

# Alternative successional pathways in the Amazon Basin

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## Summary

**1** Successional pathways were evaluated in two Amazonian secondary forest communities with different land-use histories. Sites which had been clearcut without subsequent use were dominated after 6–10 years by the pioneer genus *Cecropia* (Moraceae), whereas those used for pasture before abandonment were dominated by the pioneer genus *Vismia* (Clusiaceae).

**2** There were 58 plant families and 300 species identified in *Cecropia* stands but only 43 families and 147 species were identified in *Vismia* stands. There were 77 species in common (Sorensen similarity = 0.34).

**3** Differences in species number and composition of recruiting individuals between stand types were significant and were a function of the dominant pioneer genus, stem density, distance from primary forest, and land-use history. Regeneration under *Vismia* canopy was dominated by small *Vismia* individuals (25% of plants < 2 cm basal diameter), whereas regeneration under *Cecropia* canopy was more diverse and did not include a single young *Cecropia*.

**4** The number of regenerating plants in both secondary stand types dropped off sharply with distance (5, 25, 50, and 100 m) from primary forest, suggesting that seed dispersal was limiting plant recruitment. Species richness also declined with distance and could be explained by the decline in plant density. Species richness in *Cecropia* stands increased linearly with plant density, but in *Vismia* stands the richness increase with density was a decelerating function.

**5** For the central Amazon, secondary succession involves a more rapid return of primary forest species if deforestation is not followed by use as pasture before abandonment.

*Key-words:* *Cecropia*, pioneer, regeneration, secondary forest, *Vismia*

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## Introduction

In general, tropical forest regeneration in large treefall gaps follows fairly predictable pathways (Brokaw 1985; Denslow 1987). Successional pathways on anthropogenically altered lands, however, often appear stochastic, perhaps because prior land-use histories are extremely diverse and not well documented. After deforestation in the central Amazon, common land-uses include shifting cultivation, establishment of tree plantations, short-rotation agriculture and cattle ranching. These activities frequently leave residual effects on any subsequent forest regeneration because they deplete soil organic matter and nutrients and alter soil physical properties (Aide &

Cavelier 1994), impede organic matter decomposition and biomass accumulation (Kellman 1970), and reduce seed dispersal and recruitment of primary forest species (Nepstad *et al.* 1990; Duncan & Chapman 1999).

Secondary succession on such ‘degraded’ lands, i.e. those where the alterations in environmental conditions were anthropogenic, may proceed differently from that in natural forest openings. Studies investigating forest succession on heavily used land have shown that the suite of species that colonize and subsequently dominate floristic composition may be quite different from the classic, pioneer species in gaps in adjacent forest (Greig-Smith 1952a, 1952b; Hall & Okali 1979; Uhl *et al.* 1988; Parrota *et al.* 1997). Rather than facilitating succession or having little negative influence on it (Connell & Slayter 1977), colonizers of degraded lands may inhibit succession for a certain period of time (Kochummen & Ng 1977; Cohen *et al.* 1995) or even divert succession

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to a different forest type from the plant community at the site prior to disturbance (Sim *et al.* 1992). In eastern Amazonia Uhl *et al.* (1988) calculated that recovery to primary forest could occur on lightly used sites within 100–200 years, but 500 years or more might be required at sites with heavy land-use histories. Initial differences in the dominant colonizing species may lead in turn to differences in recruitment under their canopies, so that different land uses could result in different suites of colonizing species and different rates of forest recovery.

Such differences in successional pathways are best described by detailed quantification of floristic composition and forest structure. We already know that site effects, climate and distance from seed sources, as well as other biotic interactions, can all play a role in forest succession in the Amazon. Detecting differences in successional pathways will therefore require that vegetation comparisons be made under relatively controlled conditions, such as similar microclimate, comparable age, known land-use history and similar probabilities of seed dispersal or predation acting as main influences on colonization success. However, differences in colonization among pioneer plants and its possible effects on recruitment in the understorey have not been quantified in Amazonia (but see Parrota *et al.* 1997 for plantation forests). Although the existence of different successional pathways has not yet been verified with quantitative vegetation data, a number of researchers have recently alluded to their occurrence in central Amazonia (Stouffer & Bierregaard 1995; Foody *et al.* 1996; Lucas *et al.* 1998; Borges & Stouffer 1999).

The present study is the first controlled comparison of successional pathways for sites in central Amazonia. We compare the structure and diversity of communities that established following two different land-use histories and their understorey recruitment. We also document how distance from the nearest primary forest affects the number and composition of recruits in each successional community.

## Methods

The study area is located about 80 km north of Manaus in the state of Amazonas, Brazil, and is part of the Biological Dynamics of Forest Fragments project (BDFFP), a cooperative venture of the Smithsonian Institution and Brazil's Instituto Nacional de Pesquisas da Amazônia (INPA). The climate of the region is tropical humid with excessive rain in some months and 1 or 2 months with precipitation dropping to 100 mm (*Am* in the system of Köppen 1936). Mean temperature in Manaus is 26.7 °C; mean rainfall is 2.2 m year<sup>-1</sup>. March and April are the wettest months, with over 300 mm of precipitation, while August, September and October are the driest (normally 100–150 mm but as little as 50 mm in some El Niño years, Lovejoy & Bierregaard 1990). The predominant soils are red-yellow podzols and yellow latosols (Ranzani 1980). The dominant vegetation is dense evergreen *terra firme* forest (Veloso

*et al.* 1991), with the canopy reaching 30–37 m and emergents extending to 45–50 m. There are on average 280 tree species  $\geq 10$  cm diameter at breast height per hectare (Oliveira 1997; Oliveira & Mori 1999).

Study sites are located on three farms within the BDFFP: Esteio, Dimona and Porto Alegre. All the farms had been clearcut of primary forest at the beginning of the 1980s. We selected three areas that had been cleared in 1983, maintained as pasture for 4 years and then abandoned, and were thus 6 years old by July 1993. They were dominated by *Vismia* (mainly *V. guianensis* (Aubl.) Choisy, *V. japurensis* Reich., and *V. cayennensis* (Jacq.) Pers.). Another three areas had been abandoned after clearcut in 1983 and were therefore 10 years old, and were dominated by *Cecropia* (mainly *C. sciadophylla* Mart. and *C. purpurascens* C.C. Berg). The different types of secondary forest will hereafter be referred to simply as *Vismia* or *Cecropia* stands. These areas were the closest aged stands of each land-use type in the study area and exhibited no other apparent differences such as soil type, elevation or slope aspect. Adjacent primary forest stands are similarly remarkably uniform in above-ground biomass and soil characteristics (Laurance *et al.* 1999). The farms do contain some lower slopes and bottoms with sandier soils due to podzolization, but all transects in this study were located on upland clay soils. Weather conditions among and within the farms are relatively uniform, as the farms are scattered over 1000 km<sup>2</sup> and surrounded by continuous primary forest without major topographic variation.

Four 100-m transects were established in each of the second-growth stands. Transects ran parallel to the edge of adjacent primary forest, at perpendicular distances of 5, 25, 50 and 100 m. Primary forest edges within stand type were chosen to face different cardinal orientations. Thus, *Cecropia* transects faced east (Dimona), west (Esteio) and south (Porto Alegre), while *Vismia* transects faced north (Dimona), east and south (two widely separated sites at Esteio). There were no comparably aged *Vismia* stands adjacent to primary forest at Porto Alegre.

Along each transect five randomly located, 3 × 3 m quadrats were surveyed. All woody plants (trees, vines, palms and shrubs) rooted in each sample plot were measured for basal diameter at ground level, or higher if the stem base was swollen. Buttresses and basal swellings presented few measurement problems as most stems were small (Clark & Clark 1995). Height was measured for each plant less than 2.0 m tall, while taller individuals had their heights estimated visually to the nearest metre. Attempts were made to determine which stems were clonal, and for multiple-stemmed trees all stems were measured. Specimens of all unknown individuals were collected for identification.

It was necessary to gauge the potential vegetational changes caused by the 4-year age difference, i.e. how the 6-year-old *Vismia* stands differed from 10-year-old *Vismia* stands. We therefore compared species and size compositions of large trees ( $\geq 5$  cm diameter) in our 6-year-old *Vismia* stands with two 10-year-old *Vismia*

stands in another area at Esteio which were censused 4 years later. The latter stands are presented strictly for comparison and do not include data on plants less than 5 cm diameter. All reported comparisons of *Vismia* and *Cecropia* stands relate to 1993 censuses of the 6-year-old *Vismia* and 10-year-old *Cecropia* stands.

Data analyses were performed with randomized incomplete block ANOVAs, frequency distributions and non-metric multidimensional scaling (NMDS) using Systat version 5.0 (Wilkinson 1990) and SAS version 6.12 (SAS Institute 1997). Plants less than 20 cm tall were excluded from taxonomic and species richness analyses because they were often too difficult to identify and because they included some recent germinations that might never become established seedlings. Three taxa consistently difficult to separate to species level were treated as single taxonomic units for analysis (the *Bellucia* spp. (Melastomataceae), genus *Piper* spp. (Piperaceae) and the family Dilleniaceae). For statistical analyses of species composition, only plants identified to species or identified to genus and morphotyped to species were included. To understand whether changes in species richness were merely a function of changes in plant density, comparisons between sites and distances were performed using plant density as a covariate.

Species-area curves were constructed for each combination of stand type and distance from the primary forest. Each curve was based on five different plots on a single transect in each of three different farms. To avoid potential farm effects in the species-area curves, the species-area accumulations were stratified over farms (plot 1 from farm 1, then farm 2, then farm 3; then plot 2 ...).

## Results

A total of 2859 plants were measured, of which 121 (4%) were excluded due to unknown taxonomic identity; of the remainder, 2197 (77%) were at least 20 cm tall and 541 (19%) were less than 20 cm tall.

### STAND STRUCTURAL COMPARISONS

For both *Vismia* and *Cecropia* stands, smaller individuals were generally more common than larger individuals in terms of both height (Fig. 1) and diameter (Fig. 2). Plants less than 20 cm tall were much more common in *Vismia* stands ( $n = 464$ ) than in *Cecropia* stands ( $n = 77$ ) (Proportion test,  $Z = 16.6$ ,  $P = 0.0001$ ), whereas plants at least 20 cm tall were evenly distributed (1137 vs. 1060,  $Z = 1.67$ ,  $P = 0.10$ ). With individuals less than 20 cm tall removed from the analyses, tests for differences in size distributions between *Cecropia* and *Vismia* stands were highly significant for diameter (Kolmogorov-Smirnov test,  $D = 0.12$ ,  $P = 0.0001$ ) and moderately significant for height ( $D = 0.06$ ,  $P = 0.02$ ). *Vismia* stands appeared to have a more bi-modal height distribution than *Cecropia* stands (Fig. 1) and an excess of small basal diameters (Fig. 2). Testing only diameters greater than or equal to

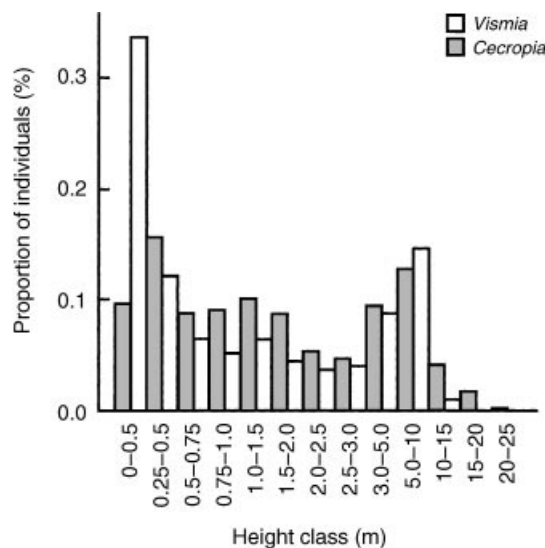


Fig. 1 Plant height distribution in *Cecropia*- and *Vismia*-dominated secondary forests.

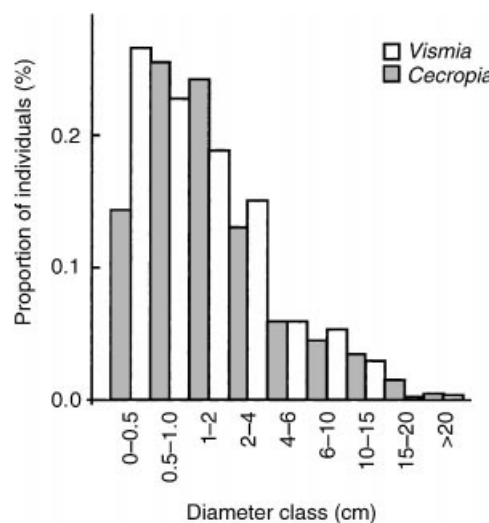


Fig. 2 Plant diameter distribution in *Cecropia*- and *Vismia*-dominated secondary forests.

0.50 cm resulted in no significant difference ( $D = 0.05$ ,  $P = 0.20$ ). Median height was similar in *Cecropia* and *Vismia* stands (1.50 vs. 1.60 m for individuals  $\geq 0.2$  m, Median test,  $n = 2197$ ,  $P = 0.39$ ) but median diameter was higher in *Cecropia* stands (1.21 vs. 1.00 m,  $n = 2106$ ,  $P = 0.006$ ). Stand type had no significant effect in parametric ANOVAs of diameter or height (Table 1).

Large diameter trees ( $\geq 5$  cm) were more numerous and consequently basal area was 20% greater in *Cecropia* stands (Table 2). Nonetheless, the diameters of the 10 largest individuals were similar (*Cecropia* mean  $\pm$  SD,  $21.4 \pm 2.7$  cm, range 19–27.3 cm vs. *Vismia*  $19.6 \pm 5.9$ , 14.2–33.5;  $T$ -test,  $t = 0.89$ ,  $P = 0.39$ ). Tall trees ( $\geq 5$  m) were taller in *Cecropia* stands ( $9.2 \pm 4.3$  m,  $n = 268$  vs.  $7.3 \pm 1.9$ ,  $n = 282$ ; Kruskal–Wallis ANOVA,  $F = 15.3$ ,  $P = 0.0001$ ).

Within 10-year-old *Cecropia* stands, *Cecropia* species comprised 34% of the basal area, whereas *Vismia*

**Table 1** The effect of stand type, farm and distance from the primary forest on number of individuals, plant diameter, height and number of individuals. Stand types are *Vismia* or *Cecropia*. Farms are Dimona, Colosso, or Porto Alegre, and distances are 5, 25, 50 and 100 m

Independent variable	d.f.	Diameter			Height			Individuals		
		MS	F	P	MS	F	P	MS	F	P
Stand	1	0.56	0.24	0.62	2.92	1.41	0.24	898	8.0	0.005
Farm (Stand)	4	1.22	0.53	0.71	0.62	0.30	0.88	131	1.2	0.33
Distance	1	15.16	6.58	0.01	13.02	6.29	0.01	6548	58.5	0.001
Stand × Distance	1	0.08	0.04	0.85	0.08	0.04	0.85	701	6.3	0.014
Distance × Farm (Stand)	4	1.48	0.64	0.63	1.24	0.60	0.66	61	0.5	0.70
Error	108	2.30			2.07			112		

**Table 2** Density and basal area, based on all stems  $\geq 5$  cm d.b.h., for the 10-year-old *Cecropia* stands and the 6-year-old *Vismia* stands reported here from 1993, together with data for two 10-year-old *Vismia* stands censused in 1997

	10-year-old <i>Cecropia</i>	6-year-old <i>Vismia</i>	10-year-old <i>Vismia</i>
Number of stands	3	3	2
No. trees $\geq 5$ cm (d.b.h.) ha <sup>-1</sup>	3280 $\pm$ 310	2440 $\pm$ 150	2100 $\pm$ 960
Basal area (m <sup>2</sup> ) ha <sup>-1</sup>	23.7 $\pm$ 6.9	19.6 $\pm$ 1.9	19.6 $\pm$ 1.3
Generic dominance (%)			
<i>Vismia</i> (Clusiaceae)	10.7 $\pm$ 9.1	46.6 $\pm$ 24.6	56.0 $\pm$ 14.4
<i>Cecropia</i> (Moraceae)	33.4 $\pm$ 22.6	8.1 $\pm$ 7.8	3.7 $\pm$ 4.4
<i>Bellucia</i> (Melastomataceae)	6.3 $\pm$ 6.0	9.4 $\pm$ 7.4	28.9 $\pm$ 20.5
<i>Laetia</i> (Flacourtiaceae)	4.0 $\pm$ 5.1	8.6 $\pm$ 4.9	0.4 $\pm$ 0.5

comprised 11% (Table 2). Within 6-year-old *Vismia* stands, *Vismia* species comprised 47% of the basal area, while *Cecropia* comprised 8%. The percentage difference (*Vismia*–*Cecropia*) was significantly different between stands (*t*-test, d.f. = 4,  $P \leq 0.05$ ).

#### DIFFERENCES BETWEEN 6- AND 10-YEAR-OLD *VISMIA* STANDS

The 6-year-old *Vismia* stands were structurally similar to the 10-year-old *Vismia*: although basal areas were identical, the number of trees  $\geq 5$  cm d.b.h. was slightly larger in the 6-year-old *Vismia* (Table 2), suggesting that self-thinning had resulted in fewer, larger trees. Both showed *Vismia* dominance, with only a minor contribution from *Cecropia* (Table 2), but one genus, *Bellucia*, showed a large increase in relative basal area from the 6-year-old to the 10-year-old stands (Table 2). Throughout the abandoned pastures, there is limited recruitment of large trees other than the dominant *Vismia* except for *Bellucia* (Table 2), which is probably dispersed into the stands by the bats that also consume *Vismia* fruits.

#### STAND DIFFERENCES IN FLORISTIC COMPOSITION

A total of 61 families, 149 genera and 370 species and morphospecies were tallied in the two stand types for the 2197 individuals at least 20 cm tall. *Cecropia* stands contained 58 families and 300 species, whereas *Vismia* stands contained 43 families and 147 species. About 15% of these plants  $\geq 20$  cm tall could not be placed

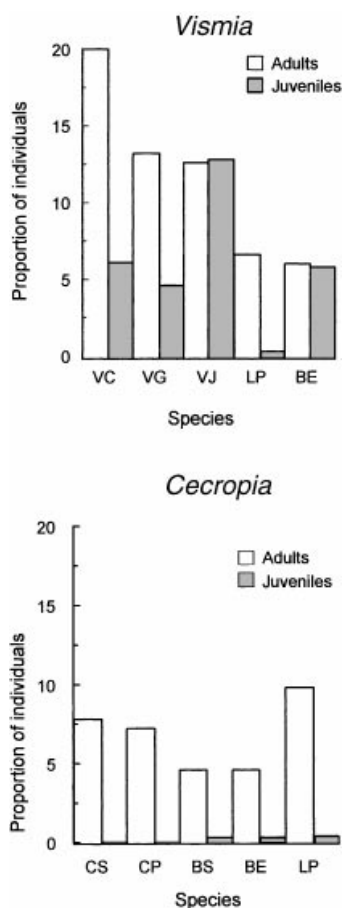
even to family (7.8% in *Cecropia* stands and 7.9% in *Vismia* stands), usually because they were too small. *Vismia* and *Cecropia* stands shared 77 species in common, yielding a Sorensen Index of Similarity of 0.34, based on presence–absence. When relative abundances were included, the Modified Sorensen Index was nearly the same, 0.32, based on species with at least five individuals (Southwood 1978).

At the familial level there were differences between stand types. Of the 10 most abundant families in each type, only four (Leguminosae, Annonaceae, Moraceae and Melastomataceae) were shared by *Vismia* and *Cecropia* stands (Table 3). The 10 most common families comprised 55.8% of the individuals in *Cecropia* stands and 75.5% of the individuals in *Vismia* stands. The families in *Cecropia* stands were more representative of the dominant arboreal families from nearby primary forest (Table 3).

A comparison of the abundance of the five most common species in the canopy ( $\geq 5.0$  cm basal diameter) with their presence as recruits ( $< 2.0$  cm basal diameter) revealed that the dominant canopy species in *Vismia* were also prevalent in the understorey (representing 72% of recruitment, Fig. 3). *Vismia* spp. contributed the three most abundant canopy species and almost 50% of the understorey recruits. In contrast, while *Cecropia sciadophylla*, *C. purpurascens*, together with *Bellucia* spp., *Laetia procera* (Poepp.) Eichl., and *Byrsonima stipulacea* were the most common canopy trees in *Cecropia* stands, there were no juveniles of *Cecropia* and a few *Bellucia* and *Laetia* in the understorey (only 2.2% of total recruits, Fig. 3). Two taxa

**Table 3** Ten most common families from *Vismia* stands and from *Cecropia* stands with their total abundance and relative abundance from 60 9-m<sup>2</sup> plots, and each family's abundance rank among trees (> 10 cm d.b.h.) in adjacent primary forest from Rankin-de-Merona *et al.* (1990)

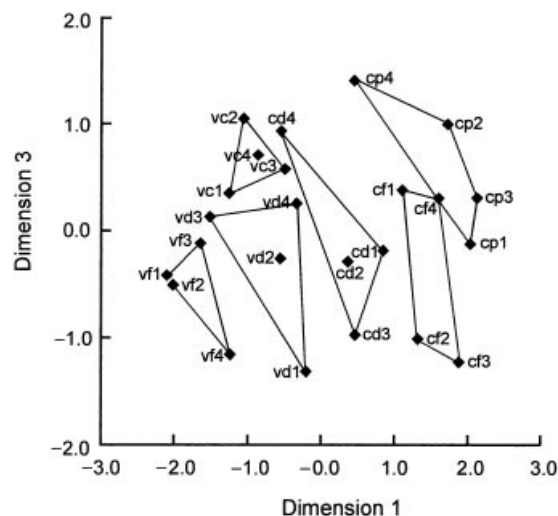
<i>Vismia</i> stands	<i>n</i>	%	Rank	<i>Cecropia</i> stands	<i>n</i>	%	Rank
Clusiaceae	364	23.1	29	Leguminosae	129	9.9	4
Piperaceae	241	15.3	–	Burseraceae	124	9.5	3
Melastomataceae	152	9.6	20	Arecaceae	89	6.8	12
Myrtaceae	146	9.3	14	Annonaceae	80	6.1	9
Leguminosae	70	4.4	4	Moraceae	69	5.3	5
Flacourtiaceae	54	3.5	27	Bignoniaceae	51	3.9	33
Annonaceae	49	3.3	9	Melastomataceae	51	3.9	20
Violaceae	40	2.5	10	Lecythidaceae	49	3.8	1
Moraceae	37	2.3	5	Rubiaceae	45	3.5	26
Monimiaceae	35	2.2	35	Euphorbiaceae	40	3.1	8



**Fig. 3** Comparison of five most common adult species ( $\geq 5$  cm basal diameter) with their presence as juveniles ( $< 2.0$  cm basal diameter) in *Cecropia*- and *Vismia*-dominated secondary forests. VC = *Vismia cayennensis*, VG = *Vismia guianensis*, VJ = *Vismia japurensis*, LP = *Laetia procera*, BE = *Bellucia* sp., CS = *Cecropia sciadophylla*, CP = *Cecropia purpurascens*, BS = *Byrsonima stipulacea*. Values are relative percentages within group.

– *Laetia procera* and *Bellucia* species – were among the five most common canopy dominants in both stand types, but only *Bellucia* in the *Vismia* stands was well represented among recruits (Fig. 3).

To determine if regeneration was different under *Vismia* and *Cecropia* canopies, floristic composition



**Fig. 4** Non-metric multidimensional scaling of the floristic composition in *Cecropia*- and *Vismia*-dominated secondary forests, showing dimensions 1 and 3. Each point represents one transect (12 in *Cecropia* and 12 in *Vismia*); labels refer to vegetation dominance (c = *Cecropia*; v = *Vismia*), site (c = Colosso, d = Dimona, f = Florestal, p = Porto Alegre), and distance from forest edge (1 = 5 m, 2 = 25 m, 3 = 50 m and 4 = 100 m) in that order. Lines connect transects in the same farm and vegetation type.

was compared for non-canopy plants ( $\leq 3$  m tall) for the 24 transects. The abundance-weighted Modified Sorensen Index of Similarity was calculated for each pair of transects, and the resulting matrix subjected to non-metric multidimensional scaling (NMDS). Optimal separation required three dimensions (SAS ‘SStress’ criterion = 13.4). The first dimension gave a clear floristic separation of plants regenerating under *Vismia* and *Cecropia* canopies (Fig. 4): neither of the other two dimensions was directly interpretable, although transects did tend to cluster by farm.

#### STAND DIFFERENCES IN SPECIES RICHNESS

An overall ANOVA (not shown) of the number of species per plot, with stand, farm, distance, number of individuals and their interaction terms as independent

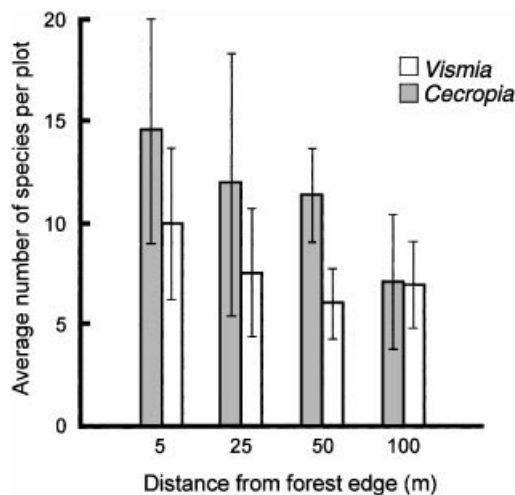


Fig. 5 Effect of distance from forest edge on number of species found in *Cecropia*- and *Vismia*-dominated secondary forests. Values are mean number of species per  $m^2 \pm$  SD.

variables, revealed only two significant effects: the number of individuals ( $P = 0.001$ ) and the interaction of stand type with the number of individuals ( $P = 0.001$ ). These results imply that the number of species per plot was a function of the number of individuals per plot, but that the relationships were different for *Cecropia* and *Vismia* stands. Separate linear regressions of ( $\log_{10}$ ) species/plot on ( $\log_{10}$ ) individuals/plot confirmed significant positive relationships for both *Cecropia* stands ( $y = 0.972x - 0.461$ ,  $r^2 = 0.70$ , one-tailed  $P = 0.001$ ) and for *Vismia* stands ( $y = 0.448x + 0.714$ ,  $r^2 = 0.32$ , one-tailed  $P = 0.001$ ), with a much steeper slope for *Cecropia*. The regression slopes indicate that the increase in species with number of individuals using non-transformed data was nearly linear for *Cecropia* plots but was decelerating for *Vismia* plots.

*Cecropia* stands had significantly more species per plot than *Vismia* stands at 5, 25 and 50 m from the forest edge ( $t$ -tests,  $n = 30$ ,  $P = 0.0001$ , 0.03 and 0.04, respectively) but not at 100 m ( $P = 0.77$ ; Fig. 5). Species-area curves (Fig. 6) show that rate of species accumulation was greater for *Cecropia* stands at any given distance. However, there were three farms with *Cecropia* stands and only two farms with *Vismia* stands leading to possible site effects. The percentage difference in the cumulative species number was therefore compared for *Cecropia* and *Vismia* sites, using all three stands of each type, or only the two in the farms where both occurred. The differences in species richness were maintained when one *Vismia* stand at Colosso and one *Cecropia* stand at Porto Alegre were excluded (data not shown). None of the species-area curves appeared to level off. There were 58% more species in *Cecropia* than in *Vismia* stands at 5 m distance when only the two sites in common were compared. The percentage difference became a little larger (99%) when all three sites were included, but the species-accumulation curve was very similar. For 100-m transects, there were 59% more species in

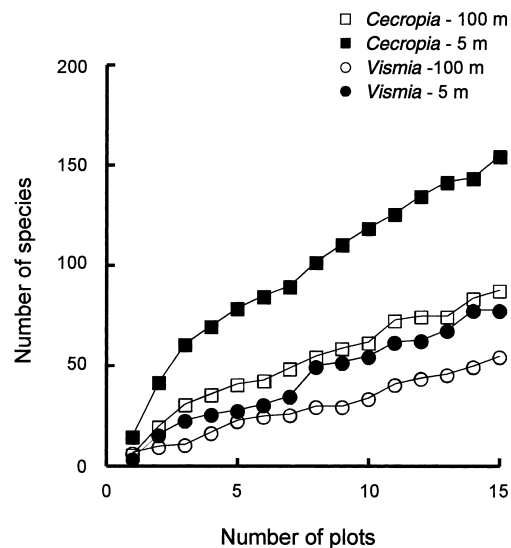


Fig. 6 Cumulative species-area curve for transects located at 5 and 100 m from forest edges in *Cecropia*- and *Vismia*-dominated secondary forests. Each sample point represents one  $3 \times 3$  m plot.

*Cecropia* than in *Vismia* stands independent of the number of sites (two or three) used for comparisons. Moreover, the recruitment communities for *Cecropia* from two farms (Florestal and Porto Alegre) were not more different from each other than the two *Vismia* samples from different areas of the same farm (Florestal and Colosso, Fig. 4, centroids not shown), indicating that comparisons using three sites did not significantly inflate differences in richness.

#### DISTANCE EFFECTS

Distance had a dramatic effect on the number of individuals per plot (Table 1,  $P = 0.001$ ). Overall, there were more than twice as many individuals at 5 m as at 100 m from the forest edge ( $2.94 \pm 1.13$  vs.  $1.46 \pm 0.72$   $m^{-2}$ ). Stand ( $P = 0.005$ ) and the stand–distance interaction ( $P = 0.014$ ) had significant, albeit minor, effects on the number of individuals, suggesting that the decline in individuals with distance was different for *Cecropia* and *Vismia* stands (Table 1, Fig. 7). Separate linear regressions of the number of individuals per plot on ( $\log_{10}$ ) distance revealed significant declines in individuals/plot with distance for both stand types, and the regression parameters were similar (*Vismia*,  $y = -1.24x + 3.84$ ,  $r^2 = 0.28$ ,  $P = 0.0001$ ,  $n = 30$ , and *Cecropia*,  $y = -1.16x + 3.71$ ,  $r^2 = 0.21$ ,  $P = 0.0002$ ,  $n = 30$ ).

In an overall ANOVA (not shown), distance had no effect on species richness when number of individuals was included as a covariate.

Distance from the forest had a statistically significant effect on basal diameter ( $P = 0.01$ ) and on plant height ( $P = 0.01$ ) (Table 1). However, these ( $\log_{10}$ ) distance effects were biologically meaningless due to the low  $r^2$ -values of the linear regressions (diameter,

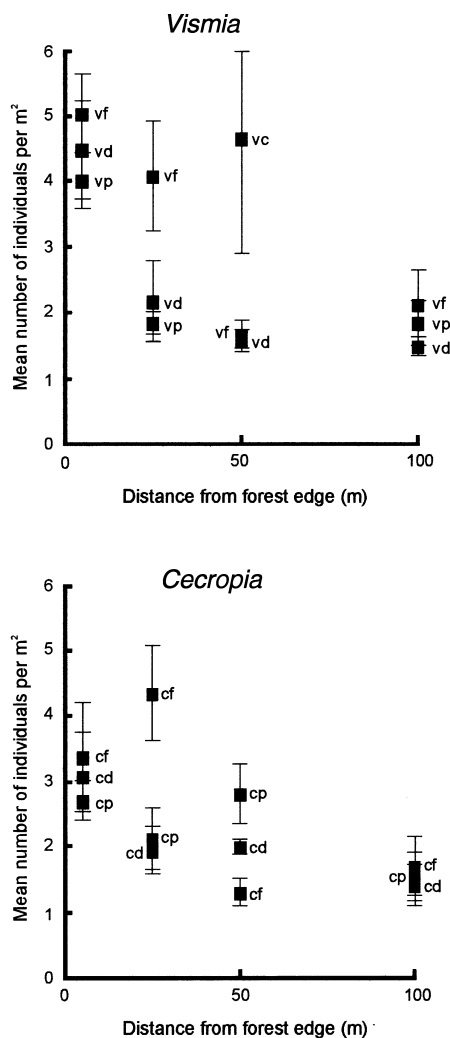


Fig. 7 Effect of distance from forest edge on number of individuals found in *Cecropia*- and *Vismia*-dominated secondary forests. Values are mean number of individuals per  $m^2 \pm SD$ .

$y = 0.66x + 1.54, r^2 = 0.009, P = 0.0001, n = 2102$ ; and height,  $y = 0.60x + 2.29, r^2 = 0.007, P = 0.0001, n = 2197$ .

## Discussion

### STRUCTURAL DIFFERENCES BETWEEN STANDS

The stands for this study were chosen on the basis of known differences in land-use history, not because of the apparent dominance by certain tree genera. Although various authors have alluded to the association between land-use history, dominant genera and successional pathways (Stouffer & Bierregaard 1995; Foody *et al.* 1996; Lucas *et al.* 1998; Borges & Stouffer 1999), these relationships have not been documented previously. Such associations were supported here with *Cecropia* three times as dominant as *Vismia* in the clearcut and abandoned stands, whereas *Vismia* was more than four times as dominant as *Cecropia* in the abandoned pasture stands (Table 3, Fig. 4).

Ten-year-old *Cecropia* stands had a larger basal area, more trees  $\geq 5$  cm basal diameter, and taller trees for trees  $\geq 5$  m in height than the 6-year-old *Vismia* stands. Their size differences may reflect the age differences but must partly be due to different species' growth rates because 10-year-old *Vismia* stands had the same basal area and fewer large trees than 6-year-old *Vismia* stands.

In addition to age, stand structural differences may be explained by individual structural characteristics of the two dominant genera, *Cecropia* and *Vismia*. These two have been reported to have significant differences in biomass allocation and allometric relationships in Brazil's Atlantic Coastal rain forest (Williamson *et al.* 1998). There, *Vismia* species had slower growth in height, a lower height : diameter ratio, thicker crowns, higher light interception and higher wood specific gravity than *Cecropia* species. While *Vismia* formed a closed-canopy monolayer, *Cecropia* species grew quickly and created a stratified canopy which allowed survival and growth of other tree species beneath its canopy. Besides influencing second-growth forest structure, these differences can have an effect on the likelihood of seedling establishment underneath their crowns, thus influencing subsequent regeneration.

### REGENERATION UNDER *VISMIA*- AND *CECROPIA*-DOMINATED CANOPIES

There were significant differences in species composition and recruitment under *Cecropia* and *Vismia* canopies that indicate different successional pathways. A large proportion of stems recruiting under *Vismia* were *Vismia* seedlings or clonal sprouts, but no *Cecropia* seedlings or sprouts were found under *Cecropia* canopies. In the context of Connell & Slayter's (1977) hypotheses, *Vismia* may have inhibited regeneration of primary forest species, whereas *Cecropia* may have facilitated regeneration or had no effect on succession.

Some or most of the smaller *Vismia* individuals may be ramets from adult trees, as *Vismia* sprouts profusely from exposed lateral roots when the main stem is damaged (Williamson *et al.* 1998; Williamson & Mesquita, in press). This would also explain the high incidence of very small stems and how such small stems of 'pioneer' species tolerate the shade of the canopy. In adjacent primary forest, the three *Vismia* species studied here (*V. japurensis*, *V. cayennensis*, *V. guianensis*) only regenerate in forest light gaps (Mesquita, unpublished data).

In contrast to *Vismia* stands, *Cecropia* stands exhibited diverse understorey regeneration that did not include a single recruit from the dominant canopy genus. Number of species per plot was greater under *Cecropia* canopies and species-area curves showed twice as many species accumulating under *Cecropia* than under *Vismia* (Fig. 6). These differences were more exaggerated closer to the primary forest, implying that dispersal from adjacent areas was important. A land-use history of repeated fires

would also have eliminated the seed bank and stump sprouts of primary forest species from the pastures, leaving only *Vismia* resprouts (Williamson & Mesquita, in press). Both increased dispersal and absence of fire could thus have operated to increase the relative species richness regenerating under *Cecropia* canopies, but the similarity of familial composition in *Cecropia* stands and adjacent forest favours dispersal and/or resprouting of primary forest species.

Further evidence of stand differences in recruitment is provided by the differences in regressions of number of species on number of individuals. Plant density explained 70% of the variation in species richness in *Cecropia* stands but only 32% in *Vismia* stands in log transformed linear regressions, and species richness increased twice as fast in *Cecropia* stands. In fact, for *Vismia*, the species–individuals regression was better fit by a decelerating curve, implying few species per individual in plots with more individuals. A further suggestion that succession under *Vismia* was different from that under *Cecropia* is provided by the ordination (NMDS) of the regeneration, which clearly separated their floristic communities.

One possibility is that the dominant species themselves have had an effect on regeneration under their canopies. Schnitzer *et al.* (2000) have found an alternate successional pathway in canopy gaps dominated by lianas, whereby regeneration was stalled in a low-canopy state for many years. They suggest that the ability of lianas to colonize and proliferate allows them to arrest regeneration by other species in gaps and to cause an altered successional trajectory. Similarly, *Vismia* species are known to be extremely persistent and to retard regeneration under their crowns (Saldarriaga 1985; Saldarriaga & Uhl 1991; Williamson *et al.* 1998). Furthermore, in French Guiana *Cecropia* litter has been shown to be more effective than *Vismia* litter in restoring soil conditions that facilitate the return of mature forest species (Maury-Lechon 1991). However, because areas dominated by *Vismia* and *Cecropia* in our study have different land-use histories, factors other than the plants themselves may have confounding effects on the regeneration pathway.

#### REGENERATION AS A FUNCTION OF DISTANCE FROM PRIMARY FOREST EDGE

The effect of distance on the number of regenerating individuals in our study concurs with results from studies documenting seed rain from the primary forest declining relatively rapidly with distance from the edge (Thomas *et al.* 1988; Willson & Crome 1989; Gorchoff *et al.* 1993; Aide & Cavellier 1994). The number of regenerating plants dropped off sharply between 25 and 50 m (Fig. 7), as did propagules arriving in seed traps at distances of 2.5–12.5 m in the Peruvian Amazon (Gorchoff *et al.* 1993). Declines are most often measured from the forest edge into clearcut and pastures, but a similar distance effect is seen here in 6- or 10-year-old

secondary forests. Therefore, there appears to be a residual effect of distance on recruitment even after secondary forests have become established, with little effect of stand type (similar regressions of number of individuals on distance). However, *Cecropia* plots had more species for a given number of individuals than *Vismia* plots, and there were therefore more species in *Cecropia* plots than in *Vismia* plots for a given distance. The two canopies may attract different dispersal agents, as the *Vismia* species are more strictly bat-dispersed and *Cecropia* fruits are consumed by birds, bats and climbing mammals. Thus, secondary forests dominated by trees with contrasting modes of dispersal may have different likelihoods of colonization by different suites of primary forest species.

Extensive deforested areas may be too far away from primary forest, and consequently from seed sources, for recolonization. Our observed decline in the number of individuals and the richness of species suggests that seed dispersal limits plant invasion, even in areas as close as 25–50 m to the forest, and may persist in structured second-growth forest.

#### WHAT DRIVES SUCCESSIONAL PATHWAYS IN THE AMAZON?

In the Amazon, natural disturbances of mature forest, such as flooding of upland low terrains, wind blowdowns and large canopy gaps, can result in succession dominated by either *Vismia* or *Cecropia*. Succession on degraded lands, however, can differ from that in natural light gaps, because seed dispersal, seed banks and sprouting (three critical forest recovery mechanisms, Uhl *et al.* 1989) are lost or severely altered.

Succession on degraded upland areas also differs from riverine succession, because regeneration on newly exposed fluvial beaches must start with the earliest stages of primary succession and under an erosional disturbance regime more severe than normally found in the upland (Salo *et al.* 1986). These riverine areas, however, can have some similarities with anthropogenically modified upland areas. Some stages of riverine succession in the Amazon, dominated by *Cecropia* (Salo *et al.* 1986), can result in mosaics of forests with higher age heterogeneity and a more continuous spatial distribution over the landscape than would be found in scattered light gaps in a forest background.

The size and degree of disturbance of deforested areas can determine the routes along which abandoned areas will become structured forests (Bazzaz 1991). In the Central Amazon, *Vismia* dominates succession in periodically burned pastures because it has the ability to resprout. Deforested areas that are neither burned nor converted to pasture are colonized by *Cecropia* and a more diverse secondary community develops from the seed bank, stump sprouts and seed rain. Such large areas dominated by one genus or the other may reflect treatment differences imposed at a landscape scale by anthropogenic activities. It is probable that original site



factors as well as land-use treatment prior to abandonment affect the success of initial pioneers. All three factors—site, land-use and first colonizers—may interact to determine the path of secondary succession, and only through field experimentation will it be possible to separate their effects. However, for now it is at least evident that in the central Amazon secondary succession immediately following deforestation leads to a more rapid return of primary forest species than when deforestation is followed by conversion to pasture and periodic burns, before abandonment.

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