

Mechanisms of plant regeneration during succession after shifting cultivation in eastern Amazonia

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Abstract The role of seed bank, seed rain, and regeneration from seedlings and sprouts after swidden agriculture was compared in 5-, 10- and 20-year-old secondary forest and in a primary forest in Bragantina, Pará, Brazil. The seed bank (0–5 cm soil depth) was largest in the 5-year-old forest (1190 ± 284 seeds m^{-2}) and decreased nearly ten-fold with age to 137 ± 19 seeds m^{-2} in the primary forest. The highest seed rain was in the 5-year-old forest (883 ± 230 seeds m^{-2} year $^{-1}$) and the least in the primary forest (220 ± 80 seeds m^{-2} year $^{-1}$). Large plants (≥ 5 cm dbh) had more individuals and species that regenerated from sprouts than from seeds and the most abundant tree species in the secondary forest stands of all ages appear to be maintained by sprouting. The smaller individuals (≥ 1 m tall, < 5 cm dbh) in the 5-year-old forest were mainly from sprouts, but those in the older secondary forests originated mainly from seeds. These results show that at the beginning of succession, although many species can be introduced to swidden fallow from seed bank and seed rain, it is the sprout that is the

main source of recruits of primary forest species in secondary forests in Bragantina.

Keywords Amazonia · Seed bank · Seed rain · Secondary succession · Slash-and-burn · Sprouting · Succession

Introduction

Initial floristic composition in disturbed forest is mainly determined by the soil seed bank, seed advance regeneration, and by the sprouting capacity of stumps and roots. Several studies have investigated the role of the seed bank and seed rain, but rarely along a gradient of forest ages (Uhl and Jordan 1984; Uhl 1987; Young et al. 1987; Saulei and Swaine 1988; Rico-Gray and Garcia-Franco 1992; Victor and Jose 1992). Sprouts have been shown important in sites manually cleared for shifting cultivation (Rouw 1993) and have been regarded by Uhl et al. (1982b) and Whitmore (1983) as being generally important in the regeneration of tropical forests.

However, the regeneration sources after repeated use of land for shifting cultivation are poorly quantified, and in particular, the long-term role of the three basic forms of plant regeneration in secondary succession after slash-and-burn agriculture is not well-documented. In addition, little is known about how the initial available regeneration sources relate to species composition in forest stands of

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different age and status (primary vs. secondary). It is common that following the rapid initial recovery of forest cover after slash-and-burn agriculture many primary forest tree species remain absent from these secondary forests for a large number of years. For example, Vieira (1996) reported that in Bragantina only 35% of the tree species recorded in a primary forest were found in nearby secondary forest stands.

This article reports a study that was carried out in the Bragantina region, eastern Amazonia, Brazil, where about 90% of the primary forest has been removed and much of the land has had at least eight cycles of slash, burn, cultivation and fallow. The objectives are to describe the seed rain, seed bank and sprouting in different-aged forest fallows and mature forest (1) to determine the relative importance of the regeneration sources to forest recovery in relation to forest age; (2) to compare the resprouting ability of tree species of different successional status; and (3) to determine the contribution of seeds and sprouts to the restoration of tree species diversity.

Material and methods

The study area

Bragantina (0°45' S, 46°16' W and 1°39' S, 48°15' W; Fig. 1) is the oldest agricultural frontier in Amazonia (Oliveira 1983). Colonisation occurred during the early 1800s by immigrants from Europe (mainly Spain, Portugal, and France) and from north-

eastern Brazil (Egler 1961; Penteadó 1967). The farming system was shifting cultivation and most individual fields were abandoned, reverting to secondary forest or *capoeiras*.

The region has a gentle relief, with elevations of not more than 50 m a.s.l. The mean annual temperature is about 25.5°C and the annual rainfall is about 2,300 mm. Most of the rain falls in January–March and there is a dry period in September–November (with less than 150 mm rain). The predominant soils are oxisols, including those under the study plots, where they are all of similar chemical and physical composition (Vieira 1996).

The secondary forest sites for this study were selected after interviewing local residents (Vieira 1996). None of the sites had been sprayed with herbicides or fertilised during cultivation. Three plots of 5 m × 50 m each (a size which is within the range of typical plot size of 0.01–1 ha used by farmers in the past) were established at random in secondary forest stands of 5, 10 and 20 years of age after abandonment and three plots of 1 ha (10 m × 1000 m) were placed randomly (but at least 100 m from the forest edge) in a 200 ha fragment of primary forest. The primary forest (Monte Verde) is lowland evergreen rain forest (*sensu* Whitmore 1984), with a canopy 30–40 m tall, and the most abundant species ≥ 5 cm dbh are *Eschweilera coriacea* (DC.) Mart. ex Berg. and *Lecythis idatimon* Aubl., both of the Lecythidaceae family. The secondary forest stands were within a radius of 3 km from Monte Verde. The most abundant species in the secondary forest was *Vismia guianensis* (Aubl.) Choisy (Clusiaceae) in the 5- and 10-year-old forests and *Croton matourensis* Aubl. (Euphorbiaceae) in the 20-year-old plots.

Soil seed bank

Four soil monoliths of 20 cm × 20 cm were collected at random in each plot to depths of 0–5 and 5–10 cm (a total of 12 samples for each forest age-class and soil depth) in January 2004. All samples were spread about 3 cm thick on separate trays of 25 cm × 40 cm, and maintained moist and well-ventilated in the open under a white shade cloth. The samples were examined every 7 d in the first two months and every 14 d thereafter. After four months the soils in the trays were turned over and observed for two more

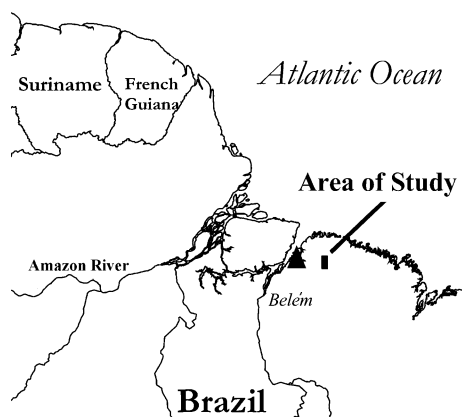


Fig. 1 Location of the study site in Bragantina, near Belém, Pará, Brazil

months. All seedlings were identified and removed as they emerged. Control trays were deemed unnecessary because the area where the seed trays were placed had no seedlings growing and the white shade cloth prevented contamination of the experimental trays; Nepstad et al. (1996) found no contamination of controls either in a seed bank site at Paragominas in Brazil.

The diversity of the seed bank was compared across forest ages by the Shannon–Wiener index and similarity by the Sørensen index (Brower and Zar 1984). For each sample depth separately the seed bank data were square root transformed (Warr et al. 1993) and analysed using a two-way nested analysis of variance with forest age-class and soil depth as fixed factors, and replicate plots within forest age class as a random factor (Zar 1996). A Tukey test was used to compare the mean seed bank size among the forest age-classes.

Seed rain

Four seed traps (cloth stretched on wood frames) of 1 m² were located randomly at 1 m above the ground in each plot. A random trap location was thought to be suitable in view of the work by Adams (1997), discussed later. The legs of the traps were covered with oily plastic to control predation. Unfortunately, the oil was readily washed off by rain. However, few insects (the only likely predators) were ever found in the traps and their effect was thought to be slight and ignored. The traps were visited every 14 d from 1 April 1993 to 31 March 1994. All visible and healthy seeds were counted and extracted. The unidentified seeds were grown up in a glasshouse for identification of the seedlings. Animal faeces and assorted fine debris that collected in the traps were placed in a well-lit germination box (FANEM model 347) with a constant temperature of 30°C and any seedlings which emerged were counted and identified. These were called hidden (not visible to the naked eye) seeds, because it was not possible to separate them before germination. When intact fruits were recovered, the number of seeds contained within them was counted or estimated using an average from a sample of fruits of the species.

The square root transformed data were analysed by a one-way analysis of variance (Zar 1996) and a Tukey test was used to compare the mean of seed rain

among the forest age-classes. Diversity and similarity were analysed as described for the seed bank.

Seedlings vs. sprouts

All larger plants (≥ 5 cm dbh) in each plot were enumerated (Vieira 1996) examined for sprouting by digging a hole around each plant to a depth of 10 cm to assess the presence of root sprouts. The presence of sprout scar on the stems was also observed. Smaller plants (< 5 cm dbh and ≥ 1 m tall) were sampled from two random subplots of 1 m \times 5 m in each of the three replicate plots in each forest age-class. The smaller plants were identified and counted and a distinction was made between seedlings and sprouts, by examining the older plant parts. Often the plants had to uprooted to check for sprouting. Root and shoot sprouts were not recorded separately.

Results

Soil seed bank

The density of germinating seeds was significantly different between the forest age-classes at both depths (Table 1, $F = 19.39$ for 0–5 cm; $F = 30.88$ for 5–10 cm; d.f. = 3, $p < 0.001$). The highest number of seeds was found in the 0–5 cm soil of the 5-year-old forest (1190 ± 284 seeds m⁻²) and decreased with age to 137 ± 19 seeds m⁻² in the primary forest (Table 1). The density of seeds at 5–10 cm was about half of that at 0–5 cm (Table 1). Between 30% and 40% of the seeds germinated after 28 d and there was a flush of germination after turning the soil over at 112 d.

Total seed bank species diversity and richness did not vary much with forest age-class (Table 1). Total species numbers in the seed bank (0–5 and 5–10 cm samples combined) were 60, 63 and 70 for the 5-, 10- and 20-year-old secondary forests and 54 for the primary forest. Species similarity amongst the forest age-classes varied from 0.48 to 0.69, with higher values between adjacent forest age-classes.

Herb (forbs and graminoids) seeds were commonest (Fig. 2) but their proportion decreased with age from 78% of the total seeds in the 5-year-old forest to 43% in the primary forest. The number of herb species was higher in the secondary forests

Table 1 Mean numbers of seeds ($m^{-2} \pm SE$), the numbers of species and their diversity in the seed bank (total sample area $0.48 m^2$) and in the seed rain ($12 m^2$) in 5-, 10- and 20-year-old

secondary forests and primary forest in Bragantina, Pará, Brazil. The mean values followed by different letters in the rows are significantly different according to a Tukey test, $p < 0.05$

	Forest-age class (years)			
	5	10	20	Primary forest
Soil seed bank				
Mean number of seeds				
0–5 cm	1190 \pm 284a	547 \pm 42b	450 \pm 56.7b	137 \pm 19c
5–10 cm	411 \pm 78.2a	260 \pm 6.2ab	162 \pm 20.5b	64 \pm 10.4c
Number of species	60	63	70	54
Species diversity (H')	1.20	1.30	1.42	1.31
Seed rain				
Mean number of seeds year ⁻¹	883 \pm 230a	527 \pm 122ab	514 \pm 169ab	220 \pm 80b
Number of species	70	93	104	134
Species diversity (H')	0.91	1.19	1.09	1.35

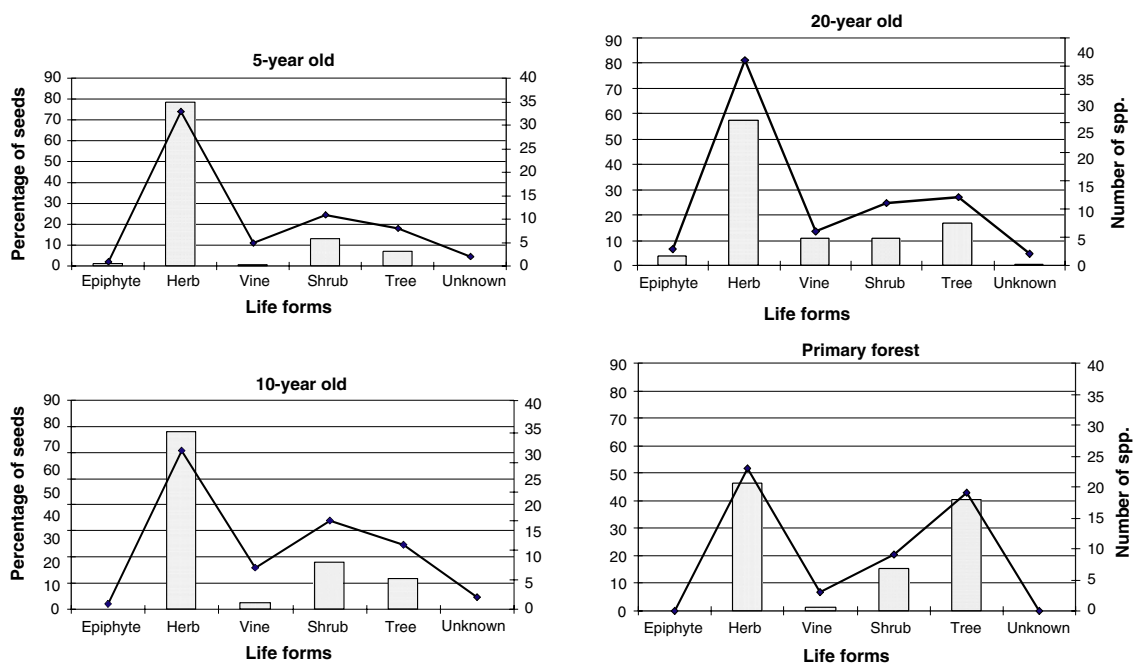


Fig. 2 The percentage of seeds and number of species belonging to different life forms in the soil seed bank at 0–10 cm depth in 5-, 10- and 20-year-old secondary forest

stands and in primary forest in Bragantina, Pará, Brazil. Columns, percentage of seeds; lines, number of species

(27–36) than in the primary forest (23). The proportion of tree seeds and species increased with forest age (Fig. 2).

The most numerous seed bank species in the secondary forests were the herbs *Borreria verticillata* (Rubiaceae) > *Cyperus luzulae* > *Lindernia crustacea* (Scrophulariaceae) > *Borreria latifolia* > the tree

Cecropia palmata (Cecropiaceae) > and the shrub *Clidemia hirta* (Melastomataceae). In the primary forest, *Cecropia palmata* accounted for 25% of the seed bank, followed by *Clidemia hirta*, the grass *Paspalum conjugatum*, and by other pioneer woody species (Table 2). There were 11 tree species that were only found in the soil seed bank of the primary

Table 2 Mean numbers of seeds m^{-2} (M) of some common species (with at least 45 seeds in all plots combined) in the seed bank (0–10 cm) of 5-, 10-, and 20-year-old secondary forest

stands and in a primary forest in Bragantina, Pará, Brazil. The ranges are for the values in the three plots in each forest-age class

Species	Life form	5-year-old secondary forest		10-year-old secondary forest		20-year-old secondary forest		Primary forest	
		M	range	M	range	M	range	M	range
<i>Axonopus compressus</i> (Sw.) Beauv.	H	2	0–6	27	0–56	106	3–231	42	12–69
<i>Borreria latifolia</i> (Aubl.) Schum.	H	627	244–981	140	38–225	102	69–125	17	0–31
<i>Borreria verticillata</i> (L.) Mey	H	1325	425–2987	317	162–594	35	12–56	12	0–38
<i>Cecropia palmata</i> Willd.	T	211	69–425	220	31–381	268	169–412	204	162–225
<i>Clidemia hirta</i> (L.) D. Don.	T	354	312–375	415	394–450	172	137–206	77	38–125
<i>Cyperus luzulae</i> Rottb.	H	717	556–837	324	269–431	302	87–494	4	0–6
<i>Diodia ocimifolia</i> (Wiild. ex R.) Bren.	H	2	0–6	8	0–25	110	6–269	4	0–6
<i>Gouania pyriformis</i> Reiss	H	–		4	0–6	179	19–481	–	
<i>Irlbachia alata</i> (Aubl.) Maas.	H	492	12–1150	129	0–219	39	0–87	–	
<i>Jacquemontia hirtiflora</i> (Mart. ex Gal.) O'Donnell	H	–		44	0–75	60	50–69	2	0–6
<i>Lasiacis ligulata</i> Hitch. & Chase	H	152	44–344	21	6–38	23	6–44	10	6–19
<i>Lindernia crustacea</i> F. Muell.	H	611	94–1306	367	44–531	110	69–169	16	6–31
<i>Mariscus flavus</i> Vohl.	H	140	81–194	335	100–494	147	112–194	40	19–56
<i>Miconia ceramicarpa</i> (DC.) Cogn.	H	204	12–319	64	6–156	14	6–25	12	0–38
<i>Paspalum conjugatum</i> Berg.	H	62	56–75	54	31–69	171	112–281	79	31–125
<i>Peperomia pellucida</i> (L.) H.B.K.	H	2	0–6	69	12–150	47	12–75	48	0–144
<i>Pterolepis trichotoma</i> (Rottb.) Cogn.	H	298	75–537	37	0–112	17	0–31	–	
<i>Scleria secans</i> (L.) Urb.	H	60	19–112	64	0–244	31	12–56	–	
<i>Stachytarpheta cayannensis</i> (Rich.) Vahl.	H	406	137–819	90	0–231	2	0–6	–	
<i>Vismia guianensis</i> (Aubl.) Choisy	T	46	25–75	44	6–88	25	6–62	19	12–25
<i>Zanthoxylum rhoifolium</i> Lam.	T	108	0–325	37	0–81	50	0–81	2	0–6
Other species (97 species)		759		562		603		279	

–, means not recorded or less than 45 seeds in all plots combined; T, tree, H, herbs (forbs and graminoids)

forest (Table 2; they all had low densities (<10 seeds m^{-2}).

Seed rain

A total of 10,591 seeds of at least 70 species, were caught in 1 year in the seed traps in the 5-year-old secondary forest, 6,320 seeds of at least 93 species in the 10-year-old, 6,170 seeds of at least 104 species in the 20-year-old and 2,641 seeds of at least 134 species in the primary forest (Fig. 3). Between 2% and 6.6% of the seeds in the secondary forest stands and 21.4% in the primary forest remained unidentified. The highest mean number of seeds was found in the 5-year-old forest (883 ± 230 seeds m^{-2} year $^{-1}$, and this value was significantly different ($p < 0.05$)

from that in the primary forest (220 ± 80 seeds m^{-2} year $^{-1}$, Table 1). The pair-wise species similarity between the seed rain in the secondary forest stands varied from 0.46 (between 5- and 20-year-old forests) to 0.51 (between 5- and 10-year-old forests and between 10- and 20-year-old forests) and the species similarity between the seed rain of secondary forests and the primary forest ranged from 0.38 to 0.45, with increasing similarity with age.

Trees contributed 61% to the total seed rain in the primary forest and 66% to 84% in the secondary forest stands. In terms of species, 30–43% were trees in the secondary forest and 44% in the primary forest (Fig. 3). Most wind- and self-dispersed seeds were vines and herbs, but included some large pioneer and mature-forest tree species. There was a high

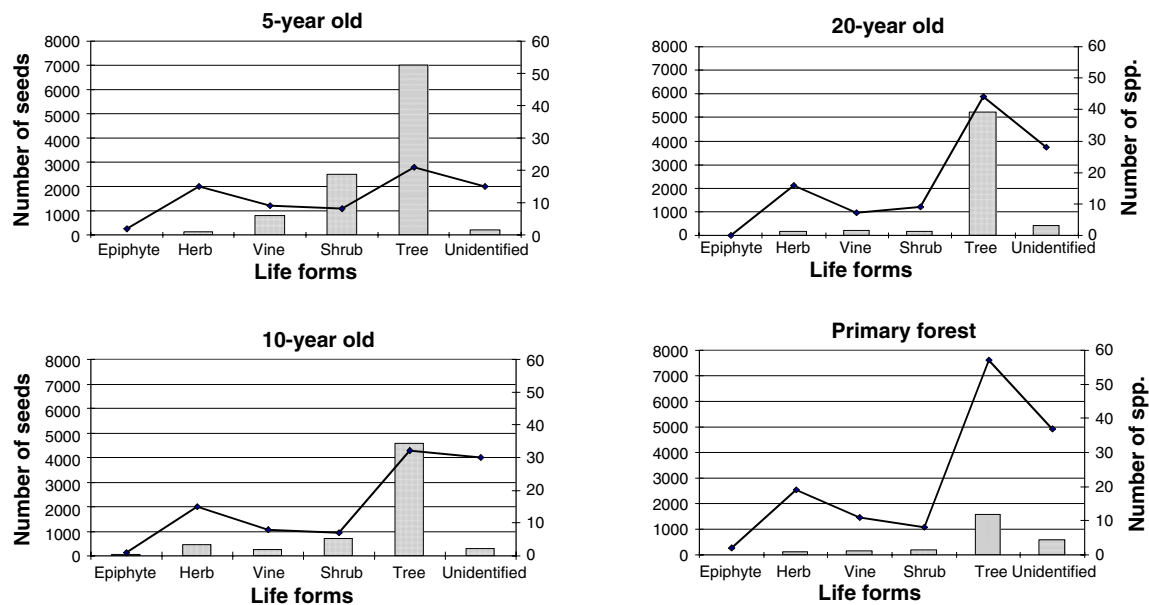


Fig. 3 The total number of trapped seeds and species in different life forms in 5-, 10- and 20-year-old secondary forest and primary forest in Braganantina, Pará, Brazil. Values are for

the total trap area of 12 m² in each forest-age class. Columns, number of seeds; lines, number of species

contribution of hidden (see above) seeds in the assorted fine debris (Fig. 3), mainly of herbs, that were recorded in the germination box. Many of these hidden seeds remained unidentified, and as a result, the species number was underestimated.

Four to five species accounted for up to 70% of the seed rain in each forest age-class (Table 3). In the 5-year-old forest, *Cecropia palmata*, *Miconia* sp. (Melastomataceae), *Myriaspora* sp. (Melastomataceae) and *Vismia guianensis* accounted for 71% of all seeds. In the 10-year-old forest, *Cecropia palmata*, *Clidemia hirta*, *Inga* sp. (Fabaceae), *Vismia guianensis* and *Zanthoxylum rhoifolium* accounted for 66% of all seeds and in the 20-year-old forest, *Cecropia palmata*, *Didymopanax morototoni*, *Vismia guianensis* and *Zanthoxylum rhoifolium* made up 70% of all seeds trapped. The seeds most commonly trapped in the secondary forests originated from trees already present, however, a few, and in low densities, arrived from the primary forest, such as the wind-dispersed *Chaenochiton klaperi* (Olacaceae) and *Erisma uncinatum* (Vochysiaceae) and the bird- and bat-dispersed species recovered from faeces *Cecropia obtusa*, *Inga alba*, *Laetia procera* (Flacourtiaceae), *Nectandra globosa* (Lauraceae), *Pouroma palmata* (Cecropiaceae), *Sacoglottis guianensis* (Humiriaceae), *Trichilia*

sp. (Meliaceae), and *Virola sebifera* (Myristicaceae). In the primary forest, most of the tree seed species trapped were pioneers such as *Cecropia palmata*, *Clidemia hirta* and *Didymopanax morototoni*; these three together accounted for 35% of all seeds trapped.

There was a peak in seed rain in June in the 5-year-old secondary forest (267 seeds m⁻², 23 species), in the 20-year-old forest (162 seeds m⁻², 19 species) and in the primary forest (55 seeds m⁻², 30 species). A second peak occurred in the 5-year-old forest in November (211 seeds m⁻², 20 species); the single peak for the 10-year-old forest was in October (124 seeds m⁻², 30 species). The small and mainly bird- and bat-dispersed seeds of the Asteraceae, Melastomataceae and Piperaceae were common throughout the year and were mostly in the debris and faeces fraction in the traps. Out the 108 identified species in the seed rain of the secondary forests, 63 (58%) were fleshy or arillate and 45 (42%) were dry. In the primary forest, 52 species (53% of identified species) had dry fruits.

Seedlings vs. sprouts

For small plants (≥ 1 m tall, < 5 cm dbh) species numbers were 62 in the 5-year-old forest, 68 in the

Table 3 Mean number of seeds m^{-2} (M) of some common species (with at least 50 seeds in all plots combined) in the seed rain of the 5-, 10- and 20-year-old secondary forests and a primary forest in Bragantina, Pará, Brazil. The ranges are for the values in the three plots in each forest-age class

Species	Life form	5-year-old		10-year-old		20-year-old		Primary forest	
		M	range	M	range	M	range	M	range
<i>Ambelania acida</i> Aubl.	T	–		–		–		4.7	0–14
Bignoniaceae sp.	L	–		0.3	0–0.5	–		4.3	0–13
<i>Cecropia palmata</i> Willd.	T	93	14–249	68	32–95	88	28–120	8.3	7–10
<i>Clidemia hirta</i> (L.) D. Don.	S	12.5	5–17	51.6	1.5–132	10	1.5–25	4.5	1.5–6
<i>Commelina</i> sp.	H	0.1	0–0.3	1.1	0–2.5	2.7	0–8	2.4	0–7.3
Convolvulaceae spp.	L	28	0–84	1	0–2.5	–		–	
<i>Cordia</i> sp.	T	–		2.9	0–8.8	1.9	0–6	0.1	0–0.3
<i>Croton matourensis</i> Aubl.	T	–		–		12	0–35	–	
<i>Didymopanax morototoni</i> (Aubl) Decne et Planch	T	0.1	0–0.3	0.3	0–0.5	58	1.3–170	78	1–230
<i>Ficus</i> sp.	T	–		22	0–66	–		8.5	0–25
<i>Gouania pyrifolia</i> Reis.	L	28.1	0–84	9.8	0–29	15	0.5–42	0.3	0–0.8
<i>Inga</i> sp.	T	0.4	0–1.3	31	0.3–51	0.2	0–0.3	0.1	0–0.3
<i>Lacistema pubescens</i> M.	T	27.2	6.8–52	14.6	0.8–35	0.8	0–1.5	3.7	1–8.8
<i>Lacmellea aculeata</i> (Ducke) Mon	T	–		–		8.3	0–25	0.1	0–0.3
Fabaceae spp.	T	–		2.4	0–6.3	0.4	0–1	4.6	0–14
<i>Mabea angustifolia</i> Spruce ex Benth.	T	1.7	0–5	0.4	0–1.3	2.4	0.3–4.3	–	
<i>Maprounea guianensis</i> Aubl.	T	–		–		6.1	0–18	–	
<i>Miconia ceramicarpa</i> (DC.) Cogn.	S	1.3	0–3	25.8	0.8–75	2.2	0.5–4	3.4	1.3–6
<i>Miconia minutiflora</i> (Bonpl.) DC.	S	93	0–265	12.8	0.5–36	21	3–54	3.7	2.3–6
<i>Miconia</i> sp.	S	86	0–188	–		2.2	0–6.5	–	
<i>Mikania banisteriae</i> Baker	S	4.4	0–13	–		–		–	
Morph 08*		3.1	0–9.3	1.6	0–2.5	0.3	0–1	0.5	0–1.5
Morph 34		–		–		11.4	0–34.2	–	
Morph 65		–		0.2	0–0.5	0.5	0–1.5	13.5	0.5–21
<i>Myriaspora</i> sp.	T	89.7	0–269	–		0.5	0–1.5	–	
<i>Paullinia pinnata</i> L.	L	–		4	0–9.3	0.1	0–0.3	–	
<i>Piper aduncum</i> L.	H	16.8	0.3–50	11	0.8–8.8	1.2	0–2	0.8	0–2
<i>Psychotria</i> sp.	H	–		3.2	0–5.8	2.8	0–7.3	0.5	0–1.5
<i>Rollinia exsucca</i> (DC ex Dunal) DC.	T	0.1	0–0.3	0.3	0–0.8	8.7	0–25.8	0.3	0–1
<i>Sabicea</i> sp.	S	4.7	0–13.5	–		–		–	
<i>Serjania</i> sp.	L	–		5.2	0.3–15	1.3	0–2.3	1.3	1–1.5
<i>Siparuna guianensis</i> Aubl.	T	0.1	0–0.3	9.4	0–28.3	0.3	0–0.8	0.2	0–0.5
Solanaceae spp.	S	–		–		–		8.8	0–26.3
<i>Tapirira guianensis</i> Aubl.	T	–		14.6	0–43.3	3.5	1–7	0.8	0–2.5
<i>Virola sebifera</i> Aubl.	T	1.2	0–3	0.2	0–0.5	0.6	0–1.8	2.3	0–6.8
<i>Vismia guianensis</i> (Aubl) Choisy	T	360.3	151–647	115	36–269	58.9	2.5–158	2.8	1.5–3
<i>Zanthoxylum rhoifolium</i> Lam.	T	–		80	0–240	156	0.3–465	–	
Other species (195 species)		35.5		37.2		37.16		61.6	

–, means not recorded or less than 50 seeds in all plots combined; * Morph is used for each separate but unidentified taxon; T, tree; H, herb (forbs and graminoids); S, shrub

10-year and 66 in the 20-year-old forest. The proportion of all stems (≥ 1 m tall, < 5 cm dbh) formed by sprouts declined from 54% in the 5-year-old forest to 19.3% in the 10-year-old forest and reached 27.6% in the 20-year-old forest. The relative importance of seeds and sprouts differed with forest age for smaller individuals. In the 5-year-old forest seeds and sprouts had the same importance while in the 10- and 20-year-old forests seeds were more important. In contrast, larger plants (≥ 5 cm dbh) had more individuals and species regenerated from sprouts than from seeds in all forest age-classes (Table 4).

The mean number of seedling species found in the 10- (58 species) and 20-year-old forests (48) were significantly higher ($p < 0.05$) than the 36 in the 5-year-old forest (Table 4). The most abundant seedling species (Table 5) in the 5-year-old forest were the trees *Rourea amazonica* (Connaraceae; 1.4 seedlings m^{-2}) and *Lacistema pubescens* (Lacistemataceae; 0.5 seedlings m^{-2}) and the herb *Psychotria colorata* (Rubiaceae; 0.4 seedlings m^{-2}). The most abundant seedlings in the 10-year-old forest were the shrub *Myrcia bracteata* (Myrtaceae; 7.1 m^{-2}) and the graminoids *Pariana* sp. and *Scleria secans* (0.6 m^{-2}); in the 20-year-old forest the most abundant seedlings were *Inga* sp. (3.2 m^{-2}) and *Myrcia bracteata* (1.6 m^{-2}).

The mean numbers of sprouts m^{-2} (≥ 1 m tall, < 5 cm dbh) were not significantly different among the forest age-classes. The highest number of sprout-

ing species (Table 4) was found in the 20-year-old forest (36 species). In the 5-year-old forest the most abundant sprouting species (Table 5) were the liana *Davilla kuntii* (Davalliaceae; 1.0 m^{-2}) and the shrub *Myrcia bracteata* (0.7 m^{-2}). Nine species (*Arrabidaea* sp., *Chrysophyllum sparsiflorum* (Sapotaceae), *Inga edulis*, *Lacistema pubescens*, *Memora flavida* (Bignoniaceae), *Myrcia floribunda*, *Myrciaria tenella* (Myrtaceae), *Rourea amazonica* and *Tabebuia serratifolia* (Bignoniaceae) were found both as seedlings and sprouts. The most abundant sprouts in the 10-year-old forest were *Rourea amazonica* (1.4 m^{-2}) and in the 20-year-old forest, *Tabernaemontana angulata* (Apocynaceae; 0.46 m^{-2}).

Discussion

Seed bank

Some studies (Guevara and Gómez-Pompa 1972; Uhl et al. 1981; Putz 1983; Swaine and Hall 1983) have shown that seed banks are important in the early stages of tropical successions. However, the relative importance and size of seed bank changes with age and with fallow origin (primary forest vs. secondary) show some variability. The present study showed a peak (1,190 seeds m^{-2}) at 5 years, followed by a decline with stand age. Guevara and Gómez-Pompa (1972) found 1,982–4,051 seeds m^{-2} in Veracruz, Mexico in a 5-year-old forest, while a primary forest

Table 4 The number of species and mean density of seeds and sprouts of two size classes (≥ 1 m tall, < 5 cm dbh; and ≥ 5 cm dbh) in the 5-, 10- and 20-year-old secondary forests in Bragantina, Pará, Brazil

Origin	Number of species (N) / Density (D)	Forest age-class (years)		
		5	10	20
≥ 1 m tall, < 5 cm dbh				
From seeds	N*	36	58	48
	D m^{-2}	4.6 (1.4–7.5)	14.7 (7.7–25.5)	11.5 (6.6–16.4)
From sprouts	N	37	19	28
	D m^{-2}	5.4 (4.3–6.1)	3.5 (0–7.5)	4.4 (2.9–5.6)
≥ 5 cm dbh				
From seeds	N	4	13	13
	D 250 m^{-2}	3.3 (1–7)	7.3 (3–10)	9 (5–13)
From sprouts	N	18	25	31
	D 250 m^{-2}	21.3 (10–34)	32.3 (21–44)	38 (32–44)

* Some species were found with both modes of regeneration

Table 5 Mean number of seedlings and sprouts m^{-2} of some common species ≥ 1 m tall, < 5 cm dbh (with at least eight individuals in all plots combined) in the 5-, 10- and 20-years-old forests in the Bragantina region, Pará. The ranges are for the values in the three plots in each forest age-class

Species	Life form	5-years-old				10-years-old				20-years-old			
		seedlings		sprouts		seedlings		sprouts		seedlings		sprouts	
		N	range	N	range	N	range	N	range	N	range	N	range
<i>Arrabidaea</i> sp.	L	0.03	0–0.1	0.03	0–0.1	0.1	0–0.3	–	–	0.43	0–1.3	–	–
<i>Bernardinia fluminensis</i> (Gard.) Planch	L	0.03	0–0.1	–	–	0.1	0–0.3	–	–	0.23	0–0.7	–	–
<i>Calyptanthes bipennis</i> Berg.	T	0.03	0–0.1	0.3	0–0.9	–	–	–	–	–	–	–	–
<i>Cassipourea guianensis</i> Aub.	T	–	–	0.03	0–0.1	–	–	–	–	0.03	0–0.1	–	–
<i>Davilla kuntii</i> St. Hill	L	–	–	1.03	0.4–2.2	0.53	0–1	0.43	0–0.9	0.13	0–0.4	0.36	0.3–0.4
<i>Diodia</i> sp.	H	0.03	0–0.1	–	–	–	–	–	–	0.26	0–0.8	–	–
<i>Gustavia augusta</i> L.	T	–	–	0.27	0–0.8	0.1	0–0.3	0.23	0–0.7	–	–	–	–
<i>Heisteria acuminata</i> (H. & B.) Engler	T	–	–	0.17	0–0.5	–	–	–	–	0.13	0–0.3	–	–
<i>Inga edulis</i> Mart.	T	0.06	0–0.2	0.13	0–0.3	–	–	–	–	0.4	0–1.1	–	–
<i>Inga</i> sp.	T	–	–	–	–	–	–	–	–	3.2	0–9.6	–	–
<i>Inga thibaudiana</i> DC.	T	–	–	–	–	0.4	0–0.9	0.36	0–1.1	0.23	0–0.3	–	–
<i>Lacistema aggregatum</i> (Berg.) Rusby	T	0.13	0–0.4	–	–	–	–	–	–	–	–	0.23	0–0.5
<i>Lacistema pubescens</i> Mart.	T	0.5	0–1.5	0.1	0–0.3	0.27	0.1–0.5	–	–	0.2	0–0.4	0.1	0–0.3
<i>Machaerium madeirense</i> Pittier	L	–	–	0.17	0–0.5	–	–	0.06	0–0.2	–	–	0.1	0–0.3
<i>Memora flavida</i> (DC.) Bur et Schum.	L	0.06	0–0.2	0.13	0–0.3	–	–	–	–	0.27	0–0.8	0.03	0–0.1
<i>Memora magnifica</i> (Mart. ex DC.) Burret	L	–	–	0.37	0–1.1	–	–	–	–	–	–	0.13	0–0.2
<i>Myrcia bracteata</i> (Rich.) DC.	T	–	–	0.7	0–2.1	7.1	0.8–17.4	–	–	1.6	0.6–3.6	–	–
<i>Myrcia floribunda</i> (West ex Willd) Berg	T	0.13	0–0.4	0.13	0–0.4	–	–	0.03	0–0.1	0.1	0–0.3	0.1	0–0.3
<i>Myrcia tenella</i> (DC.) Berg.	T	0.06	0–0.2	0.13	0–0.4	–	–	–	–	0.6	0–2	–	–
<i>Panicum pilosum</i> Swartz.	H	0.13	0–0.4	–	–	0.5	0–1.1	–	–	–	–	–	–
<i>Pariana</i> sp.	H	–	–	–	–	0.6	0–1.9	–	–	0.27	0–0.8	–	–
<i>Protium trifoliolatum</i> Engl.	T	–	–	–	–	–	–	–	–	0.3	0–0.9	–	–
<i>Psychotria colorata</i> (Willd. ex R&S) M.Arg.	H	0.4	0–0.7	–	–	0.53	0–1.5	–	–	0.27	0.2–0.8	–	–
<i>Rourea amazonica</i> (Baker) Radlk.	T	1.37	0–3.9	0.03	0–0.1	0.2	0–0.5	1.37	0–4.1	0.23	0–0.7	–	–
<i>Rourea ligulata</i> Backer	T	–	–	–	–	0.5	0–1.5	–	–	–	–	–	–
<i>Scleria secans</i> (L.) Urb.	H	0.13	0–0.4	–	–	0.6	0–1.8	–	–	0.16	0–0.5	–	–
<i>Smilax schomburgkiana</i> Kunth.	L	–	–	0.23	0–0.7	0.1	0–0.3	0.36	0–1.1	–	–	–	–
<i>Tabebuia serratifolia</i> (Vals.) Nichols.	T	0.17	0–0.4	0.3	0–0.9	–	–	–	–	–	–	–	–
<i>Tabernaemontana angulata</i> Mart ex M.Arg.	S	0.03	0–0.1	–	–	–	–	–	–	0.43	0–1.1	0.46	0–1.4
<i>Trichilia micrantha</i> Benth.	T	–	–	–	–	0.1	0–0.3	–	–	0.37	0–0.6	–	–
<i>Trichilia</i> sp.	T	–	–	–	–	0.83	0–2.5	–	–	0.06	0–0.2	–	–
Other species (99 species)		2.11		0.35		2.14		0.66		1.60		1.09	

–, means not recorded or less than eight individuals recorded in all plots combined; T, tree; H, herb (forbs and graminoids); S, shrub

had 344–862 m⁻². Young et al. (1987) found that the seed bank began to increase 84 d after forest clearance in Costa Rica, had a peak at 4–7 years, and then declined. Uhl (1987) found a marked seed bank decline during succession in San Carlos de Rio Negro, Venezuela. In contrast, Rico-Gray and Garcia-Franco (1992) found no changes with secondary forest age in seed banks in Yucatán, Mexico, while Abdulhadi and Lamb (1988) found higher seed bank density and species richness in old (>20 years) secondary forests than in mature forest and 2-year-old secondary forests in Australia. Nagy and Proctor (1999) have reported higher mean numbers of seeds after dry land rice cultivation from fallows in Kalimantan, Indonesia where the fields were of secondary forest origin (460–1,415 m⁻²; 0–2 years of age) than where they were of primary forest origin (100–340 m⁻²; 0–1 year of age). Another study in the same area estimated the size of the seed bank at 175 m⁻² in primary forest and 4,300 in a 3-year-old fallow (Prajadinata 1996).

The seed banks of the Bragantina primary forest were within the range (55–860 seeds m⁻²) reported from other tropical rain forests (Guevara and Gómez-Pompa 1972; Hall and Swaine 1980; Uhl et al. 1981; 1982a; Putz 1983; Uhl and Clark 1983; Putz and Appanah 1987; Chandrashekhara and Ramakrishnan 1993) and were mainly of woody pioneers. The number of seed bank species in the Bragantina primary forest (54) and secondary forests (60–70) were within the range and of 4–79 for primary forest and 8–67 for secondary forest found in other studies (e.g. Young et al. 1987; Garwood 1989; Skoglund 1992).

In general, there is a decrease in seed bank with depth (Putz 1983; Garwood 1989). This was the case in Bragantina (Table 1) with some species more abundant near the surface, others in deeper layers, while some showed an almost uniform distribution. Differences in the depth profile of the seed bank have been attributed to differences in soil texture, cultivation history, and changes in seed rain (Garwood 1989).

In Bragantina most of the seed bank species had small seeds (range 1–400 mg; $n = 19$). According to Whitmore (1983), species with persistent seed banks produce large numbers of small, well-dispersed seeds. Of the 96 species found in the secondary forest seed banks, 14 were trees; 12 of them pioneer and two shade-tolerant (*Neea* sp. Nyctaginaceae and *Trichilia* sp.). Four of the pioneer species occurred

both in primary and secondary forest (*Annona densicoma* Annonaceae, *Casearia decandra* Flacourtiaceae, *Cecropia palmata*, *Croton matourensis*). In contrast, only two pioneer tree species were found in the seed bank of degraded pastures near Paragominas, Pará (Nepstad et al. 1996) and the same number in a 5-year-old secondary forest in Bragantina (Denich 1991). In common with other workers (e.g. Rico-Gray and Garcia-Franco 1992), there was little similarity between species composition of established woody vegetation and the seed bank. From the total of 140 tree species (≥ 5 cm dbh) recorded from all the secondary forest plots (Vieira 1996) only 14 occurred in the seed bank (*Banara guianensis* Flacourtiaceae, *Casearia decandra*, *C. grandiflora*, *Cassia fastuosa* (Fabaceae), *Cecropia palmata*, *Croton matourensis*, *Lacistema pubescens*, *Mabea angustifolia* (Euphorbiaceae), *Miconia minutiflora*, *Myriaspore egensis*, *Neea* sp., *Trema micrantha*, *Vismia guianensis*, *Zanthoxylum rhoifolium*). This shows that the seed bank makes a limited direct contribution to tree regeneration during succession. This observed pattern is partly due to the fact that some tree species that contribute to the vegetation cover in the very early stages of succession (0–3 years) soon die out.

Seed rain

Seeds from seed rain can contribute directly to regeneration, or may become incorporated into the seed bank. The quantification of seed rain for tropical successional vegetation is rare (Young et al. 1987). In this study, more seeds were collected from secondary than primary forest and Young et al. (1987) found the same pattern in Costa Rica, but reported values four to six-fold higher for 3- and 11-year-old secondary forests (3,366 and 3,700 seeds m⁻² year⁻¹, respectively) and for primary forest (1,233 seeds m⁻² year⁻¹). In Bragantina, the total number of species captured in the traps from the seed rain increased from 69 in the 5-year-old forest to 133 in the primary forest. Young et al. (1987) reported more species in the seed rain in the young vegetation than in the primary forest (75 vs. 48), however, this might have been explained in part by their using only half as much trap surface area in the primary forest. Denslow and Gomez Diaz (1990) reported 588 seeds m⁻² year⁻¹ in tree-fall gaps in Costa Rica and pointed out that many seeds may have

originated from the surrounding farmlands. Some studies showed that animals facilitate the deposition of some seeds. For example, Nepstad et al. (1996) have found that 400 times more seeds fell into traps beneath trees in an abandoned pasture in eastern Amazonia than in traps in the open because of birds and bats attracted by the fleshy fruits. Vieira et al. (1994) described a similar phenomenon beneath the fleshy-fruited shrub *Cordia multispicata* (Boraginaceae). However, the same pattern has been observed for other non-fleshy fruit bearing trees by Adams (1997), who found a high seed fall beneath and outside the canopy of *Cecropia palmata*, *Tapirira guianensis* (Anacardiaceae) and *Vismia guianensis*.

In Bragantina, seed rain plays an important role in the regeneration of forests and is probably also responsible for the large seed bank found in the studied secondary forests. Similarly, seed rain was found important in young regrowth in a study in Costa Rica where the number of seeds in the annual seed rain was equal to or greater than that in the soil (Young et al. 1987). By contrast, in cases such as that reported for the forests of San Carlos, Venezuela (Uhl and Clark 1983) where there were fewer pioneer seeds in the annual seed rain than in the upper 4–5 cm of the soil, the seed bank is likely to be equally important for regeneration after disturbance.

Seedlings and sprouts

Sprouting from stems and roots has been reported to be common after disturbance (Uhl et al. 1988; Putz and Brokaw 1989; Kauffman 1991) but the regrowing vegetation depends on various regeneration sources (Noble and Slatyer 1980). In Bragantina, the majority of cleared fields are cultivated immediately after burning, without the removal of the stumps. As a result, the initial regeneration from the seed bank and from sprouts in the fallows is high (81–86% of individuals and from 68 to 81% of the species ≥ 5 cm dbh originated from sprouts, or from sprouts and seed). The apparent absence of seedlings of the medium-sized pioneer species (with high seed bank and seed rain) might have been due to the exclusion from the study of seedlings less than 1 m tall or high seedling mortality or both. The smaller individuals (≥ 1 m tall, < 5 cm dbh) in the 5-year-old forest were mainly observed arising from sprouts (partly because the sprout stems had not advanced to the larger size

category of > 5 cm dbh), but those in the older secondary forests established mainly from seeds, suggesting that the vigour of growth from sprouts confers an advantage in the early years of secondary forest growth. In later years, sprouting becomes relatively less important as new plants establish from seed, some of which arrive as immigrants. For example, Uhl et al. (1982a) working at San Carlos de Rio Negro, Venezuela, found in a 3-year-old forest that 54% of the individuals ≥ 5 cm tall were sprouts, while in a 5-year-old forest in the same area only 17% were sprouts (Uhl and Jordan 1984). Earlier work at San Carlos had shown that sprouting was the most common means of regeneration after forest cutting (Uhl et al. 1981). They found 6.37 sprouts m^{-2} vs. only 0.95 seedlings m^{-2} (all individuals ≥ 5 cm tall). Also, in his study in 5-year-old forests in Bragantina, Denich (1991) found that the majority of individuals were from sprouts.

In this study, whereas pioneer species predominated among secondary forest seedlings, the sprouts included some primary forest species such as *Andira retusa* (Fabaceae), *Couratari guianensis* (Lecythidaceae), *Eschweilera pedicelata*, *Guatteria poeppigiana* (Annonaceae), *Sacoglottis guianensis*, *Swartzia racemosa* (Fabaceae), and *Talisia subalbans* (Sapindaceae). Many of these species had no or poor seed rain and seed bank and sprouting may represent their only way of regeneration in the secondary forests.

Seed bank, seed rain and the regeneration of species

The role of the seed bank and that of the seed rain in succession seems varied (Skoglund 1992). Experimental studies in recently cleared forests (Uhl et al. 1981; 1982b; Young et al. 1987; Lawton and Putz 1988) have demonstrated that most of the woody colonising species growing from seeds originate from the seed bank. In this study, it is likely that some of the seed bank resulted from seed rain during the period of cultivation of annual crops before the area was abandoned. This included the 15–17 species observed both in the seed rain and seed bank. In the absence of longer-term seed rain data and information on seed longevity it was not possible to quantify the contribution of the seed rain to the seed bank.

Since pioneer tree species generally have smaller seeds than primary forest trees (Foster and Janson

1985) it is not surprising that they dominate the seed bank and seed rain in secondary forests. Pioneer and late secondary forest species dominate less disturbed sites such as forest gaps after tree fall or logging, while herb species dominate repeatedly burned and disturbed sites (Hall and Swaine 1980; Nagy and Proctor 1999). In Papua New Guinea two-thirds of the tree seeds in the seed rain and seed bank of a small patch of old regrowth forest (about 55 years) were from species abundant in the surrounding young vegetation (<2 years) but absent from the patch itself (Saulei and Swaine 1988). In primary forests, the seed bank is less important compared with the current seed rain, or the seedling bank in regeneration (Putz and Appanah 1987). The large seed bank of young secondary forests results from the high rate of input from the taller successional secondary forest plants (Young et al. 1987). In this study, the accumulated seed bank was higher than the annual seed rain (Table 1) in all forest age-classes. Others, such as Uhl and Clark (1983) found that there was a low seed rain compared with seed bank size (180 seeds m⁻² in the seed bank vs. 50 seeds m⁻² year⁻¹ in the seed rain) and they concluded that seed longevity might be considerably greater than 1 year for pioneer species. Cheke et al. (1979) also found that the seed bank numbers in the soil were much greater than those in the annual seed rain in their sites in Thailand.

Finally, it has been repeatedly observed that primary forest species other than those that sprout are slow to establish in secondary forest (e.g. Prajadinata 1996; L. Nagy et al. pers. comm.). It is also true for Bragantina, where only 35% of the 268 tree species of a primary forest were found in nearby secondary forests Vieira (1996). As 84% of tree species in the primary forest depend on animals for their seed dispersal, the absence of animals from heavily disturbed forest and structurally unsuitable sites could be a barrier to the arrival and establishment of zoochorous species in secondary forests (Vieira 1996) and delay succession.

Conclusion

In the secondary forests studied, species had different combinations of regenerative traits. The most abundant medium-sized pioneer species (*sensu* Swaine and Whitmore 1988) had large seed banks, high seed

rain and many adults (e.g. *Cecropia palmata*, *Vismia guianensis*, *Zanthoxylum rhoifolium*) but no or few seedlings; large pioneers (e.g. *Croton matourensis*, *Inga* sp., *Tapirira guianensis*) had a low seed rain, a modest seed bank, some seedlings and the ability to sprout. Large mature-forest species such as *Gustavia augusta* (Lecythidaceae) and *Virola sebifera* were poorly represented in the seed bank, seed rain and as seedlings, and were more commonly found as sprouts in the secondary forest stands. Other abundant pioneer species and a few primary forest species were recorded as seeds in the seed bank or seed rain and were also present as seedlings. Finally, the most abundant pioneer tree species in all successional stages sampled had a large seed bank and seed rain and as a result they can rapidly re-colonise new open areas by seeds, while other pioneer and some primary forest species are only present in the secondary forest because of their capacity to regenerate from sprouts after felling and burning. Sprouting, as our study has shown, is important both in the early development of secondary forest cover and in maintaining late successional tree species early on during succession.

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