

Tree recruitment and mortality over eight years after logging in a terra firme rain forest in Brazilian Amazonia

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Abstract

Data on recruitment and mortality are reported for trees ≥ 5 cm dbh from 257 species at the Tapajós National Forest over an eight-year period after selective logging and in a nearby unlogged control area. Recruitment increased with time after logging while mortality was very high immediately after logging due to felled and damaged trees but slowed down by year 5 after logging. In the unlogged forest, recruitment and mortality were nearly equal during the period. Both recruitment and mortality rates were higher for light-demanding species than for shade-tolerants in the logged area over the study period, but in the undisturbed forest this situation was reversed. The effect of logging on dynamics of commercial species was positive, insofar as their mortality represented less than 15% of their recruitment. In the undisturbed forest, mortality and recruitment of commercial species were in equilibrium.

Key-words: Amazonian forest, Tapajós National Forest, forest dynamics, tree species recruitment, tree species mortality

Recrutamento e mortalidade de árvores durante oito anos após da exploração numa floresta de terra firme na Amazônia brasileira

Resumo

Dados de recrutamento e mortalidade são apresentados para árvores com ≥ 5 cm de 257 espécies na Floresta Nacional do Tapajós, durante um período de oito anos após a exploração seletiva e em uma área vizinha não-explorada. O recrutamento aumentou com o tempo após a exploração, enquanto que a mortalidade foi muito alta imediatamente após a exploração devido às árvores derrubadas e danificadas, porém decresceu até o quinto ano após a exploração. Na floresta não-explorada, recrutamento e mortalidade foram quase iguais durante o período. As taxas de recrutamento e mortalidade foram mais altas para as espécies intolerantes à sombra do que para as tolerantes na área explorada durante o período estudado, porém na floresta não-explorada essa situação foi inversa. O efeito da exploração na dinâmica das espécies comerciais foi positivo, considerando que a mortalidade representou menos do que 15% do recrutamento. Na floresta não-explorada, o recrutamento e a mortalidade das espécies comerciais estavam em equilíbrio.

Palavras-chaves: Floresta amazônica, Floresta Nacional do Tapajós, dinâmica de florestas, recrutamento de árvores, mortalidade de árvores.

Introduction

Data on ingrowth, mortality, and diameter increment are needed for predicting future stand tables in tropical rain forest. Spatial and temporal patterns of natural mortality in time and space is strongly related to maximum longevity of trees, size class distribution, relative abundance of species, and size and number of canopy gaps (Swaine *et al.* 1987b). Wind is perhaps the commonest cause of death for trees that are uprooted or snapped, but there are other possible causes including fungal pathogens, herbivores, senescence, lightning, drought and suppression. Uhl (1982) stated that the most apparent cause of death for trees 1-10 cm dbh (diameter at breast height, 1.3 m) in a *terra-firme* forest in Venezuelan Amazonia was mechanical damage, mainly because of branches or trees falling on other individuals. Most of the trees in >10 cm dbh class died as a consequence of stem snapping.

This paper seeks to analyze the ingrowth and mortality rates of trees ≥ 5 cm dbh in Tapajós National Forest over an eight-year period. The focus is on forest dynamics after logging, compared to an

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undisturbed area, in order to provide information for making decisions about silvicultural approaches to be adopted in the Brazilian Amazonia. Ingrowth and mortality rates were compared in the post-logging period and in the control area, and the effects of logging on the dynamics of species of economic interest were explored.

Material and Methods

The study area

The study area is in Tapajós National Forest (2°40' - 4°10'S, 54°45' - 55°30'W) near kilometer 114 of the Santarém-Cuibá Road (BR 163) in the municipality of Belterra, State of Pará, Brazil. Tapajós National Forest area is about 600 000 ha at an altitude of *c.* 175 m above the sea level. The climate is classified by Köppen as Ami, mean annual air temperature is *c.* 25°C, mean relative humidity is 86% (76-93%), mean annual rainfall is 2110 mm with high rainfall from March to May, and low rainfall from August to November (Carvalho 1982). The topography is mostly level or slightly rolling. Soil is allic to moderate yellow latosol with heavy clay texture (60-94% clay), with inclusions of concretionary yellow latosol, derived from clay stone (Fundação de Pesquisas Florestais do Paraná 1986). Following the general pattern for the soils of *terra firme* Amazonian forests, it is low in nutrients. Dubois (1976) classified the forest type as zonal primary high *terra firme* forest without *babaçu* palm (*Orbygnia barbosiana* Burret).

This area was selected because it is representative of the majority of *terra firme* dense forest in the region. It is also sufficiently remote from settlements to have been disturbed by the cutting of trees for building materials or fuel. Apparently the only disturbances in the area were hunting of animals for food, collecting edible fruits, tapping of some *Hevea brasiliensis* trees, and barking trees of medicinal species such as *Aniba canellila* (H.B.K.) Mez, *Tabebuia serratifolia* (Vahl.) Nicholson and *Stryphnodendron barbatimao* Mart. Those activities probably did not cause any serious damage or substantially alter the structure and composition of the forest.

Methods

The research was initiated in 1981 by conducting 100% pre-felling forest inventory of trees ≥ 45 cm dbh in 144 ha. At the time of the initial inventory, all lianas were cut and 48 permanent sample plots were established and measured for the first time within the 144 ha. In 1982 the area was logged. The subsequent measurements took place one, five and seven years after logging (1983, 1987 and 1989, respectively). A 36 ha unlogged control area with 12 permanent plots was established in 1983. It was first measured then and later in 1987 and 1989.

The forest structure was similar in both the T1 and T2 areas before logging and in the control block (Carvalho 1992). An experienced Embrapa research team carried out logging. Chainsaws were used for cutting. An attempt was made at directional felling and a wheeled skidder was used, operating in trails previously planned and opened by a bulldozer. Particulars of each treatment are as follows:

- T1.-** This treatment consisted of cutting trees of 38 species ≥ 45 cm dbh. This dbh limit was applied because it is the minimum permitted by the Brazilian Forest Law for felling trees in natural forests. The 38 species were selected from a list of commercial species in the regional timber market based on their abundance, basal area and timber volume recorded in a previous forest inventory carried out in the study area (Silva *et al.* 1985). In this treatment, 14 trees ha⁻¹ were cut (69 m³ ha⁻¹).
- T2.-** Cutting of trees of the same 38 commercial species as in T1 but ≥ 55 cm dbh. This diameter limit was applied because generally the sawmills in the Tapajós region are set to use logs ≥ 45

cm diameter. The top diameter of a bole might only measure 45 cm if its dbh is at least 50 cm, although this varies from one species to another. The decision to take 55 cm as the cutting limit assumed that all trees felled would have a diameter greater than 45 cm at any part of their bole. This does not allow for any loss of timber, which occurs with trees of 45 cm dbh -the traditional cutting limit in Amazonia. In this treatment, 11 trees ha⁻¹ were cut (78 m³ ha⁻¹).

T0.- The control area remained in its natural untreated condition.

The statistical design of the treatments constituted four randomized blocks. Each treatment was replicated four times, with one 9 ha treatment plot per block. The control was a separate block also divided into four plots, each of 9 ha. Each plot was sub-divided into nine 1 ha quadrats. Three of which were selected at random. A 50 m x 50 m permanent sample-plot was set in the center of each. Following the procedure of Silva and Lopes (1984), each permanent sample-plot was divided into 25 subsample-plots of 10 m x 10 m and marked with permanent top-red-painted stakes. All individuals ≥ 5 cm dbh were number-tagged, identified and measured. In total, each treatment was applied over 36 ha, and included 3 ha of measured sample-plots.

The guidelines proposed by Synnott (1979) and Whitmore (1989b) for the measurement of the permanent sample-plots in tropical rain forests were followed. Further procedures in measurement were based up on Hutchinson (1982) and Silva and Lopes (1984), described in Silva (1989).

Individual trees were identified by their vernacular names in the forest. Botanical specimens were collected from less common trees for later identification in the Embrapa Herbarium. Whenever possible, identification was made to the species level (Carvalho 1992). Species were classified by their wood quality group and ecological class. The wood quality groups were: commercial.- species presently sold in the national or international market; potential.- species likely to be sold in the near future, mainly on account of their wood properties; non-commercial.- species not marketable or species whose wood is not yet sufficiently known. This classification was based on wood characteristics and timber markets in Brazil and abroad, according to Brasil-IBDF (1980, 1981, 1988), Brasil-SUDAM (1981), Silva (1989) and Teixeira *et al.* (1988).

The species were further classified as light-demanding or shade-tolerant species, based on seedling requirement for solar radiation observed casually in the field during the study period (Carvalho 1992), and according to distinguishing characters suggested by Swaine and Whitmore (1988) and Whitmore (1989a, 1990).

Ingrowth recruitment in this paper is considered as the number of trees that entered the smallest size class (5 cm dbh) at each measurement following the first. It is also presented as the percentage of the total number of trees in the previous measurement. The annual percentage average recruitment is calculated as the relation between new individuals in the measurement at the end of the study period and the number of trees in the first measurement, divided by 8 years. Mortality during the first year after logging included felled trees and those that died as a consequence of logging operations.

Results and Discussion

Ingrowth

Ingrowth after logging of trees ≥ 45 cm dbh over the eight-year period was 1051 trees ha⁻¹, corresponding to 131 trees ha⁻¹ year⁻¹, while after logging of trees ≥ 55 cm dbh ingrowth was 982 trees ha⁻¹, or 123 trees ha⁻¹ year⁻¹. In the unlogged forest ingrowth was 99 trees ha⁻¹ in six years, or 16 trees ha⁻¹ year⁻¹ (Table 1). Analysis of variance showed no significant difference between the logged treatments in the period from before logging to five years after logging, but a difference was found from five to seven years after logging, when the less intensively logged plots (11 trees harvested per

Table 1. Ingrowth (number of trees per hectare) in Tapajós National Forest in Brazilian Amazonia over an eight-year period

Treatment	Unit	Period					
		BL-1Y (2yr)	1Y-5Y (4yr)	BL-5Y (6yr)	5Y-7Y (2yr)	1Y-7Y (6yr)	BL-7Y (8yr)
Logged >45cm dbh	N/ha	440	930	943	711	1037	1051
	N/ha /yr	220	232	157	355	173	131
Logged >55cm dbh	N/ha	450	891	914	885	960	982
	N/ha/yr	225	223	152	442	160	123
Control		1M-2M (4 yr)		2M-3M (2 yr)		1M-3M (6 yr)	
	N/ha	66		36		99	
	N/ha/yr	16		18		16	

T1 = logging of trees ≥ 45 cm dbh, T2 = logging of trees ≥ 55 cm dbh, T0 = unlogged area

BL = before logging, 1Y = one year after logging, ..., 1M = first measurement, ..., N = number of trees.

ha) showed a higher ingrowth rate. Overall, average ingrowth was greater in the last two years of the study period in the logged forest plots (Fig. 1). As expected ingrowth was significantly higher in the logged than in the unlogged forest. Similar results were reported for Trengganu, where Tang and Wan-Razali (1981) reported a mean ingrowth rate higher in the fifth year after logging than in the first, considering trees >10 cm dbh. On the other hand, Silva (1989) reported that recruitment had "dramatically fallen" between year 4 and year 6, and between year 6 and year 8 after more intensive logging in Tapajós Forest, 47 km from the present study area.

Ingrowth varied differently over time for guilds of species, as well as for each species depending on its peculiar silvicultural characteristics, as also observed by Alder (1983). Light-demanding species showed more ingrowth than shade-tolerant over the entire period in the two logged treatments, but in the undisturbed area this situation was reversed (Figure 1). In the logged forest, ingrowth of shade-tolerant species declined from year 1 to year 5 after logging, while light-demanding species showed a continual increase during the study period, always being more abundant in the more intensively logged plots. In the unlogged area shade-tolerant species showed a very slight increase in ingrowth ($2 \text{ trees ha}^{-1} \text{ year}^{-1}$) from the second to the third measurement, while the light-demanding species showed similar values over the study period. Ingrowth of both shade-tolerant and light-demanding commercial species increased with time after both logged treatments, but in the undisturbed forest it was almost constant ($1 \text{ tree ha}^{-1} \text{ year}^{-1}$) during the period.

Species with average ingrowth $>5 \text{ trees ha}^{-1}$ in the logged forest were *Inga* spp, *Rinorea flavescens*, *Cecropia sciadophylla*, Sapotaceae group, *Jacaranda copaia* and *Protium* spp. In the unlogged area only the genus *Inga* showed recruitment of $>5 \text{ trees ha}^{-1} \text{ year}^{-1}$. Species with ingrowth of 2 - 5 trees $\text{ha}^{-1} \text{ year}^{-1}$ were *Duguetia echinophora*, *Protium* spp., group Sapotaceae and *Rinorea flavescens*.

The annual mean ingrowth of trees >5 cm dbh during the eight-year study period were 12% after heavy logging (≥ 45 cm dbh), 11% after less intensive logging (≥ 55 cm dbh) and only 1.4% in the unlogged forest. Light-demanding species showed ingrowth of 46% in more intensive logging (trees ≥ 45 cm dbh), 25% in less intensive logging (≥ 55 cm dbh) and only 0.6% in control, while the shade-tolerant had 8% in more intensive logged plots, 9% in less intensive logged plots and 1.2% in control plots. Ingrowth of commercial species was 15% in more intensive logging, 12% in less intensive logging and 1% in the undisturbed area.

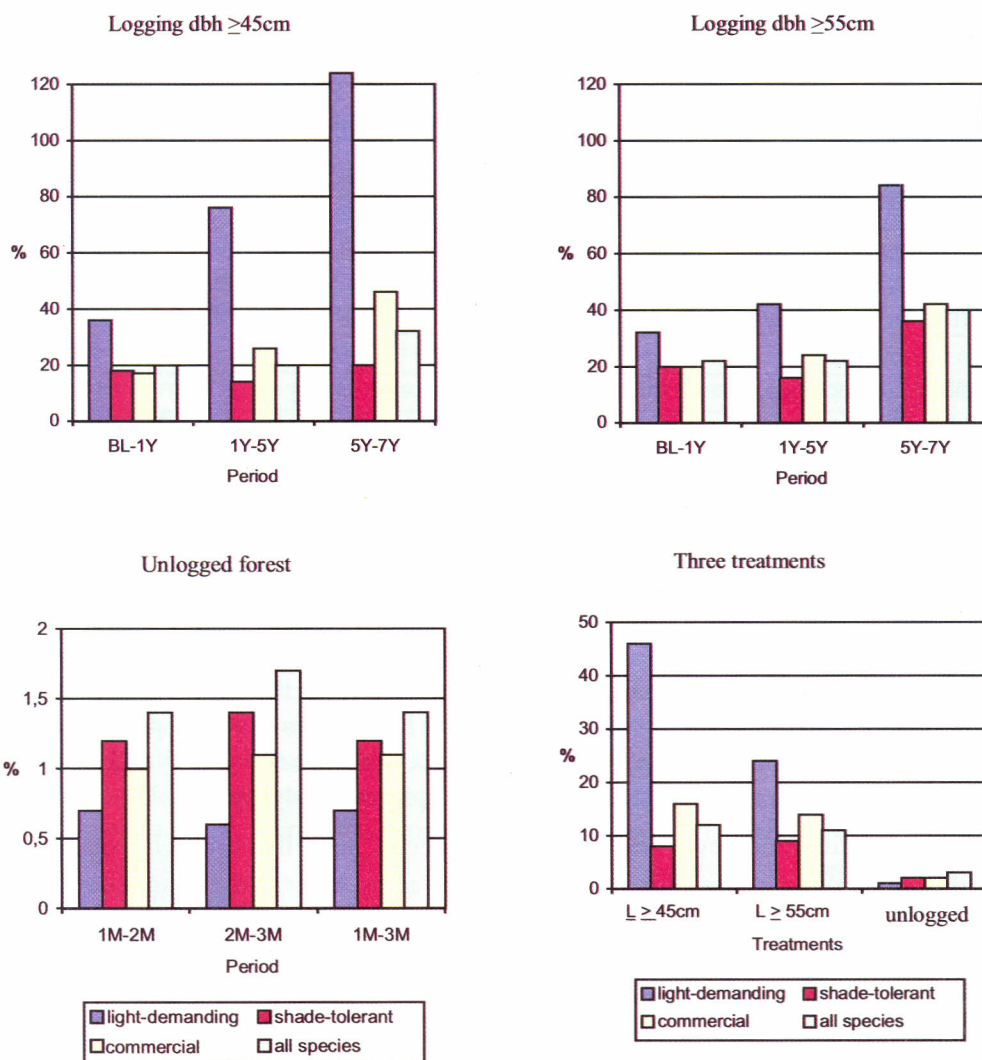


Figure 1. Ingrowth of trees ≥ 5 cm dbh during eight years in Brazilian Amazonia. Percentages refer to number of new trees compared to existing trees in previous measurement
 BL = before logging, 1Y = 1 year after logging, ..., 1M = first measurement in the unlogged area, ...

Mortality

Annual mortality over the eight-year period was 4.3% after logging of trees ≥ 45 cm dbh, 3.1% after logging of trees ≥ 55 cm dbh, and 1.3% in the unlogged area. The percentages in the logged forest also included cut trees and those which died from logging damage, because they could not be separated easily in the first measurement after logging. But excluding those individuals and taking only the period after exploitation, the periodic annual averages were 2.1% after logging of trees ≥ 45 cm dbh and 1.6% after logging of trees ≥ 55 cm dbh (Table 2).

Sites where more trees were cut, showed a higher mortality rate (11.1%) immediately after logging than did logging of trees ≥ 55 cm dbh (7.5%), although the difference was not statistically significant. During the rest of the period after logging, mortality after logging of trees ≥ 45 cm dbh was slightly greater than that after logging of trees ≥ 55 cm dbh (Figure 2). Comparing mortality between logged and unlogged forest, a significant difference was only found immediately after logging, due presumably to the inclusion of cut trees in calculation.

Table 2. Mortality of trees ≥ 5 cm dbh in Tapajós National Forest in Brazilian Amazonia over an eight-year period

Treatment	Unit	Period			
		BL-1Y	1Y-5Y	5Y-7Y	BL-7Y
Logging of trees ≥ 45 cm	N/ha	240	71	60	371
	N/ha/yr	120	18	30	46
	Percent	11,1	2,0	2,5	4,3
Logging of trees ≥ 55 cm	N/ha	161	62	43	266
	N/ha/yr	81	15	22	33
	Percent	7,5	1,5	1,9	3,1
Unlogged forest			1M-2M (4 yr)	2M-3M (2 yr)	1M-3M (6 yr)
	N/ha		51	38	89
	N/ha/yr		13	19	15
	Percent		1,2	1,7	1,3

BL = before logging, 1Y = one year after logging, ..., 1M = first measurement, ..., N = number of trees

Mortality rates at five years after logging were lower than that reported by Tang (1976) in a five-year period in Trengganu, Malaysia, where he found 2.8% for low logging intensity, 6.9% for medium and 10.2% for high. He pointed out that mortality rates following logging declined with time and tended to peak in the second year after logging. In our study, data did not indicate mortality peak in the second year after logging, but it was higher 5-7 year after logging, than it was 1-5 year after logging. There were similar findings in the undisturbed forest. This could be due to the natural dynamics of the forest or to some abnormality in the climate or in another environmental factor. Silva (1989) reported a similar finding in another logging study in Tapajós Forest, where mortality rates declined up to the fourth year after logging, then rose again until year 6 after logging and remained nearly stable until the end of the eight-year study period. Annual mortality rate found by Silva (1989) was of 2.8%, but he considered in the calculation live fallen trees and broken individuals less than 3 m high in addition to dead trees. A subsequent study made by Silva *et al.* (1995) in the same plots during eleven years (1981-1992) reported an annual mortality rate of 2.2%.

Annual average mortality in the unlogged forest (1.3%) was similar to the findings of Swaine *et al.* (1987b) in their review of research in 18 tropical sites on three continents. They commented that the annual mortality rates of trees in those tropical forests were between 1% and 2%, varying within local sites and between successive periods. The rate of 1.3% in the present study was lower than 2.03% found for individuals ≥ 10 cm dbh by Lieberman and Lieberman (1987) at La Selva in Costa Rica, 2.06% by Manokaran and Kochummen (1987) in Sungei Menyala Forest Reserve in Malaysia, and 1.77% for trees ≥ 30 cm dbh by Swaine *et al.* (1987a) at Kade, Ghana. But mortality in the present study was higher than 1.12% found by Nicholson (1965) and 1.06% by Nicholson (1979) in Sabah, North Borneo, 1.04% found by Lang and Knight (1983) in Barro Colorado, Panama, and 1.07% by Nicholson *et al.* (1988) in Queensland.

Comparing the ecological guilds of species, mean mortality was higher for light-demanding species than for shade-tolerant during the entire study period in the logged area, while in the undisturbed forest the reverse was observed; the same patterns were observed for ingrowth (Figure 2). This result in the unlogged area was different from those of Manokaran and Kochummen (1987) in Sungei Menyala Forest Reserve in Malaysia, where high mortality rates occurred in both pioneer and late seral species. The extremely high mortality rates of light-demanding species from year 5 to year 7 after logging in the Tapajós study (Figure 2) can be explained by the increasing number of deaths of short-lived pioneer species up to the end of the period, probably as a response to the

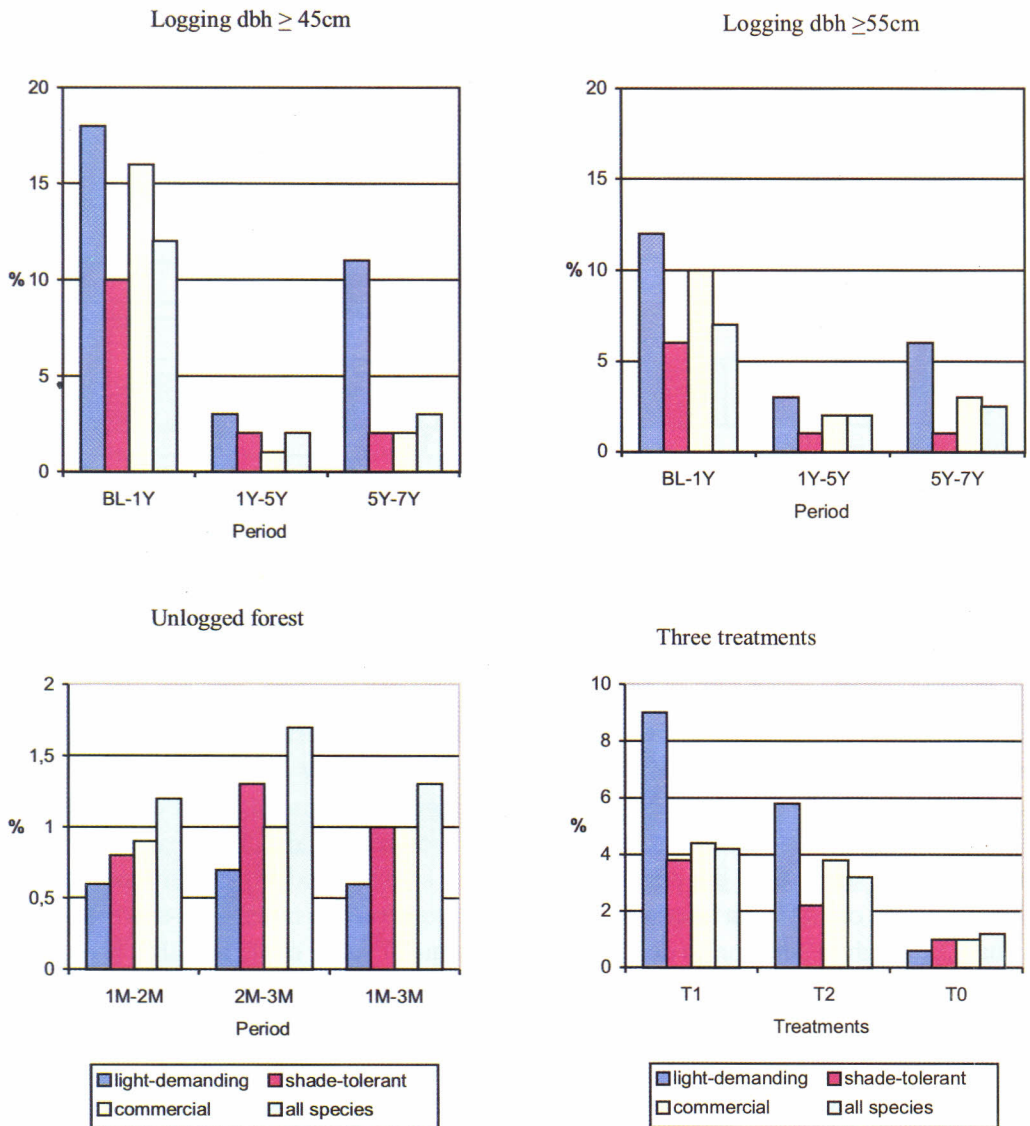


Figure 2. Mortality of trees ≥ 5 cm dbh during eight years in Brazilian Amazonia. Percentages refer to number of dead trees compared to existing trees in previous measurement

BL = before logging, 1Y = 1 year after logging, ..., 1M = first measurement in the unlogged area, ...

reduction of light in the area due to closing canopy. After logging of trees ≥ 45 cm dbh, the mortality for light-demanding species rose from 3% to 11% 5-7 years after logging. Only light-demanding species in the genus *Inga* were among the ten species with higher mortality rates in year 5 after logging, but in year 7 there were three other pioneer species (*Cecropia obtusa*, *Cecropia sciadophylla* and *Jacaranda copaia*), as well as *Inga* spp among the ten species with highest mortality rates. After logging of trees ≥ 55 cm dbh, where mortality of light-demanding species increased from 2% to 6%, *Inga* spp were the only pioneer species among the ten with higher mortality rates five years after logging, but by seven years after logging there were the following light-demanding species with higher mortality rates: *Inga* spp, *Jacaranda copaia*, *Cecropia obtusa*, *Neea floribunda* and *Cecropia sciadophylla*. The mortality rate of shade-tolerant species increased from 1.5% to 1.7% from the fifth to the seventh year after logging of trees ≥ 45 cm dbh, while it had a slight decrease from 1.2% to 1.1% after logging of trees ≥ 55 cm dbh.

In the unlogged area there were three light-demanding species in the second measurement and four in the third, among the ten species with higher mortality rate (*Inga* spp., *Tachigalia myrmecophylla*, *Tachigalia* spp. and *Sclerolobium guianensis*). Shade-tolerant species were chiefly responsible for the observed increase in mortality rates in the unlogged area; they increased from 0.9% to 1.3% while the light-demanding increased from 0.58% to 0.63%. Commercial species had annual mortality rates of 1.1% from year 1 to year 7 after logging in T1, and 1.7% in T2. Also in the undisturbed forest the annual mortality rate was 1% for commercial species during the whole study period, which suggests that logging did not greatly affect the survival of this species group.

Dynamic balance

According to some authors (eg. Uhl 1982, Whitmore 1984), gaps have greater recruitment than mortality. During the building phase recruitment + mortality would tend towards equilibrium for a short time, then mortality would exceed ingrowth, and the mature phase would be in balance. In this study, as already seen, ingrowth increased with time in the logged forest, while mortality rates, even though lower than ingrowth, were very high immediately after logging, slowing down up to year 5 after logging, and keeping low rates until the end of the study period (Fig. 3). Most species considered separately had ingrowth higher than mortality in the logged area over the period, while in the undisturbed forest a great number of species showed the same rate in ingrowth and mortality, although a few showed large differences. In general, in the unlogged forest differences between ingrowth and mortality were not large, agreeing with Whitmore (1984) that deaths are more or less balanced by replacements in climax forests. In addition, Swaine *et al.* (1987b) pointed out that there is a dynamic balance in natural undisturbed forests, where dead trees are continually replaced by new recruits. In La Selva, Costa Rica, Lieberman and Lieberman (1987) found an equal rate of mortality and recruitment for individuals ≥ 10 cm dbh over a 13-year period. Manokaran and Kochummen (1987) reported that mortality and ingrowth rates differed in the first years of a 34-year period in an unlogged Malayan forest but were in balance in the last ten years, and the recruitment increased in response to increase of mortality. Uhl (1982) commented that the structure of a *terra firme* forest in Venezuelan Amazonia was 'relatively' stable considering that mortality was approximately balanced by ingrowth. The only consulted study in unlogged forest that showed a very low ingrowth (0.71%) compared with mortality (1.6%) was carried out by Pires and Prance (1977) during a 15-year period at Mocambo Reserve in Belém, Brazilian Amazonia.

Conclusion

Ingrowth increased with time after both intensities of logging while mortality was very high immediately after logging due to felled and damaged trees, slowed down up to year 5 after logging, then kept low rates until the end of the eight-year study period. In the unlogged forest, ingrowth and mortality were nearly balanced during the period.

Both ingrowth and mortality rates were higher for light-demanding species than for shade-tolerant in the logged areas, but in the undisturbed forest this situation was reversed.

The effect of logging on dynamics of commercial species was positive insofar as ingrowth exceeded mortality by a factor of 6 after both intensities of logging. In the undisturbed forest, both mortality and ingrowth of commercial species were in equilibrium.

The logging made the forest more dynamic, considering that the unlogged area had ingrowth and mortality balanced, while in the logged forest the ingrowth was higher than mortality. As expected, the more intensive logged plots were more dynamic with higher ingrowth and mortality rates.

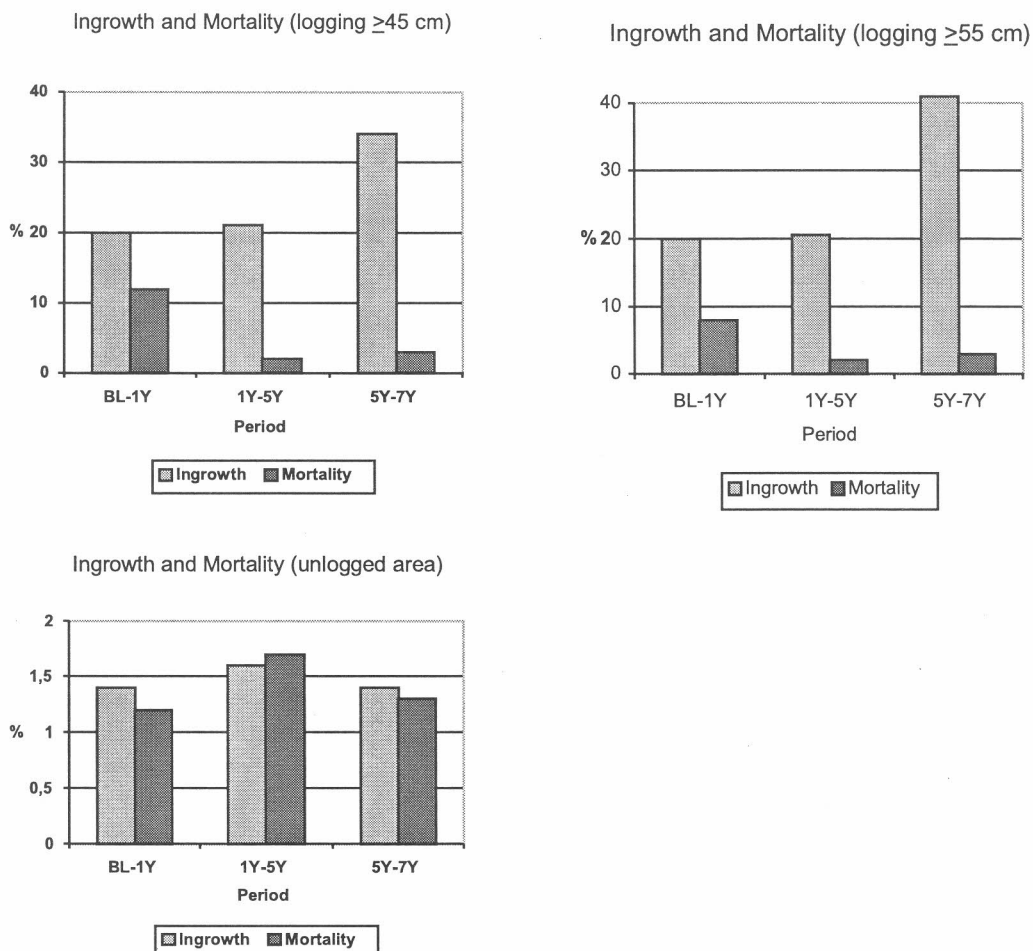


Figure 3. Ingrowth and mortality of trees > 5 cm dbh over an eight-year period in Brazilian Amazonia. Percentages refer to ingrowth or mortality
 BL = before logging, 1Y = 1 year after logging, ..., 1M = first measurement in the unlogged area.

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