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# The Role of Sprouts in the Restoration of Atlantic Rainforest in Southern Brazil

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## Abstract

The relative importance of sexual reproduction (seed) and sprouting as sources for regeneration in Brazilian Atlantic Forest was evaluated in three different successional forest stages: young forest, immature forest, and late-successional forest. Young plants (10–100 cm tall) of tree species were classified into the following categories: (1) seedlings that are nonsprouting—plants that originated through sexual reproduction as seeds; (2) stem base sprouting—plants that sprouted at the base of an existing plant; and (3) underground stem sprouting—plants that sprouted from subterranean stems of an existing plant. A total of 1,030 individuals of 48 species were collected. Underground stem sprouting is the rarest form of propagation, with stem base sprouting somewhat more common and possibly associated with recovery of damaged parts. The greatest contribution to regeneration was due to seeds: 92% of the

individuals counted in 67% of the plant species. However, 13 species were “facultative” sprouters as seedlings and sprouters were observed in this group. The three forest ages differed in the proportion of regeneration strategies; in immature forest, sprouting was more common (15%) than in young (7%) and late-successional (3%;  $p < 0.05$ ) forest. In these three forest stages, germinating seeds are the major source of new plants; although sprouting as a reproductive strategy is rare, it is related to recovery after damage of an already existing plant and may be due to previous land use history (agriculture) and low soil fertility. Restoration using natural regeneration should consider these factors to understand seed arrival as seed is the main source of regeneration.

**Key words:** asexual reproduction, regeneration modes, *restinga*, seed reproduction, sprouting, tropical rainforest.

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## Introduction

The Atlantic Forest, the most diverse of any Brazilian forest system, originally extended along the entire eastern coast of Brazil and into the bordering regions of Paraguay and Argentina. Due to agriculture and urban growth (70% of the Brazilian population is urban), this biome has been reduced to a small fraction of its former size. Today, the Atlantic Forest is considered a global “hot-spot” of biological diversity and is therefore extremely important for conservation (Myers et al. 2000). Although some remnants of Atlantic Forest are currently protected in reserves, the largest tracts of forest were totally or partially destroyed in the twentieth century. Because these deforested areas are usually abandoned, forest recovery depends on the complex interaction of allochthonous and autochthonous regeneration processes.

In the ecological restoration of tropical forests, planting forest species based on a conceptual framework of ecological succession is an efficient strategy for establishing the original forest structure and function (Young 2000). Several initiatives have been successful in the tropics (Parrotta 1991; Ferreti & Britez 2005), but the high cost of these methods impedes their application in forest

rehabilitation (Metzger 2003). If the degree of disturbance was low and if the forest fragments remain, natural regeneration (by seed, sprouting, or advanced regeneration) is preferred and ecological processes recover after some variable time interval (Parrotta et al. 1997; Reis & Kageyama 2003). Understanding the regeneration process is therefore essential for developing management plans for the restoration and maintenance of Atlantic Forest.

In disturbed tropical forests, recovery of the original forest diversity and species abundance may be initiated through a variety of mechanisms. The seed bank and seed rain, along with sprouting from existing roots or stems of plants that survived the disturbance, may initiate restoration (Alvarez-Buylla & Garcia-Barrios 1991; Martínez-Ramos & Soto-Castro 1993; Everham & Brokaw 1996; Dalling & Denslow 1998). The relative importance of these two regeneration mechanisms (seed or sprouting) will determine the successional process and, ultimately, community structure of the mature forest.

Sprouting may result in several individuals (clones) originating from one parent plant (Silvertown 1987). Although sexual reproduction will provide greater genetic variability (Harper 1977), vegetative propagation through ramets may result in the survival of resistant individuals (Miller & Kauffman 1998). Sprouts have advantages, including an already established root system with a large surface area for water and resource acquisition and high stored energy reserves. These advantages may confer greater chances of plant survival and recovery of damaged

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parts (Sakai et al. 1995; Kennard et al. 2002) and therefore may offset the benefits gained from sexual reproduction, especially when seedling establishment is limited (Sakai et al. 1995).

Although studies have tended to neglect the importance of sprouting in favor of processes associated with sexual reproduction (Bond & Midgley 2001), some studies have examined the importance of sprouting in tropical forests (e.g., Kammesheidt 1998; Miller & Kauffman 1998). Although we understand that sprouting often occurs in Atlantic Forests (Sá 1996; Tabarelli & Mantovani 1999; Rodrigues et al. 2004), the importance of this method of propagation has never been quantified. The first step to understanding the role that sprouting may play in forest conservation is to examine the relative investment in seed (sexual reproduction) and sprouting (asexual reproduction) in disturbed environments. With these data, we may then examine the ability of species to recover and consequently the regenerative capacity of the forest. Management plans may then be developed for conservation strategies and, based on those data, may recommend natural or artificial propagation to restore forest structure and function.

In this study, we examined the role and importance of sprouting in regeneration in the Atlantic Forest of southern Brazil. Specifically, we answer the following questions: (1) is sprouting common in this forest?; (2) if so, in what proportion of individuals and species does it occur?; (3) do plants have specific regions (aboveground or belowground level) from which sprouting most commonly occurs?; (4) is sprouting associated with plant size?; and (5) is the relative importance of sprouting constant along successional stages of forest recovery?

## Methods

### Study Site

The study site is in a region of Atlantic Forest within a protected reserve (Palmito State Forest, total area of approximately 300 ha) in the municipality of Paranaguá (lat 25°35'S, long 48°32'W, at sea level), in the state of Paraná, southern Brazil. The climate (Af in Koppen's classification) is tropical and superhumid, with neither a pronounced dry season nor frosts (Iapar 1978). The 46-year running average temperature is 21°C. Average annual precipitation is 2,218 mm and is always greater than 60 mm even in the driest month (Britez & Marques 2005). Soils (spodzols) are sandy (90–98% sand) and acidic (3.2–3.9 pH; C. Wisniewski, 2006, Universidade Federal do Paraná, personal communication).

The southern coast of Brazil is in the Atlantic Rainforest biome, which includes a complex of vegetation types (mainly forest and scrub) on both upland and lowland areas. In lowland areas, where the soil is comprised of marine (Holocene) deposits, the vegetation type is locally called "restinga" (Araujo 1992). In the Palmito reserve, the vegetation type is *restinga* forest, very similar in flor-

istics and structure to those typical of lowland Atlantic forests that are not over Holocene deposits (Silva et al. 1994). However, the vegetation in the reserve has been modified by 100 years of human occupation. Historically, agricultural practices were rudimentary, with subsistence cultivation based on slash-and-burn agriculture. In the Palmito reserve, forest cutting, planting, and burning occurred successively during several years of pineapple and manioc cultivation. As a result of these practices, today, the reserve is a mosaic of different successional stages including a very small area of old-growth forest. A 0.5-ha area of each of the three forest successional stages was chosen for the study: young forest (21 years old as of 2003), immature forest (34 years), and late-successional forest (59 years). The young forest contains two, more or less, well-defined strata (upper and lower), with a canopy height of approximately 8 m, has relatively low plant species diversity (Shannon–Wiener's diversity index  $H' = 0.95$  for trees >5 cm diameter at breast height [dbh]), and is dominated by *Ilex theazans*. The immature forest has three (upper, middle, and lower) strata, with a canopy height of 12 m and greater diversity ( $H' = 2.16$ ). The late-successional forest also has three strata, with a canopy height of 16 m and even greater diversity ( $H' = 3.29$ ; F. M. Ramos et al., unpublished data). The three forest sites are within close proximity to each other (approximately 1,000 m).

### Sampling

In each of the three forest stages, five 2 × 2-m plots were established along a transect (8 m between plots). Due to the irregular distribution of forest in the Palmito reserve (i.e., patches of early- and late-successional forest are very close), a limited area was defined. In each of these plots, all individuals of tree species that were 10–100 cm tall were collected. Our sampling technique was determined by the asymptote of a species area curve, showing that the sample size was sufficient to include all or nearly all species. Each individual was very carefully excavated to gather both aerial and subterranean parts and uniquely labeled. Plants were taken to the laboratory, where they were identified, counted, and diameter at soil level and height measured. Plants were identified by comparison with either adults in the same area or specimens in the herbarium of the Botany Department of the Universidade Federal do Paraná. Species names and authorities were checked in Missouri Botanical Garden tropical database ([www.mobot.org](http://www.mobot.org)).

In the laboratory, plants were carefully examined to determine connections between two or more aerial parts. When connections existed, indicating sprouting, the form of the connection was noted as aboveground or belowground and stem or root. When necessary, anatomical slides were prepared for microscopic examination to determine the form of the connection between the plants. Plants were assumed to have originated from seed in the absence of evidence of sprouting.

### Data Analysis

Plant density and species richness were counted, and Shannon–Wiener's diversity index ( $H'$ ) was estimated for each plot in each forest stage (Pielou 1975). Forest stages were compared by the Sorensen Similarity Index ( $S$ ). To test whether sprouting was associated with plant size in each forest stage, average diameter and height of plants that had sprouted were compared among the three forest stages (analysis of variance [ANOVA], Tukey; Zar 1999). Sprouting probability (proportion of sprouting plants) and type of sprouting were compared among areas by contingency analysis (Zar 1999). All the tests were two tailed and considered significant at  $p < 0.05$ .

### Results

Forty-eight species and 1,030 individual plants were collected (Appendix 1). The species area curve reached an asymptote at 16 m<sup>2</sup>, which shows that our sampling areas were sufficient for an accurate estimate of the community (Fig. 1). The three forest stages had a similar species composition: young and immature forests— $S = 0.73$ , immature and late-successional forest— $S = 0.70$ , and the greatest difference was between the young and late-successional forest, where  $S = 0.49$ . Richness and diversity ( $H'$ ) varied among the forest stages, with late-successional forest being the most rich and diverse and the young forest the least (Table 1). The most common species, by forest stage, were *Gomidesia fenzliana* in the young forest; *Ocotea pulchella*, *G. fenzliana*, and *Myrsine venosa* in the immature forest; and *O. pulchella* and *Calophyllum brasiliense* in the late-successional forest (Appendix 1).

Plants arose in three main ways: (1) from seed, non-sprouting seedlings; (2) stem base sprouting, which arises from the stem above the soil level usually after breakage; and (3) underground stem sprouting, which arises from an underground stem normally parallel to the soil surface. Of the 48 species, 32 were strictly seedlings, 3 strictly sprouters (stem base or underground stem sprouting), and 13 “facultative sprouters,” in which plants arose through stem base sprouting, underground stem sprouting, or seed (Fig. 2). Of the 16 sprouting species, 8 were only stem base sprouting (*Amaioua guianensis*, *Clethra scabra*, *Erythroxylum amplifolium*, *Guapira opposita*, *Guatteria australis*, *Myrcia racemosa*, and unknown species 7 and 8),

4 only underground stem sprouting species (*Alibertia color*, *Blepharocalyx salicifolius*, *Conomorpha peruviana*, and Myrtaceae sp. 1), and 4 included both sprouting types (*G. fenzliana*, *Ilex theazans*, *O. pulchella*, and *M. venosa*; Fig. 2). Of the 1,030 individuals, 92.3% showed no evidence of sprouting ( $n = 950$ ), 6.4% showed stem base sprouting ( $n = 66$ ), and 1.3% showed underground stem sprouting ( $n = 14$ ).

Average plant height and diameter among the three regeneration types were different (ANOVA;  $F = 22.97$ ,  $p < 0.05$  and  $F = 36.02$ ,  $p < 0.05$ , respectively). Average height ( $\pm$  SE) of the seedlings (14.4 cm  $\pm$  0.57) was lower than that for both types of sprouters (stem base sprouting = 28.9  $\pm$  2.16 and underground stem sprouting = 23.5  $\pm$  4.7; Tukey,  $p < 0.05$ ), which were similar ( $p > 0.10$ ). The diameter followed the same pattern, with seedlings (2.13 cm  $\pm$  0.14) less than both stem base sprouters (4.4  $\pm$  0.53) and underground stem sprouters (3.7  $\pm$  1.15; Tukey,  $p < 0.05$ ).

The three forest stages differed in regeneration strategy. Seedlings were much more common than both types of sprouting in all the three forest stages ( $\chi^2 = 25.1$ ,  $df = 2$ ,  $p < 0.05$ ), even after removal from the analysis of *G. fenzliana* (the most common species in these three areas), this result was then verified ( $\chi^2 = 19.0$ ,  $df = 2$ ,  $p < 0.05$ ). Only 15% of the individuals in the immature forest showed any type of sprouting (average = 7.2  $\pm$  4.6 sprouters per plot), whereas in the young forest (9.0  $\pm$  6.8 sprouters per plot) and late-successional forest (1.4  $\pm$  0.5 sprouters per plot) this percentage was even lower (7 and 3%, respectively; Fig. 3). In comparing only the sprouting plants, the proportion of stem base sprouting and underground stem sprouting differed in the three forests stages ( $\chi^2 = 17.8$ ,  $df = 2$ ,  $p < 0.05$ ). Stem base sprouting occurred more frequently (66%) than underground stem sprouting (34%) in the immature forest and the young forest (97 and 3%, respectively). In the late-successional forest, only eight plants showed stem base sprouting (3% of the total) and no underground stem sprouting was found.

### Discussion

A low frequency of sprouting was typical of all the three forest stages, and clearly, more plants arise from seed than sprouting in this restinga forest. Sprouting appears to be occasional and may be associated with recovery after

**Table 1.** Structural parameters of the regeneration strata (plants  $\leq 1$  m tall) of three successional stages (sampling area = 20 m<sup>2</sup> each) of Atlantic Rainforest in Paranaguá, southern Brazil.

	Young Forest (21 Years Old)	Immature Forest (34 Years Old)	Late-Successional Forest (59 Years Old)
Total abundance ( $n$ )	514	287	229
Average ( $\pm$ SD) abundance (plants per plot)	102.8 ( $\pm$ 79.4)	57.4 ( $\pm$ 22.8)	45.8 ( $\pm$ 28.2)
Total richness ( $n$ )	24	31	30
Average ( $\pm$ SD) richness (plants per plot)	11.2 ( $\pm$ 5.5)	13.2 ( $\pm$ 5.6)	13.0 ( $\pm$ 1.2)
$H'$	2.18	2.36	2.42

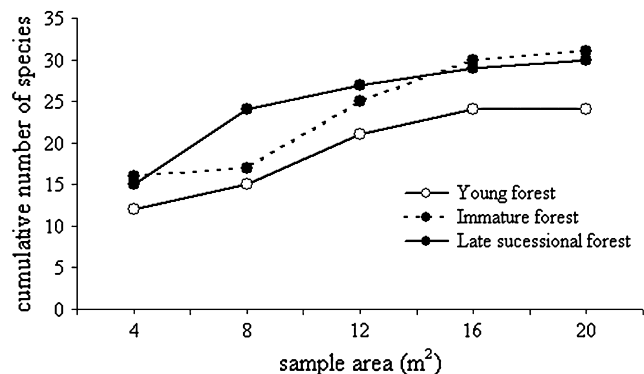


Figure 1. Species area curves for sampling areas in this study in the Atlantic Rainforest in Paranaguá, southern Brazil. Curves show asymptotes within the number of samples of this study, verifying that most or all species present were sampled.

damage, rather than a dominant form of reproduction. In general, in tropical forests, many more species sprout than were observed in this study. Fifty-two percent of species and 85% of individuals were found to sprout in disturbed forests (Everham & Brokaw 1996) compared to 33 and 8%, respectively, found here. Although shrub and tree species of Atlantic forests frequently propagate by sprouting (Negrelle 1995; Cirne & Scarano 2001), in this study, we show that the contribution of sprouting to forest regeneration is less important.

Sprout rarity in the Palmito reserve may be caused by intensive pineapple and manioc cultivation and associated with characteristics typical of restinga forests. Although slash or burn can stimulate tree sprouting, the continued or excessive use of slash-and-burn agriculture may limit

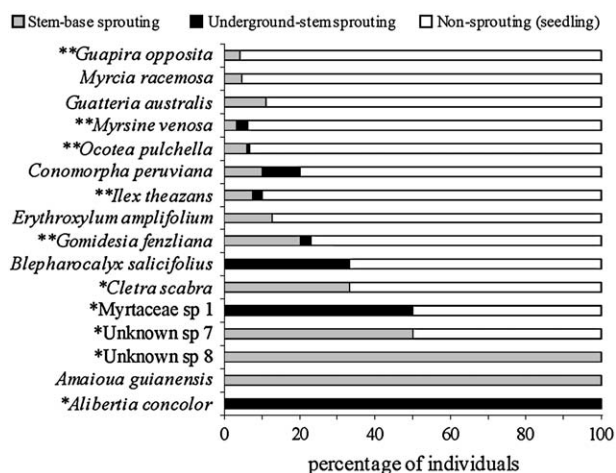


Figure 2. Percentage of individuals of each plant species with non-sprouting (seedling), stem base sprouting, or underground stem sprouting, in the three successional stages of Atlantic Rainforest in Paranaguá, southern Brazil. \* indicates rare species (abundance of  $\leq 5$ ) and \*\* indicates very common species (abundance of  $\geq 50$ ). Another 32 recorded species were 100% nonsprouting (regenerated only from seed).

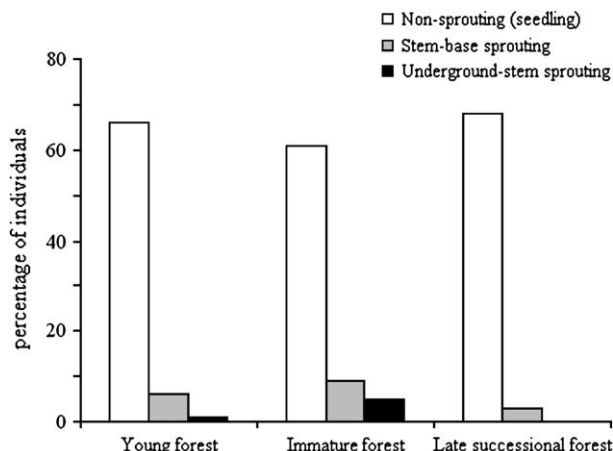


Figure 3. Percentage of nonsprouting (seedling), stem base sprouting, and underground stem sprouting individuals in the three successional stages of Atlantic Rainforest in Paranaguá, southern Brazil. Young forest,  $n = 514$ ; immature forest,  $n = 287$ ; and late-successional forest,  $n = 229$  ( $\chi^2 = 25.1$ ,  $df = 2$ ,  $p < 0.05$ ).

sprout formation (Hartmann et al. 2002). Additionally, the poor soils typical of restinga (approximately 95% sand with low concentrations of phosphorus and potassium; Britze 2005) may limit carbohydrate storage in the roots and stem and thus inhibit sprouting. This type of forest may favor species that reproduce sexually (Marques & Oliveira 2005) rather than by sprouting.

Although sprouting is relatively unimportant here in terms of numbers, plants that arose from sprouting are larger in height and diameter because bud formation only occurs following the development of a vascular cambium. In addition, in the study area, plants greater than 5 cm dbh had different numbers of stems depending on successional stage (young plants =  $3.69 \pm 0.48$ , immature plants =  $1.38 \pm 0.82$ , and mature plants =  $1.29 \pm 1.47$ ; F. M. Ramos et al., unpublished data). This suggests that growth confers an advantage in branching and sprouting; so in this study with an upper size class limit, we may have underestimated sprouting. Other studies have shown that plants arising from sprouting are often larger and more resistant (Goto et al. 1996; Miller & Kauffman 1998) and contribute more to total dominance (volume) (Kennard et al. 2002). Conversely, seedlings often suffer greater mortality (Goto et al. 1996; Marques & July 2000). Thus, although sprouting is numerically less important than germination as a source of plants, sprouted plants may have a growth advantage by initially being larger and having greater reserves, perhaps improving long-term survival.

Stem base sprouting was more common than underground stem sprouting and arose from plants that were damaged in some way. Observations in the study area suggest that damage is caused by tree falls, mammals in the understorey (including man), pathogens, or herbivores. Although sprouting of a damaged part may occur, it is an accidental event and hence most likely to be a survival

rather than reproduction strategy (Sakai et al. 1995; Goto et al. 1996; Bond & Midgley 2001).

Aboveground plant formation that arises from underground systems is due to the development of buds on roots or stems (Silvertown 1987). Tree species most commonly arise from root buds (Kammesheidt 1999; Hayashi et al. 2001; Rodrigues et al. 2004), however, surprisingly not in any of the species in the forest studied here. On the other hand, sprouting from underground stem buds, which is normally found in herbaceous plants and shrubs (Rizzini & Heringer 1966; Mallik 1993; Apezato-da-Glória 2003), occurred in eight tree species in the Palmito reserve.

Four of the 13 species that reproduce both by seed and sprout are in different successional stages (Appendix). These species invest heavily in sexual and asexual reproduction, which may be characteristics of pioneer species (Harper 1977). The large investment in reproduction apparently leads to dominance of these species. Tropical species preferably reproduce by seed (Miller & Kauffman 1998), but it is possible that the potential for asexual reproduction is also present and when manifested, may be considered “facultative resprouting” by providing the advantage of vegetative propagation when sexual reproduction is limited (Goto et al. 1996). Additionally, plants that reproduce in more than one way may persist and thereby stabilize community composition (Eriksson 2000).

In the late-successional forest, fewer plants had sprouts than those in the immature forest or young forest (3 vs. 15 and 7%, respectively). Although sprouting may be more or less constant in early-successional forests with a predominance of secondary species (Kammesheidt 1998, 1999), some species in late-successional or climatic stages may also tend to sprout (Fernández-Palacios & Arévalo 1998; Kammesheidt 1999; Kennard et al. 2002). In this study, there was a greater frequency of sprouting in the immature and young forests. This is probably related to the exclusivity of some sprouting species in these forests (*Blepharocalix salicifolius*, *Erythroxylum amplifolium*, *Guapira opposita*, and Myrtaceae sp. 1) and with the greater total abundance in the early-successional stages than in the late-successional forest.

Sexual reproduction (seed) and sprouting both influence forest composition and consequently capacity for natural restoration. Nevertheless, soil characteristics and land use history also have an important influence on the type of regeneration that takes place. Specifically, in restinga forests in coastal Paraná, where a combination of low soil fertility and agricultural practices may have limited sprouting, propagation by sprouting is less important than reproduction by seed. Additionally, species richness in the late-successional stage (30 species with dbh > 5 cm) is much less than that of undisturbed restinga forest (53 species) (Silva et al. 1994), which suggests that natural regeneration is limited due to the lack of sprouting or not enough time has passed to reach the expected number of species.

In Atlantic forests of Brazil, some attempts have been made at artificial restoration by planting (Kageyama et al.

2003; Ferreti & Britez 2005), but natural restoration is much more common, especially in conservation areas (Tabarelli & Mantovani 1999) where financial resources are limited (Dourojeanni & Pádua 2001). Thus, future restoration plans, especially in areas like the restinga (e.g., with poor soils), must consider land use history as well as the raw material for sprouting, such as viable stumps remaining from forest cutting, and the sprouting ability of the species involved, all of which will influence the speed and quality of forest restoration.

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**Appendix.** Tree species and their abundance in three successional stages of Atlantic Rainforest in Paranaguá, southern Brazil.

Family	Species	Abundance		
		YF	IF	LSF
Anacardiaceae	<i>Tapirira guianensis</i> Aubl.	—	—	12
Annonaceae	<i>Guatteria australis</i> A. St.-Hil.	10	—	6
	<i>Xylopia langsdorfiana</i> St.-Hil. & Tul.	—	1	—
Aquifoliaceae	<i>Ilex</i> sp.	—	1	—
	<i>Ilex theazans</i> Mart.	31	6	3
Arecaceae	<i>Euterpe edulis</i> Mart.	—	—	2
	<i>Geonoma schottiana</i> Mart.	2	5	2
Celastraceae	<i>Maytenus robusta</i> Reissek	2	12	2
Clethraceae	<i>Clethra scabra</i> Pers.	—	—	3
Clusiaceae	<i>Calophyllum brasiliense</i> Cambess.	2	6	29
	<i>Clusia criuva</i> Cambess.	30	1	1
Erythroxylaceae	<i>Erythroxylum amplifolium</i> Baill.	7	1	—
Euphorbiaceae	<i>Alchornea triplinervia</i> (Spreng.) Müll. Arg.	2	1	—
	<i>Maprounea brasiliensis</i> A. St.-Hil.	1	—	—
Fabaceae	<i>Andira fraxinifolia</i> Benth.	—	2	3
	<i>Machaerium uncinatum</i> Vell. (Benth.)	—	1	—
Lauraceae	<i>Ocotea aciphylla</i> (Nees) Mez	—	—	7
	<i>O. pulchella</i> (Ness) Mez	131	79	89
Melastomataceae	<i>Miconia cabussu</i> Hoehne	—	4	—
	<i>M. cinerascens</i> Miq.	—	—	2
Meliaceae	<i>Guarea macrophylla</i> Vahl	1	—	5
Myrsinaceae	<i>Conomorpha peruviana</i> A. DC.	—	10	1
	<i>Myrsine venosa</i> A. DC.	69	56	7
Myrtaceae	<i>Blepharocalyx salicifolius</i> (Kunth) O. Berg	2	4	—
	<i>Calyptanthus rubella</i> (O. Berg) D. Legrand	2	—	1
	<i>Gomidesia feniziana</i> O. Berg	112	57	6
	<i>M. multiflora</i> (Lam.) DC.	1	1	—
	<i>M. racemosa</i> (O. Berg) Kiaersk.	4	5	13
	Myrtaceae sp. 1	—	2	—
	Myrtaceae sp. 2	3	3	—
	Myrtaceae sp. 3	5	1	—
Nyctaginaceae	<i>Guapira opposita</i> (Vell.) Reitz	69	3	—
Podocarpaceae	<i>Podocarpus sellowii</i> Klotzsch ex Endl.	—	—	9
Rosaceae	<i>Prunus myrtifolia</i> (L.) Urb.	5	3	—
Rubiaceae	<i>Alibertia concolor</i> (Cham.) K. Schum.	—	1	3
	<i>Amaioua guianensis</i> Aubl.	—	—	2
	Rubiaceae sp.	1	6	—
Sapindaceae	<i>Matayba guianensis</i> Aubl.	4	7	12
Theaceae	<i>Ternstroemia brasiliensis</i> Cambess.	18	2	—
Unknown	Unknown 1	—	2	1
	Unknown 2	—	3	—
	Unknown 3	—	—	1
	Unknown 4	—	1	2
	Unknown 5	—	—	1
	Unknown 6	—	—	1
	Unknown 7	—	—	2
	Unknown 8	—	—	1

IF, immature forest; LSF, late-successional forest; YF, young forest.