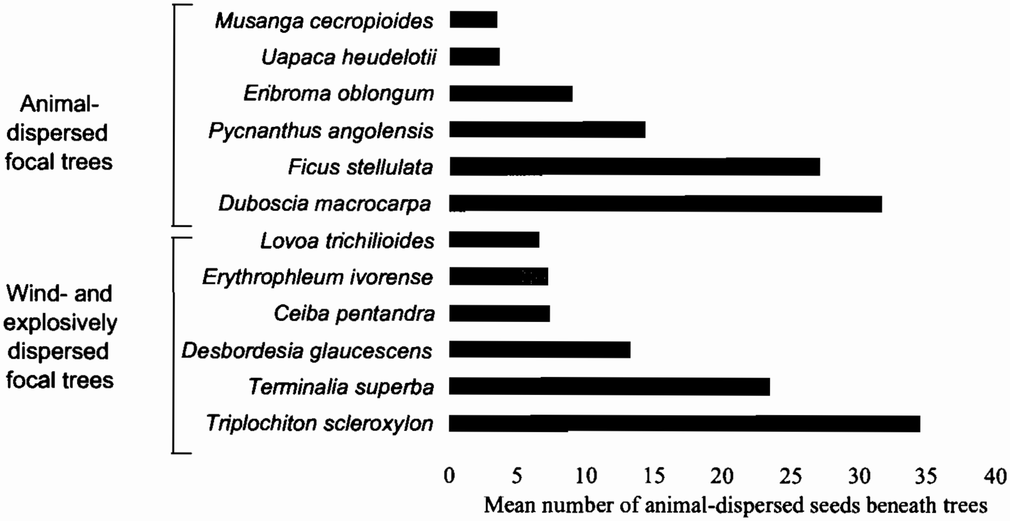


Figure 4. Mean number of foreign animal-dispersed seeds per trap mo^{-1} under different species of remnant trees in the fields. *Musanga cecropioides*, *Uapaca heudelotii*, *Eribroma oblongum*, *Pycnanthus angolensis*, *Ficus stellulata* and *Duboscia macrocarpa* are endozoochorous species, while the others are wind- and explosively dispersed. Seeds of *E. ivorense*, which have no obvious dispersal mechanism, are included in the letter category. The apparently small number of seeds deposited beneath *M. cecropioides* is an artefact; 'foreign' seed rain included only seeds of species other than the remnant tree. Since seeds of this species dominated seed rain beneath all remnant trees, only a small proportion of the total seed rain beneath *M. cecropioides* was 'foreign'.

(Fleming & Williams 1990, Guevara & Laborde 1993, Holl 1998, Slocum 1997). Such results show that determinant factors in attraction of seed dispersers are more complex than might be expected from the literature, and that presence of a food reward for frugivores may not be the most important factor. Frugivorous animals familiar with fruiting trees may frequently check trees that produce fruits unpredictably (Slocum 1997). Seed dispersers may also visit these trees for other reasons, using them as nesting sites, calling perches, or because they provide shelter from predators (Cardoso *et al.* 1996, McClanahan & Wolfe 1987, McDonnell & Stiles 1983, Wegner & Merriam 1979). Birds with mixed diets may visit trees to eat items other than fruits. Many of the frugivorous birds observed in fields at Nkongmeyos are also insectivorous (Table 5). They may visit species such as *Triplochiton scleroxylon*, *Terminalia superba*, or *Lovoa trichilioides*, that are attacked by insects such as caterpillars of saturniid moths (*Anaphe venata*, *Westermania cuprea* and *Catopyla dysorphnaea*, respectively) (CTFT 1976) and at the same time disperse seeds of mature-forest plants. In fact, greatest seed rain beneath non-fleshy-fruited species occurred beneath *Triplochiton scleroxylon* and *Terminalia superba* (Figure 4).

Rapid reconstitution of forest

Presence of remnant trees in fields greatly enhances the abundance and diversity of seeds deposited, as shown in this study. This result, along with the effect of remnant trees on microhabitats at ground level, makes the areas beneath remnant trees important foci for regeneration of forest species (Carrière 1999). The resulting rapid reconstitution of forest is probably essential to the sustainability of the fallow period (about 15 y) observed in this agricultural system, which is surprisingly short for the acid, nutrient-poor and fragile soils typical of this region. The way in which regeneration is initiated is fundamental, and it determines the structure and the specific composition of the developing plant community for many years after (Janzen 1988). By favouring the rain of animal-dispersed seeds, remnant trees enhance diversity of regenerating vegetation in several ways. First, they favour establishment of a diversity of seedlings, rather than dominance by a few aggressive clonally growing herbaceous plants, as observed in areas away from these trees (Carrière 1999). Second, by enhancing rain of animal-dispersed seeds more than they enhance rain of wind-dispersed seeds, they favour establishment of plants that upon sexual maturity will themselves continue to attract frugivores, thus durably enhancing diversity of both plants and animals in regenerating forest.

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APPENDIX 1

List of species (determined at least to the family level, 68 of 100 species total) whose seeds were found in traps (A = Animal-dispersed; W = Wind-dispersed; E = Ectozoochorous; P = Explosively dispersed). Of the remaining 32 undetermined species, 27 were animal-dispersed (a) and 5 were not (W, E, or P).

Family Seed species	Dispersal mode
Amaranthaceae	
Achyranthes aspera Linn.	A
Anacardiaceae	
Undetermined T81	A
Annonaceae	
Enantia chlorantha Oliver	A
Polyalthia suaveolens Engl. & Diels	A
Xylopia aethiopica (Dunal) A. Rich.	A
Xylopia hypolampra Mildbr.	A
Xylopia quintasii Engl. & Diels	A
Xylopia sp1	A
Xylopia sp2	A
Xylopia sp3	A
Xylopia staudtii Engl. & Diels	A
Undetermined T77	A
Apocynaceae	
Holarrhena floribunda (G. Don) Dur. & Schinz	W
Rauvolfia mannii Stapf	A
Rauvolfia vomitoria Afzel.	A
Asteraceae	
Chromolaena odorata (L.) R. M. King & H. Robinson	W
Undetermined T5	E
Undetermined T11	E
Undetermined T105	W
Bombacaceae	
Ceiba pentandra (L.) Gaertn.	W
Caricaceae	
Carica papaya L.	A
Leguminosae – Caesalpinioideae	
Erythrophleum ivorense A. Chev.	P
Combretaceae	
Terminalia superba Engl. & Diels	W
Combretum sp1	W
Combretum sp2	W
Pteleopsis hylodendron Mildbr.	W
Connaraceae	
Undetermined T31	A
Convolvulaceae	
Calycobolus sp.	W
Cucurbitaceae	
Undetermined T49	A
Dioscoreaceae	
Dioscorea sp1	W
Dioscorea sp2	W

Appendix 1. *cont.*

Family Seed species	Dispersal mode
Euphorbiaceae	
Discoglypremna caloneura (Pax) Prain	A
Manihot esculenta Crantz	P
Phyllanthus discoideus (Baill.) Müll. Arg.	A
Uapaca heudelotii Baill.	A
Menispermaceae	
Undetermined T126	A
Leguminosae – Mimosoideae	
Albizia sp.	W
Piptadeniastrum africanum (Hook. f.) Brenan	W
Moraceae	
Ficus sp1	A
Ficus sp2	A
Ficus sp3	A
Ficus sp4	A
Ficus sp5	A
Milicia excelsa (Welw.) C. C. Berg.	A
Musanga cecropioides R. Br.	A
Myristicaceae	
Pycnanthus angolensis (Welw.) Exell	A
Olacaceae	
Heisteria sp.	A
Undetermined T 117	A
Leguminosae – Papilionoideae	
Crotalaria sp1	P
Crotalaria sp2	P
Pterocarpus soyauxii Taub.	W
Undetermined T41	P
Undetermined T111	P
Undetermined T85	W
Rubiaceae	
Atractogyne sp.	A
Pausinystalia macroceras (K. Schum.) Pierre ex Beille	W
Undetermined T125	A
Sapotaceae	
Pachystela sp.	A
Solanaceae	
Capsicum frutescens L.	A
Solanum sp1	A
Solanum sp2	A
Tiliaceae	
Corchorus sp.	A
Ulmaceae	
Holoptelea grandis (Hutch.) Mildbr.	W
Trema guineensis (Schum. & Thonn.) Ficalho	A
Undetermined T120	A