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# Seed Rain and Seed Limitation in a Planted Gallery Forest in Brazil

Karina C. Barbosa<sup>1</sup> and Marco A. Pizo<sup>2,3</sup>

## Abstract

With seeds collected monthly during one year from 53 1-m<sup>2</sup> seed traps, we investigated the seed rain and seed limitation in a gallery forest planted in 1994 in SE Brazil. Contrasting animal- (zoochorous) and wind-dispersed (anemochorous) plants we investigated (1) which aspects of the composition and structure of the vegetation influence the abundance and species richness of the seed rain; (2) if such influences differ between zoochorous and anemochorous seeds; (3) if the abundance and richness of the seed rain sampled under zoochorous and nonzoochorous plant species differ; and (4) if seed limitation (given by the proportion of sites to which seeds were not dispersed) differs between zoochorous and anemochorous plant species, and also between species that have been planted and those that further colonized the area (colonists). Seed rain was intense and dominated by anemochorous

species. The overall seed rain was not influenced by the vegetation parameters we analyzed (canopy height and cover, plant size, abundance, and richness) or by the plant species above the seed trap. The abundance and richness of zoochorous seeds in a given spot was influenced by the abundance and richness of zoochorous plants in its immediate vicinity. Seed limitation was higher for anemochorous than zoochorous species and higher for planted than for colonist species. We concluded with recommendations for the initial establishment of a planted forest, including the homogeneous distribution of zoochorous plants to permit a spatially homogeneous zoochorous seedfall, which will likely enhance the chances of survival and successful establishment of seeds.

**Key words:** anemochory, restored forest, seed dispersal, seed limitation, zoochory.

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## Introduction

The number of forest restoration projects is increasing in Brazil in recent years, especially in the highly threatened Atlantic Forest (*sensu* Morellato & Haddad 2000) in the state of São Paulo, where specific legislation has recently been enacted to regulate and orientate restoration efforts (Barbosa 2003). Law enforcement obliges land owners and private companies to plant native species in order to restore a given stretch of cleared land in compensation for past or future environmental damages. By virtue of its importance as a protective belt against soil erosion and pollution running into water courses and its role as movement corridors for animals and plants, gallery forest is a priority ecosystem for such restoration projects (Rodrigues & Leitão Filho 2000). Cerri et al. (2000) estimated that 13,000 km<sup>2</sup> of this type of forest need to be restored in the state of São Paulo.

Despite the growing body of knowledge regarding restoration protocols in Brazilian lands summarized in recent publications (Barbosa & Macedo 2000; Rodrigues & Leitão Filho 2000), we still need learn much more about some basic processes that influence the structure and composi-

tion of restored forests. For instance, seed rain forms the template for later regeneration and plant recruitment and is critical for the success of a given restoration project (Zimmerman et al. 2000). Seed rain is influenced by patterns of seed limitation, which can be understood as the failure of seeds to arrive at all suitable sites (Muller-Landau et al. 2002). Patterns of seed rain and seed limitation have hitherto received no attention in restored forests in Brazil.

In this study we investigated seed rain and seed limitation in a restored gallery forest in the state of São Paulo, planted 10 years ago. Given that the predominance of animal- (zoochorous) versus wind-dispersed seeds (anemochorous) in the seed rain may lead to completely different regeneration pathways (Janzen 1988) and that both dispersal modes are usually included in varying proportions in restoration projects in Brazil, we contrasted zoochorous (endozoochorous *sensu* van der Pijl 1982) and anemochorous seed rains in relation to parameters of the vegetation structure and composition that potentially influence them. It has been shown that the structure of the vegetation influences the activity of seed dispersers (McDonnell & Stiles 1983), as well as the deposition of wind-dispersed seeds (Augsburger & Franson 1988; Loiselle et al. 1996). Moreover, the composition of the overstorey vegetation may dictate the amount and composition of the seed rain deposited in a given spot (Parrotta 1995). Seed limitation was examined according to the dispersal mode (zoochorous and anemochorous) and the origin of the

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<sup>1</sup> Programa de Pós-graduação em Biologia Vegetal, Departamento de Botânica, Universidade Estadual Paulista (UNESP), Caixa Postal 199, 13506-900 Rio Claro, SP, Brazil

<sup>2</sup> Plant Phenology and Seed Dispersal Research Group, Universidade do Vale do Rio dos Sinos (UNISINOS), Centro 2, 93022-000 São Leopoldo, RS, Brazil

<sup>3</sup> Address correspondence to M. A. Pizo, email mapizo@unisinors.br

seeds in the area, that is, if from planted or colonist (plants that were not planted but colonized the restored forest since planting) species. Results of short-term seed limitation studies should be interpreted with caution because the strength of seed limitation may diminish over time, especially for pioneer plant species that maintain an active, long-lasting seed bank (Clark et al. 1999; Dalling et al. 2002). However, we deal with seed limitation data in a comparative not absolute way.

Specifically, the following questions were addressed: (1) which aspects of the composition and structure of the vegetation influence the abundance and species richness of the seed rain; (2) does such influence, if any, differ for zoochorous and anemochorous seeds; (3) does the abundance and richness of the vertebrate-generated (zoochorous) seed rain differ under zoochorous and non-zoochorous plant species; and (4) does seed limitation differ between zoochorous and anemochorous plant species, and also between species that have been planted and those that further colonized the area? With this series of questions we intended to provide clues for the selection and spatial arrangement of planted species in future restoration projects.

## Methods

### Study Site

The study was carried out from September 2002 to August 2003 in a restored gallery forest located at Fazenda São Carlos (lat 21°47'S, long 46°47'W), municipality of Santa Cruz das Palmeiras, state of São Paulo, SE Brazil. The relief in the study area is moderately undulated covered with latosols. The original forest had been completely cleared for rice and sugar plantations until 1994 when the restoration process began by planting 40 different plant species representing a mix of pioneer to late-successional species (Appendix 1). The planting covered an elongated area of 12 ha running along the water course with a maximum width of 50 m. Zoochorous, anemochorous, and autochorous dispersal syndromes (sensu van der Pijl 1982) were all represented among the planted species. Over the years, several plant species, mainly early-successional species, invaded and became established in the area (Appendix 1). As a result, after 10 years of growth the forest was reasonably well developed, with over 80 plant species, a 0.5- to 3-cm-thick leaf litter covering the ground, average canopy height and cover of 10.5 m and 86%, respectively (Table 1). The dominant plant families in terms of number of individuals and species were Bignoniaceae, Caesalpinaceae, Mimosaceae, Papilionaceae, and Verbenaceae (Appendix 1).

Climate is moderately seasonal, with dry winters from May to August. Annual precipitation is around 1,300 mm, and annual mean temperature is 22°C (Gisler 2000). Small (<1 ha), severely degraded forest fragments are present in the landscape but several hundred meters distant from the

**Table 1.** Vegetation parameters sampled in 5-m-radius circular plots centered on 53 seed traps set in a restored gallery forest in SE Brazil.

Parameters	Code <sup>a</sup>	Mean	SD	CV (%)
Canopy height (m)	CHEIGH	10.51	2.92	27.75
Canopy cover (%)	CCOVER	86.24	7.47	8.66
Plant height (m)	MHEIGH	5.41	1.19	22.04
Plant diameter (cm)	MDIAM	7.95	2.75	34.59
Plant abundance <sup>b</sup>				
Zoochorous	NOINDZ	12.26	10.51	85.73
Anemochorous	NOINDA	17.45	15.88	91.02
Autochorous	—	1.17	2.47	211.22
Total	NOIND	31.74	14.99	47.24
Plant richness <sup>b</sup>				
Zoochorous	NOSPPZ	4.55	2.61	57.47
Anemochorous	NOSPPA	3.98	1.97	49.38
Autochorous	—	0.38	0.66	174.13
Total	NOSPP	9.42	3.38	35.92
Distance seed trap-border (m)	DIST	6.61	5.07	76.74

Means, standard deviations (SD), and the coefficient of variation (CV) are presented for each parameter.

<sup>a</sup> Codes are provided only for parameters used in the PCA (see text).

<sup>b</sup> Plant abundance and richness based on the number of plants and species (>1.3-m height) sampled in the plots.

restored forest. The largest native forest fragment was 72 ha and was 8 km away. The surrounding matrix was formed mostly by sugar cane plantations and also by a few human settlements. Seed dispersers dropping seeds from the canopy were represented by small- to medium-sized frugivorous birds, bats, and marsupials (M. A. Pizo, 2002, personal observation).

### Seed Rain

Seed rain was sampled from September 2002 to August 2003 in 1-m<sup>2</sup> seed traps composed of wooden boxes lined with a fine plastic net (1-mm mesh) and suspended 10 cm from the ground. Seed traps were spaced at least 15 m from each other. Initially, 60 seed traps were placed beneath four of the most common planted species, *Schinus terebinthifolius* (Anacardiaceae), *Trema micrantha* (Ulmaceae), *Croton urucurana* (Euphorbiaceae), and *Schizolobium parahyba* (Caesalpinaceae), avoiding plants with overlapping canopies. Each individual tree received one single trap. Depredations in the first months of data collection reduced the number of seed traps to 53, there being 16 under *S. terebinthifolius*, 10 under *T. micrantha*, 16 under *S. parahyba*, and 11 under *C. urucurana*. These species were chosen because they form two distinct classes regarding dispersal syndromes: *S. terebinthifolius* and *T. micrantha* are dispersed by birds, whereas *S. parahyba* and *C. urucurana* are dispersed by the wind and the plant itself (autochoric), respectively (Lorenzi 1992). Moreover, these plants are among the most common species used in restoration programs in SE Brazil (Barbosa et al. 2003). Therefore, an evaluation of their roles as seed arrival foci seems appropriate to inform future restoration programs

by recommending the use of tree species that most efficiently promote seed deposition.

Seed traps were emptied once a month and the material collected was brought to the lab where seeds were counted and identified. Identification of most of the seeds was made possible by a reference collection assembled during the study and also by consulting specialists at the Instituto de Botânica de São Paulo (IBt). Seed lengths were taken from Lorenzi (1992, 1998), and for unidentified species, seeds were measured with calipers.

### Vegetation Structure and Composition

Vegetation structure and composition were sampled at 5-m-radius circular plots (78.5 m<sup>2</sup>) centered at each seed trap. Inside each plot we counted, identified, and measured the height and diameter at breast height (dbh) of all the plants >1.3-m height (lianas were not common and were not sampled). Plant height was measured with a graduated pole, whereas dbh was derived from trunk circumference measured with a tape. Exactly above each seed trap we measured canopy height with the graduated pole and canopy cover with a concave densiometer (Lemmon 1957). To account for the semideciduous nature of the vegetation, canopy cover measurements were taken twice a year, at the dry (July) and wet seasons (March), and the mean of the two measurements was used for analyses. Additionally, we measured the nearest distance from each seed trap to the border of the restored forest.

Because the planted species were known, identification of most plants sampled inside the plots was not a problem. Plant samples of the remaining species, that is, those that were not planted but colonized the forest during the past 10 years, were prepared and delivered to specialists at the IBt for identification. Dispersal syndrome and successional stage were assigned to each plant species based on the previous experience of the authors, on the literature (e.g., Lorenzi 1992, 1998), consultation with specialists, and the morphology of the diaspores.

### Data Analyses

Because we were interested in the seed rain generated by effective seed dispersal, that is, the movement of seeds away from parent plants, and not in seeds that were simply dropped beneath a parent tree without being dispersed, for most of the analyses, unless otherwise noted, we did not consider seeds that had been collected under a conspecific tree (hereafter “undispersed seeds”; see Slocum & Horvitz 2000 for a similar procedure). Although we might have inadvertently discarded from the analyses seeds that have been effectively dispersed to a conspecific tree, we believe that these seeds are a minority in relation to really undispersed seeds (Jordano & Godoy 2002).

To investigate the effects of vegetation structure and composition upon seed rain we first performed an analysis of principal components (PCA) to reduce the independent

variables represented by the various vegetation parameters to a few synthetic principal components (PCs) (Manly 1994). Separate analyses were made for all the seeds irrespective of dispersal syndromes, for zoochorous seeds only, and for anemochorous seeds. Due to the low abundance of autochorous plant species in the area, and the low representation of their seeds in the seed rain (see below), we did not analyze them as a separate category. For the analysis of all seeds irrespective of dispersal syndromes the following variables (and respective codes) were used in the PCA: mean height (MHEIGHT) and mean diameter (MDIAM) of plants, number of individual plants (NOIND) and species (NOSPP) sampled inside plots, canopy height (CHEIGH) and cover (CCOVER), and distance to the forest border (DIST). For the zoochorous and anemochorous seeds, to these variables we added number of individuals and species of zoochorous (NOINDZ and NOSPPZ) and anemochorous (NOINDA and NOSPPA) plants, respectively. However, among zoochorous plants we did not consider *Enterolobium contortisiliquum* and *Hymenaea courbaril*, which had no seed dispersers (terrestrial mammalian herbivores; Hallwachs 1986) in the study area. Using the varimax rotation technique (Manly 1994), we extracted those PCs with eigenvalues  $\geq 1.0$  and used them in standard multiple regression analyses that had abundance and richness of collected seeds as dependent variables (Zar 1996). When the multiple regression model result was significant, we looked to standardized partial regressions coefficients (beta coefficients) to learn about the unique contribution of each independent variable to the prediction of the dependent variables (Zar 1996).

We analyzed the effects of tree species upon two dependent variables of vertebrate-generated (zoochorous) seed rain, namely seed abundance and richness. For this we used multivariate analyses of variance with two covariates (MANCOVA) having the tree species as the independent variable, and the richness and abundance of zoochorous plants in the plots as covariates. To test the relationship between both covariates taken together and the dependent variables, we performed a within-group correlation, which was followed by multiple regression analyses to access the contribution of each covariate upon each of the dependent variables.

We calculated seed limitation as the proportion of seed traps not receiving seeds after the one year of seed collection (“fundamental seed limitation” sensu Muller-Landau et al. 2002). Thus, seed limitation can be expressed as:

$$\text{Seed limitation} = 1 - a/n$$

where  $a$  is the number of seed traps reached by any seed of a given species and  $n$  the total number of seed traps.

We tested for the effects of dispersal syndromes (zoochorous and anemochorous) and origin in the area (i.e., if

planted or colonist) on seed limitation using analyses of covariance that had the abundance of plants, as revealed by the number of individuals censused on plots, as covariate. Syndrome and origin in the area were tested separately. Because we did not know if seeds dropped beneath parent trees (undispersed seeds) could result in established seedlings, we did two sets of analyses: one that took into account all the seeds (dispersed and undispersed), thus avoiding overestimation of seed limitation for the four focal plant species (i.e., *S. terebinthifolius*, *T. micrantha*, *S. parahyba*, and *C. urucurana*), and one that emphasized the role of seed dispersal on seed limitation and considered dispersed seeds only.

To normalize data, abundance values, either of individual plants inside plots or seeds collected, were log transformed, whereas angular transformation was applied to limitation data (Zar 1996). All analyses were performed using the version 5.5 of STATISTICA (Statsoft 1999), with 0.05 as the significance level. Means  $\pm$  SD were presented unless otherwise noted.

## Results

A total of 88,552 seeds were collected, most of them (62.9%) were considered undispersed (Table 2). Undispersed seeds were 0–97.7% of the seeds collected at a given seed trap. Dispersed seeds amounted to 32,792 seeds (618.7 seeds/m<sup>2</sup> or 51.6 seeds m<sup>-2</sup> month<sup>-1</sup>) representing 31 species (20 families), 13 being zoochorous (14,530 seeds or 44.3% of total seeds collected), 14 anemochorous (16,788 seeds, 51.2%), and 4 autochorous (1,474 seeds, 4.5%; Table 2). With the exception of one liana and one herb, most of the seeds (95.8%) came from tree species (Table 2). Pioneer (12 out of 27 identified species, 44.4%) and nonpioneer species (55.6%) were represented among trapped seeds. Seeds of pioneer species predominated in the seed rain (17,143 seeds, 52.3%; Table 2). In relation to the origin in the area, 22 seed species (5,927 seeds or 18.1% of total seeds collected) came from planted species, whereas 9 came from species that colonized the area (26,865 seeds, 81.9%). Among the most common seeds collected were *Tecoma stans*, *Maclura tinctoria*, and *Schinus terebinthifolius*. Whereas *S. terebinthifolius* is a planted, bird-dispersed species, *T. stans* and *M. tinctoria* are colonists, the former being an exotic anemochorous species and the latter dispersed by birds and bats (Table 2, Appendix 1). Length of trapped seeds ranged from 2 to 40 mm (10.7  $\pm$  9.7,  $n$  = 31). Zoochorous seeds were particularly small (85% of 13 species with <6 mm in diameter), ranging from 2 to 20 mm in length (6.5  $\pm$  4.7,  $n$  = 13).

The cumulative curve of seed collection showed that only a few species were added to the dataset after the fifth month of study in December 2002 (Fig. 1A). In fact, the bulk of seedfall in terms of abundance and richness occurred from September to December 2002, and, to

a lesser extent, in July and August 2003. The first months of the 2002 dry season were of very low seedfall (Fig. 1B).

## The Influence of Vegetation Structure and Composition on Seed Rain

A total of 1,913 plants representing 84 plant species (29 families) were sampled within the plots, resulting in a total plant density of 4,117 plants/ha (Appendix 1). In general, plants were thin and not very tall (Table 1), with a basal area of 35.2 m<sup>2</sup>/ha. Anemochorous plants were more abundant than zoochorous and autochorous plants (56.3%, 39.8%, and 3.9% of total plants sampled, respectively). Individuals from planted species represented 43.5% of total sample, the remaining representing individuals from species that colonized the area (Appendix 1). Some parameters of the structure of the vegetation at the study area were fairly homogeneous (e.g., canopy height and cover, plant height and diameter), as expected for a recently planted forest (Table 1). Abundances of zoochorous, anemochorous, and autochorous plant species were highly variable, as was the richness of autochorous species, denoting small-scale spatial variation in the relative abundance of the different dispersal syndromes. Distance from seed trap to the border of the forest also varied considerably, but no seed trap was set more than 25 m from the forest border (Table 1).

From the PCA carried out to investigate the determinants of total seed rain we selected the three first PCs, which together accounted for 73.8% of total variance (Table 3). The first PC is explained by a gradient of plant size and abundance, with mean plant height and diameter (highly correlated parameters:  $r$  = 0.82,  $n$  = 53,  $p$  < 0.001) having large positive loadings on it, whereas number of plants had a negative load. In other words, the first PC basically distinguished between plots with a high density of small plants from plots with more scattered tall plants. The second PC was related to canopy cover and distance to the forest border, both with positive loadings. The third PC was influenced by canopy height, also with positive loading (Table 3). The multiple regression model involving the three PCs was not significant, neither for abundance ( $r^2$  = 0.03,  $F_{[3,49]} = 0.55$ ,  $p$  = 0.65) nor for richness ( $r^2$  = 0.05,  $F_{[3,49]} = 0.81$ ,  $p$  = 0.49) of total seed rain.

When we added the abundance and richness of zoochorous plant species to the parameters analyzed in the PCA, the three first PCs explained 72.3% of total variation (Table 3). The parameters that most strongly influenced the first and third PCs did not change, but the second PC was related to the richness of plants in general and to the abundance and richness of zoochorous plants in particular, which had positive loadings on it (Table 3). It is important to note that the overall abundance of plants is influenced by the abundance of zoochorous plants, being positively correlated with it ( $r$  = 0.78,  $n$  = 53,  $p$  < 0.001). Multiple regression involving the three PCs and abundance of zoochorous seeds was highly significant ( $r^2$  = 0.23,  $F_{[3,49]} = 4.92$ ,

**Table 2.** Seed species collected in 53 1-m<sup>2</sup> seed traps from September 2002 to August 2003 in a restored gallery forest in SE Brazil, with information on successional stage (pioneer species, indicated with an asterisk, and nonpioneer species), exotic species (indicated by a plus sign), dispersal syndrome, habit, seed size, total number of seeds collected, number of seed traps in which each seed species was collected, and seed limitation.

Family/Species	Dispersal Syndrome <sup>a</sup>	Habit <sup>b</sup>	Seed Length (mm) <sup>c</sup>	Number of Seeds <sup>d</sup>	Number of Seed Traps	Seed Limitation
Anacardiaceae						
<i>Schinus terebinthifolius</i> *	Z	T	5	2,408/13,009	31/52	0.42/0.02
Arecaceae						
<i>Syagrus romanzoffiana</i>	Z	T	20	32	1	0.98
Asteraceae						
<i>Vernonia</i> sp.*	A	H	2	1,367	46	0.13
Bignoniaceae						
<i>Tabebuia chrysotricha</i>	A	T	15	618	14	0.74
<i>Tabebuia ochracea</i>	A	T	20	1	1	0.98
<i>Tecoma stans</i> *+	A	T	7	10,231	34	0.36
Bombacaceae						
<i>Chorisia speciosa</i>	A	T	8	25	3	0.94
Boraginaceae						
<i>Cordia sellowiana</i> *	A	T	10	47	9	0.83
Euphorbiaceae						
<i>Alchornea glandulosa</i> *	Z	T	4	34	14	0.74
<i>Croton floribundus</i> *	U	T	4	9	1	0.98
<i>Croton urucurana</i> *	U	T	2	348/13,588	20/34	0.62/0.36
Lauraceae						
<i>Nectandra megapotamica</i>	Z	T	9	1	1	0.98
Lecythidaceae						
<i>Cariniana estrellensis</i>	A	T	40	23	4	0.92
<i>Cariniana legalis</i>	A	T	30	90	3	0.94
Leguminosae						
Morphospecies 03	U	—	4	136	15	0.72
Leguminosae—Caesalpinoideae						
<i>Schizolobium parahyba</i> *	A	T	30	6/41	5/14	0.91/0.73
<i>Pterogyne nitens</i>	A	T	15	219	4	0.92
Leguminosae—Mimosoideae						
<i>Leucaena</i> sp.*+	U	T	7	981	4	0.92
Leguminosae—Papilionoideae						
<i>Centrolobium tomentosum</i>	A	T	27	1	1	0.98
<i>Platypodium elegans</i>	A	T	14	6	4	0.92
Malpighiaceae						
<i>Heteropteris</i> sp.	A	L	10	1	1	0.98
Moraceae						
<i>Maclura tinctoria</i>	Z	T	3	5,951	48	0.09
Myrsinaceae						
<i>Myrsine ferruginea</i> *	Z	T	3	56	17	0.68
Rubiaceae						
<i>Genipa americana</i>	Z	T	8	471	20	0.62
Solanaceae						
<i>Cestrum schlechtendalii</i>	Z	T	4	1,912	42	0.21
Sterculiaceae						
<i>Guazuma ulmifolia</i> *	Z	T	3	407	8	0.85
Ulmaceae						
<i>Trema micrantha</i> *	Z	T	3	1,249/29,122	36/51	0.32/0.04
Verbenaceae						
<i>Cytharexylum myrianthum</i>	Z	T	10	46	5	0.91
Morphospecies 01	A	—	3	4,153	46	0.13
Morphospecies 04	Z	—	6	2	1	0.98
Morphospecies 05	Z	—	6	1,961	7	0.87
Mean (±SD)				1,057.5/2,727.1 (2,170.5/6,164.2)	14.4/16.3 (15.6/17.8)	0.73/0.69 (0.29/0.33)

<sup>a</sup> A, anemochorous; U, autochorous; Z, zoochorous.<sup>b</sup> T, tree; L, liana; H, herb.<sup>c</sup> Taken from Lorenzi (1992, 1998), and, for unidentified species, from authors' data.<sup>d</sup> For the four focal species (i.e., *Schinus terebinthifolius*, *Croton urucurana*, *Schizolobium parahyba*, and *Trema micrantha*) figures refer to dispersed seeds only (i.e., not considering seeds collected under a conspecific tree) and all the seeds collected, respectively.

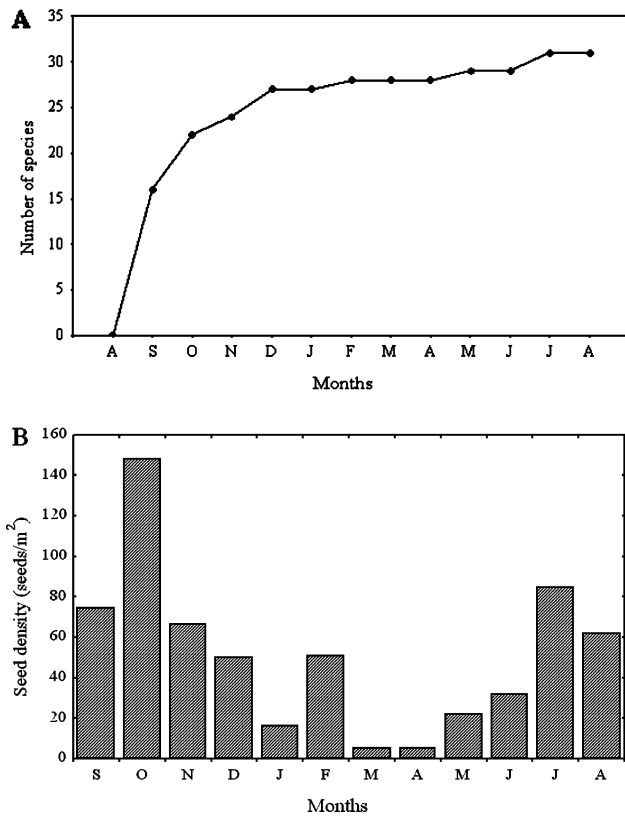


Figure 1. Cumulative curve of seed species collected (A), and seed density (B) sampled in 53 1-m<sup>2</sup> seed traps placed at a restored gallery forest in Brazil from September 2002 to August 2003.

$p = 0.004$ ), as was the regression with richness of zoochorous seeds ( $r^2 = 0.17$ ,  $F_{[3,49]} = 3.51$ ,  $p = 0.02$ ). The abundance of seeds was significantly influenced by PC2 and PC3, but in opposite directions, whereas only PC2 signifi-

cantly influenced seed richness (Table 4). Suspecting that the negative influence of PC3 upon the abundance of zoochorous seeds had to do with the abundance of some anemochorous species that are among the tallest plants in the study area (e.g., *Schizolobium parahyba*), thus contributing to elevated canopy height, we correlated the abundance of anemochorous species and canopy height, which was positive and highly significant ( $r = 0.49$ ,  $n = 53$ ,  $p < 0.001$ ).

The three first PCs extracted from the PCA carried out to investigate the determinants of the anemochorous portion of the seed rain explained 70.1% of total variance and, for the first two PCs, rendered results similar to the PCA for zoochorous seeds (see above), with the obvious difference that PC2 was related to the abundance and richness of anemochorous plant species, and also with canopy height, all with positive loadings (Table 3). This association between richness and abundance of anemochorous plants and canopy height reflects the already stressed fact that some of these plants are among the tallest ones at the study area and their presence contributes to elevated canopy height. The third PC was related to canopy cover and distance to the forest border, both with positive loadings. The multiple regression model involving the three PCs was not significant neither for abundance of anemochorous seeds ( $r^2 = 0.07$ ,  $F_{[3,49]} = 1.25$ ,  $p = 0.30$ ) nor for their richness ( $r^2 = 0.05$ ,  $F_{[3,49]} = 0.89$ ,  $p = 0.45$ ).

In summary, the overall seed rain was not influenced by the vegetation parameters we analyzed, nor by distance to forest border. By taking into account the dispersal syndromes, however, we could distinguish wind- from vertebrate-generated seed rain, and correlates with vegetation structure and composition appeared. Unlike anemochorous seeds, the abundance and richness of vertebrate-dispersed seeds in a given spot was influenced by the abundance and richness of zoochorous plants in its immediate vicinity.

**Table 3.** Rotated factors (factor loadings extracted by PCA) for the vegetation parameters measured to investigate the determinants of seed rain at a restored gallery forest in SE Brazil.

Parameter Codes	All Seeds			Zoochorous Seeds			Anemochorous Seeds		
	Factor 1	Factor 2	Factor 3	Factor 1	Factor 2	Factor 3	Factor 1	Factor 2	Factor 3
CHEIGHT	0.15	-0.21	<b>0.86</b>	0.18	0.01	<b>0.85</b>	0.21	<b>0.65</b>	-0.22
CCOVER	-0.01	<b>0.85</b>	-0.02	0.16	0.57	-0.40	0.01	-0.08	<b>0.84</b>
MHEIGHT	<b>0.93</b>	0.15	0.11	<b>0.95</b>	-0.05	0.00	<b>0.94</b>	-0.01	0.10
MDIAM	<b>0.91</b>	-0.06	0.10	<b>0.90</b>	-0.16	0.10	<b>0.92</b>	0.02	-0.11
NOIND	<b>-0.71</b>	0.06	0.53	<b>-0.60</b>	0.41	0.45	<b>-0.64</b>	0.58	0.10
NOINDZ	—	—	—	-0.16	<b>0.83</b>	-0.30	—	—	—
NOINDA	—	—	—	—	—	—	-0.32	<b>0.81</b>	-0.17
NOSPP	-0.47	0.45	0.40	-0.24	<b>0.83</b>	0.17	-0.34	0.44	0.54
NOSPPZ	—	—	—	-0.20	<b>0.91</b>	-0.10	—	—	—
NOSPPA	—	—	—	—	—	—	-0.01	<b>0.84</b>	0.02
DIST	0.05	<b>0.69</b>	-0.15	0.11	0.25	-0.47	0.04	-0.18	<b>0.64</b>
Eigenvalues	2.51	1.49	1.15	3.43	1.87	1.21	3.05	1.90	1.36
Variance (%)	35.94	21.37	16.49	38.10	20.79	13.44	33.90	21.09	15.14

Separate analyses were carried out for all seeds collected irrespective of dispersal syndrome, for zoochorous seeds only, and for anemochorous seeds only. An m-dash indicates that the parameter was not included in the analysis. Loadings that strongly affect each factor are formatted in bold. Parameter codes according to Table 1.

**Table 4.** Results of regression analyses involving the PCs (Factors) extracted from the PCA, and the abundance and richness of zoochorous seeds (dependent variables) collected in a restored gallery forest in SE Brazil.

Variables	Brief Description of Variables <sup>a</sup>	Beta Coefficient	t	p
<b>Abundance</b>				
Factor 1	Abundance (–) and size (+) of plants	–0.02	–0.19	0.84
Factor 2	Richness of all plants (+), and abundance (+) and richness (+) of zoochorous plants	0.37	2.99	<b>0.004</b>
Factor 3	Canopy height (+)	–0.30	–2.39	<b>0.02</b>
<b>Richness</b>				
Factor 1		–0.05	–0.40	0.69
Factor 2		0.38	2.92	<b>0.005</b>
Factor 3		–0.17	–1.35	0.18

Significant regressions are formatted in bold. Degrees of freedom are 49 in all the analyses.

<sup>a</sup>The influence (if positive or negative) of each parameter on each of the factors extracted from the PCA is indicated in parentheses. See Table 3 and text for more details.

### Influence of Plant Species on Seed Rain

Apart from the low number of seeds collected below *S. parahyba*, the other three focal plant species did not differ greatly in the abundance of zoochorous seeds collected below them (Fig. 2A). Within-plant variation in seed abundance was, however, more pronounced, especially for *S. terebinthifolius*, *Trema micrantha*, and *Croton urucurana* (Fig. 2A). Seed richness was fairly homogenous both within and between plant species (Fig. 2B). As a result, and contrary to expectations, the abundance and richness of the zoochorous seed rain did not differ among plant species (MANCOVA: Wilk's lambda = 0.93,  $p = 0.76$ ). Within-group correlation revealed that covariates, namely abundance and richness of zoochorous plant species, and dependent variables were significantly correlated (Wilk's lambda = 0.65,  $p = 0.0004$ ). Regression models involving the two covariates were significant for the abundance ( $r^2 = 0.22$ ,  $F_{[2,47]} = 6.79$ ,  $p = 0.002$ ) and richness of zoochorous seeds ( $r^2 = 0.26$ ,  $F_{[2,47]} = 8.16$ ,  $p = 0.0009$ ). Of the two covariates, the abundance more than the richness of zoochorous plant species influenced the abundance (beta coefficients: 0.36 and 0.12, respectively) and richness (0.85 and 0.46, respectively) of zoochorous seeds. Once again these results point to the importance of the forest composition in the immediate vicinity of a given spot to the zoochoric seed rain that falls in that particular spot.

### Patterns of Seed Limitation

Seed limitation varied substantially among species, from almost nonexistent (e.g., *Maclura tinctoria*) to very strong ( $>0.90$ ; Table 2). For 18 of 31 seed species,  $>80\%$  of seed traps failed to receive any seed. After controlling for the abundance of plants, zoochorous and anemochorous plants differed in the strength of seed limitation, with the latter being more seed limited, both when considering all the seeds ( $F_{[1,18]} = 6.10$ ,  $p = 0.02$ ) or only dispersed seeds ( $F_{[1,18]} = 5.10$ ,  $p = 0.04$ ). Planted and colonist species differed in seed limitation only in the more conservative analysis that considered only dispersed seeds, which

revealed higher seed limitation for planted species ( $F_{[1,21]} = 8.73$ ,  $p = 0.007$ ). When all the seeds were taken into account (i.e., dispersed and undispersed seeds), no significant difference was found ( $F_{[1,21]} = 3.01$ ,  $p = 0.09$ ), although the trend of higher seed limitation for planted species remained (planted:  $0.75 \pm 0.32$ ,  $n = 17$ ; colonist:  $0.59 \pm 0.36$ ,  $n = 10$ ).

### Discussion

The density of seeds sampled in the restored forest ( $618.7$  seeds  $m^{-2} yr^{-1}$ ) was intermediate between those reported for two fragments (345 and 250 ha) of native semideciduous forests located within 200 km of the study area ( $1804.2$  and  $442.0$  seeds  $m^{-2} yr^{-1}$  in Penhalber & Mantovani 1997, and Grombone-Guaratini & Rodrigues 2002, respectively). However, it should be noted that the seed density we got may be underestimated because some seeds, if any, might have been removed from seed traps by terrestrial seed predators prior to our samplings. Greatly differing from these native forests was the paucity of liana seeds sampled in the restored forest, a consequence of the general scarcity of lianas in the study area, which contrasts with the usually high abundance of lianas in fragments of semideciduous forests where they may profoundly influence forest physiognomy (Morellato & Leitão-Filho 1996). The rarity of lianas in our study area may be related to the low abundance of viable liana seeds in the seed bank when the forest was planted and the difficulty of the predominantly anemochorous seeds of lianas (Morellato & Leitão-Filho 1996) dispersing to the restored forest from nearby native forest fragments, several hundred meters distant.

Although intense, the seed rain was dominated by a few planted (e.g., *Trema micrantha*, *Schinus terebinthifolius*, *Croton urucurana*) and colonist species (e.g., *Tecoma stans*, *Maclura tinctoria*, morphospecies 01). These species characteristically produce great numbers of fruits annually (Lorenzi 1992; Barbosa & Macedo 2000; Lorenzi et al. 2003), and, except for *M. tinctoria* and *Leucaena* sp., all of

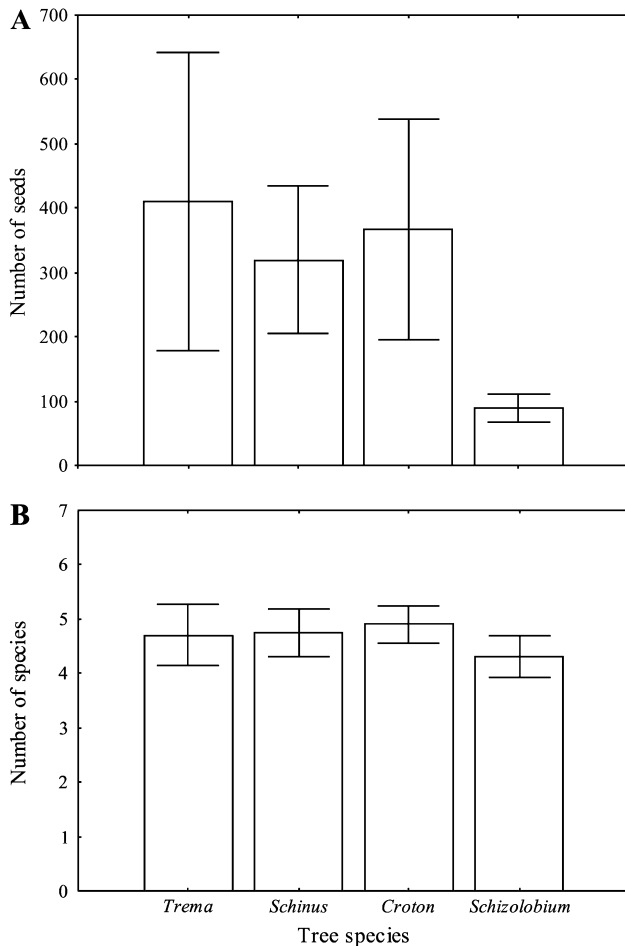


Figure 2. Mean number of zoochorous seeds (A) and seed species (B) collected below four different tree species originally planted in a restored gallery forest in Brazil. Tree species and number of 1-m<sup>2</sup> seed traps below them were as follows: *Trema micrantha*, 10 seed traps; *Schinus terebinthifolius*, 16; *Croton urucurana*, 11; and *Schizolobium parahyba*, 16. The first two species have fleshy fruits, whereas *Croton* and *Schizolobium* have dry fruits. Seeds collected under conspecifics (undispersed seeds; see text) were not considered here. Vertical lines refer to standard errors.

them occur in great abundances at the study area (Appendix 1). In addition, the zoochorous species have their seeds dispersed by small frugivorous birds and/or bats, which are the main agents responsible for seed dispersal in degraded tropical areas (Medellin & Gaona 1999; Pizo 2004). Therefore, high fruit production, high abundance, and efficient seed dispersal are key features that permitted these species dominate the seed rain. As a corollary it follows that the remaining species failed in at least one of these aspects, either they did not produce fruit during the study year, occurred in very low abundance, or did not have their seeds dispersed. The last possibility is especially critical for zoochorous species with large seeds, which usually suffer the lack of appropriate seed dispersers in disturbed areas (Silva & Tabarelli 2000; Pizo 2004). For instance, the palm *Syagrus romanzoffiana* has the largest

seed (13-mm diameter) among the zoochorous species collected, and despite the fact that it is not rare in the study area (Appendix 1) and has produced lots of fruits, seeds were collected in only one seed trap possibly because its seed dispersers, medium- to large-sized birds and mammals (Galetti et al. 1994; Guix & Ruiz 1997), are absent from the study area. Obviously, we cannot wait for natural colonization of such large-seeded species in restored forests, and they should be planted in the area to be restored (Martínez-Garza & Howe 2003).

In relation to dispersal modes, the seed rain was dominated by anemochorous species in abundance and richness, which did not differ from other natural semideciduous forests in SE Brazil (Penhalber & Mantovani 1997; Grombone-Guaratini & Rodrigues 2002). However, the high abundance of anemochorous seeds is largely due to the contribution of only one species, *T. stans*, an exotic tree commonly used as an ornamental plant in the human settlements that surround the restored forest from where it likely colonized. Judging by its high local abundance (23.5% of all plants sampled) and great seed production, *T. stans* is a very successful colonist species that may dominate the area in the near future causing great concerns. As an exotic species it may prevent the reestablishment of native species (Vitousek 1990), and as a wind-dispersed plant it may drive the restoration process in an unwanted direction. Although wind-dispersed plants may be important for the initial colonization of a given site (Finegan & Delgado 2000), its eventual predominance in the study area may slow down the progress of forest restoration. As Janzen (1988) pointed out, forest fragments dominated by anemochorous plants are usually unattractive to vertebrate seed dispersers, thus potentially diminishing the arrival of zoochorous seeds. This is especially critical for small, isolated forest fragments immersed in an inhospitable matrix as the study area, where lack of seed dispersal, particularly of zoochorous seeds, is a primary factor limiting forest recovery (Holl et al. 2000; Zimmerman et al. 2000).

The parameters of the structure of the vegetation we considered did not influence the abundance and richness of the seed rain as a whole, which is likely a result of the structural homogeneity of the planted forest. For the deposition of zoochorous seeds, more important than the structure of the vegetation or the plant species growing over a given spot is the composition of the vegetation in its immediate vicinity. In forested habitats, with a greater assortment of fruit-bearing plants and consequently foraging opportunities, a concentration of zoochorous species attracts seed dispersers repeatedly and promotes the deposition of animal-dispersed seeds (Clark et al. 2004; Lázaro et al. 2005). Therefore, if deposition of zoochorous seeds is a goal in restoration projects (Wunderle 1997), the spatial distribution of planted species, especially of zoochorous ones, should be carefully considered.

The high fruit production characteristic of many plant species in the study area, coupled with the already



mentioned lack of dispersal of some large-seeded species, likely contributed to the high between-species variation of seed limitation. Somewhat surprising was the fact that anemochorous species were more seed limited than zoochorous species. One could expect zoochorous species being more seed limited due to their dependence on animals, sometimes lacking or uncommon in disturbed areas (Silva & Tabarelli 2000), for seed dispersal. However, the majority of zoochorous seeds collected were small, thus readily dispersed by the small frugivorous birds and/or bats that occur in disturbed areas (Medellin & Gaona 1999; Pizo 2004). Moreover, it is possible that some planted anemochorous species (e.g., *Myroxylum peruiferum*, *Cariniana* spp.) had not reached their full reproductive maturity, thus contributing to increase the overall seed limitation of the anemochorous species pool. In relation to the origin in the area, colonist species were less seed limited than planted species, a difference that arose from the intrinsic characteristics of colonist species that make them good colonizers, that is, high seed production and efficient seed dispersal (Aide et al. 2000). As a consequence, if seed limitation indeed regulates population recruitment, colonist species may dominate the restored forest with time (e.g., *T. stans* cited above; see Appendix 1 for density), especially if plants with characteristically low fruit production and/or seed dispersal are present in high proportion among the planted species.

In conclusion, the development of the planted forest we studied is apparently going well. It now has many more species than originally planted, and seeds of potentially colonist species arrive in abundance. The invasion of the exotic anemochoric tree *T. stans* is, however, of great concern because it may dominate the forest in detriment of native species, thus driving the restoration process in an unwanted way. The invasion of exotic plant species should be a preoccupation for those interested in restoring a native forested habitat. Given that the abundance and richness of zoochorous plants positively influence the deposition of zoochorous seeds, we further recommend that for the initial establishment of a planted forest zoochorous plants should be homogeneously distributed to permit a spatially homogeneous zoochorous seedfall. If the chances of survival and establishment of a given seed vary spatially, as is often the case (Forget et al. 2005), a spatially homogeneous seedfall will likely result in enhanced opportunities of successful establishment.

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**Appendix.** Number of individuals and relative density (%) of plant species sampled in 53 5-m-radius circular plots at a restored gallery forest in SE Brazil, with information on successional stage (pioneer species, indicated with an asterisk, and nonpioneer species), exotic species (indicated by a plus sign), habit, dispersal syndrome, and origin in the area (i.e., if planted or colonist; see text for definition).

Family/Species	Habit <sup>a</sup>	Dispersal Syndrome <sup>b</sup>	Origin in the Area <sup>c</sup>	Number of Individuals	Relative Density
<b>Anacardiaceae</b>					
<i>Lithraea molleoides</i> *	T	Z	C	3	0.16
<i>Schinus terebinthifolius</i> *	T	Z	P	170	8.89
<b>Annonaceae</b>					
<i>Annona cacans</i>	T	Z	C	6	0.31
<b>Arecaceae</b>					
<i>Acrocomia aculeata</i>	T	Z	C	1	0.05
<i>Syagrus romanzoffiana</i>	T	Z	C	19	0.99
<b>Asteraceae</b>					
<i>Baccharis dracunculifolia</i> *	H	A	C	6	0.31
<i>Vernonia ferruginea</i> *	H	A	C	18	0.94
<i>Vernonia polyanthes</i> *	H	A	C	2	0.10
<i>Vernonia</i> sp. 1*	H	A	C	2	0.10
<i>Vernonia</i> sp. 2*	H	A	C	1	0.05
<i>Vernonia</i> sp. 3*	H	A	C	8	0.42
<b>Bignoniaceae</b>					
<i>Jacaranda mimosifolia</i>	T	A	C	60	3.14
<i>Tabebuia</i> cf. <i>rosea</i>	T	A	C	13	0.68
<i>Tabebuia chrysotricha</i>	T	A	P	28	1.46
<i>Tabebuia impetiginosa</i>	T	A	C	4	0.21
<i>Tabebuia ochracea</i>	T	A	C	2	0.10
<i>Tecoma stans</i> *+	T	A	C	450	23.52
<i>Zeyheria tuberculosa</i>	T	A	C	3	0.16
<b>Bombacaceae</b>					
<i>Chorisia speciosa</i>	T	A	P	11	0.58
<b>Boraginaceae</b>					
<i>Cordia superba</i> *	T	Z	P	3	0.16
<i>Cordia trichotoma</i>	T	Z	C	1	0.05
<b>Cecropiaceae</b>					
<i>Cecropia pachystachya</i> *	T	Z	C	10	0.52
<b>Euphorbiaceae</b>					
<i>Alchornea glandulosa</i> *	T	Z	C	37	1.93
<i>Croton floribundus</i> *	T	U	P	9	0.47
<i>Croton urucurana</i> *	T	U	P	59	3.08
<b>Lauraceae</b>					
<i>Nectandra megapotamica</i>	T	Z	P	15	0.78
<i>Ocotea odorifera</i>	T	Z	P	5	0.26
<b>Lecythidaceae</b>					
<i>Cariniana estrellensis</i>	T	A	P	13	0.68
<i>Cariniana legalis</i>	T	A	P	11	0.58
<b>Leguminosae—Caesalpinoideae</b>					
<i>Bauhinia variegata</i> *	T	A	C	1	0.05
<i>Delonix regia</i> +	T	U	C	1	0.05
<i>Hymenaea courbaril</i>	T	Z	P	16	0.84
<i>Pterogyne nitens</i>	T	A	P	34	1.78
<i>Schizolobium parahyba</i> *	T	A	P	75	3.92
<i>Senna bicapsularis</i> *	S	A	C	2	0.10
<b>Leguminosae—Mimosoideae</b>					
<i>Albizia hassleri</i> *	T	A	C	2	0.10
<i>Anadenanthera falcata</i>	T	A	C	1	0.05
<i>Enterolobium contortisiliquum</i> *	T	Z	P	39	2.94
<i>Inga uruguensis</i> *	T	Z	C	14	0.73
<i>Leucaena</i> sp.*+	T	U	C	2	0.10
<i>Piptadenia colubrina</i>	T	A	C	20	1.05
<i>Piptadenia gonoacantha</i> *	T	A	C	2	0.10

## Appendix. Continued.

Leguminosae—Papilionoideae						
<i>Centrolobium tomentosum</i>	T	A	P	19	0.99	
<i>Lonchocarpus muehlbergianus</i>	T	A	P	18	0.94	
<i>Machaerium acutifolium</i>	T	A	C	1	0.05	
<i>Myroxylum peruiiferum</i>	T	A	C	1	0.05	
<i>Platypodium elegans</i>	T	A	P	6	0.31	
<i>Pterocarpus violaceus</i>	T	A	P	18	0.94	
<i>Pterodon pubescens</i>	T	A	C	11	0.58	
<i>Tipuana tipu</i> +	T	A	P	12	0.63	
Meliaceae						
<i>Cedrela fissilis</i>	T	A	P	66	3.45	
<i>Guarea guidonia</i>	T	Z	P	9	0.47	
Moraceae						
<i>Maclura tinctoria</i>	T	Z	C	6	0.31	
Myrsinaceae						
<i>Myrsine ferruginea</i> *	T	Z	C	1	0.05	
<i>Myrsine cf umbrosa</i> *	T	Z	C	1	0.05	
Myrtaceae						
<i>Psidium cattleianum</i>	T	Z	P	2	0.10	
<i>Psidium guajava</i>	T	Z	C	16	0.84	
Phytolaccaceae						
<i>Gallesia integrifolia</i> *	T	A	P	61	3.19	
Piperaceae						
<i>Piper amalago</i> *	H	Z	C	1	0.05	
<i>Piper glabratum</i> *	H	Z	C	12	0.63	
<i>Piper sp.</i>	H	Z	C	15	0.78	
<i>Pothomorphe umbellata</i>	H	Z	C	1	0.05	
Rhamnaceae						
<i>Colubrina glandulosa</i>	T	Z	C	17	0.89	
<i>Rhamnidium elaeocarpus</i>	T	Z	C	1	0.05	
Rosaceae						
<i>Eriobotrya japonica</i> +	T	Z	C	1	0.05	
Rubiaceae						
<i>Genipa americana</i>	T	Z	P	4	0.21	
Rutaceae						
<i>Balfourodendron riedelianum</i> *	T	A	P	2	0.10	
<i>Esenbeckia leiocarpa</i>	T	U	P	5	0.26	
<i>Murraya paniculata</i> +	T	Z	C	6	0.31	
<i>Zanthoxylum rhoifolium</i>	T	Z	C	13	0.68	
<i>Zanthoxylum riedelianum</i>	T	Z	C	10	0.52	
Sapindaceae						
<i>Sapindus saponaria</i> *	T	Z	P	50	2.61	
Solanaceae						
<i>Cestrum schlechtendalii</i>	T	Z	C	173	9.04	
<i>Solanum erianthum</i> *	S	Z	C	1	0.05	
<i>Solanum granuloso-leprosum</i> *	T	Z	C	7	0.37	
Sterculiaceae						
<i>Guazuma ulmifolia</i>	T	Z	P	34	1.78	
Ulmaceae						
<i>Celtis iguanae</i> *	S	Z	C	1	0.05	
<i>Trema micrantha</i> *	T	Z	P	32	1.67	
Verbenaceae						
<i>Aegiphila lhotzkiana</i> *	T	Z	C	1	0.05	
<i>Aegiphila sellowiana</i> *	T	Z	P	7	0.37	
<i>Aloysia virgata</i> *	T	A	C	75	3.92	
<i>Cytharexylum myrianthum</i>	T	Z	P	4	0.21	
<i>Lantana camara</i> *	S	Z	C	12	0.63	
<i>Lantana sp.</i> *	H	Z	C	1	0.05	

<sup>a</sup>T, tree; S, shrub; H, herb.

<sup>b</sup>A, anemochorous; U, autochorous; Z, zoochorous.

<sup>c</sup>P, planted; C, colonist. Not all plant species originally planted in the area were sampled.