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GROWTH AND YIELD OF A TROPICAL RAIN FOREST IN THE BRAZILIAN AMAZON 13 YEARS AFTER LOGGING

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ABSTRACT

Successive inventories of a silvicultural experiment in *terra firme* rain forest within the Tapajós National Forest in the Brazilian Amazon are examined to provide guidelines for operational forest management on a sustainable basis. The experiment was logged in 1979 without additional silvicultural treatment, but included protection from further logging and encroachment ("log and leave"). Thirty-six permanent plots established in 1981, were remeasured in 1987 and 1992.

Logging changed the canopy structure and altered the composition of the stand, reducing the number of shade tolerant species and stimulating light demanding species. There was a nett increase in stem number and stand basal area during the 11 year observation period, and this trend also holds for most of the individual species. The stand basal area 13 years after logging was about 75% of that in a comparable unlogged forest. Logging stimulated growth, but this effect was short-lived, lasting only about 3 years, and current growth rates are similar to those in the unlogged forest.

Between the first and second remeasures, average diameter increment decreased from 0.4 to 0.2 cm yr⁻¹, mortality remained relatively constant at 2.5% per year, while recruitment (at 5 cm dbh) decreased from 5% to 2%. Total volume production declined from approx. 6 to 4 m³ha⁻¹yr⁻¹, while commercial production remained about 0.8 m³ha⁻¹yr⁻¹. New commercial species increased the commercial volume in 1992 from 18 to 54 m³ha⁻¹, and the increment to 1.8 m³ha⁻¹yr⁻¹.

Results from this experiment provide the first quantitative information for management planning in the Tapajós Forest, and may guide the choice of cutting cycle and annual allowable cut. Silvicultural treatment to stimulate growth rates in forest areas zoned for timber production should be considered as a viable management option. Extrapolations of these results to an anticipated 30–35 year

cutting cycle must be interpreted with caution. On-going remeasurement and analysis of these and other plots over the next 30 years or more are necessary to provide a stronger basis for management inferences.

INTRODUCTION

The socioeconomic importance of forestry in the Brazilian Amazon is unquestionable. In Pará State, for example, in 1990, wood ranks second in income generation, surpassed only by mining (Yared 1990). However, wood production must become sustainable, or social, economic and ecological implications may have serious repercussions (see e.g., Johnson and Cabarle 1993). Sustainable forest management for timber production is therefore an important issue in the Brazilian Amazon.

The Brazilian Institute of Environment and Renewable Natural Resources (IBAMA), the agency responsible for forest policy and law enforcement, requires that all timber companies with a log intake exceeding 12 000 m³yr⁻¹ must submit and follow a forest management system for the sustainable production of timber. Since the beginning of the 1980s, over 380 forest management projects have been approved, over an area of approximately 700 000 ha.

One prerequisite for sustainable forest management is reliable information on growth and yield for different

management regimes and silvicultural options. But little information on growth and yield is available for tropical rain forest in the Amazon region. Some permanent plots were established in 1956, but few data and results have been published (e.g. Moraes 1970; Pires 1978). Growth monitoring in silvicultural experiments in Amazônia began in the early 1980s, and by 1989 about 105 ha of permanent plots had been established, mainly in Pará State. To date, only preliminary analyses of these data have been completed (e.g. Carvalho 1992; Higuchi 1987; Silva *et al.* 1989).

Here, we examine a silvicultural experiment established in the Tapajós Forest in 1979. The experiment involved logging without additional silvicultural treatment such as poisoning or climber cutting, but included protection from further logging and encroachment ("log and leave" *sensu* Poore *et al.* 1989, p. 7). Silva (1989) made a detailed analysis of this experiment 8 years after logging. The present paper is a continuation of this analysis, and draws on additional plot remeasures made in 1992. It describes changes in the main stand parameters 13 years after logging, and provides data to aid the formulation of forest management plans in the Brazilian Amazon.

This paper draws on successive inventories of silvicultural experiments to provide management guidelines for operational forest management on a sustainable basis. It

illustrates the expedient transfer of research results to practice, in a region lacking such a tradition and with few research sites or results to draw upon.

METHODS

The research was conducted in a 64 ha experimental site denoted RP012 in the Tapajós National Forest, 67 km south of Santarém City, in the State of Pará, Brazil, longitude 55°00'W and latitude 2°45'S (Fig. 1). The area experiences a humid tropical climate and has an annual rainfall of about 1900 mm, with the heaviest rains from December to May. There is a short dry season of 2–3 months which has less than 60 mm of rain. The monthly temperatures are fairly constant through the year, varying from 24 to 26°C. The Tapajós Forest is a typical *terra firme* rain forest, and has a standing volume of about 150–200 m³ha⁻¹ in trees larger than 45 cm dbh.

The experiment site was logged in 1979 using chainsaws and attempts at directional felling. A wheeled skidder was used on skidding trails previously opened by a bulldozer. On average, logging removed 75 m³ha⁻¹ from 16 trees ha⁻¹, all over the felling limit of 45 cm dbh.

In 1981, 36 permanent sample plots, each 0.25 ha (50 m square), were laid out at random over the area. The plots comprised 25 quadrats of 10 x 10 m to allow better control of

measurements. In each quadrat, all trees ≥ 5 cm dbh were numbered and tagged, and several variables were measured (Silva 1989). Seedlings and saplings were measured in selected sub-plots but are not considered in the present study. The present study draws on three variables: dbh, stem identity class and crown illumination class (Table 1). Dbh and stem identity class were recorded for all trees (≥ 5 cm dbh), but crown illumination was determined only for trees ≥ 10 cm dbh. The crown illumination class was modified (after Hutchinson 1982) from the five Crown Illumination Scores proposed by Dawkins (1958; see also Lamprecht 1989, p.42; Alder and Synnott 1992, p.81), to ensure consistent evaluation of this important variable. Readers in temperate zones should recall that the sun is overhead in the tropics, and that direction of neighbouring trees has little influence on crown illumination. Diameters were recorded to the nearest millimetre. Stand parameters were calculated using a standard package for the analysis of permanent sample plot data (SINFCON).

RESULTS AND DISCUSSION

Stand structure

In 1981, two years after logging, 22 species comprised c. 60% of the stand basal area (BA) over 5 cm dbh. Of these species, 14 were shade tolerant and 8 were light demanding. Ten species (45% of BA) were commercial (Table 2). The same

species contributed the bulk of the bole volume over 20 cm dbh. The most abundant species, *Rinorea guianensis* (Violaceae) is shade tolerant and frequently dominates the undergrowth in the Tapajós Forest, but rarely exceeds 35 cm dbh.

In 1992, the same species still comprised 60% of the stand basal area but the ranking had changed: *Rinorea* ranked 5th. *Bixa arborea* (Bixaceae), a fast growing light demander which benefitted from the canopy opening, ranked first in basal area, followed by two other pioneers, *Inga* sp. (Leguminosae) and *Cecropia sciadophylla* (Moraceae).

Another study of species composition before and after logging (90 m³ha⁻¹ were extracted) in the Tapajós Forest found no major changes in species ranking (Carvalho 1992). Shade tolerant species, viz. Sapotaceae (9 species) and *Rinorea guianensis* ranked 1st and 2nd before logging and the same Sapotaceae and *Mimosa guianensis* (Olacaceae) dominated 7 years after logging. Common pioneer species such as *Cecropia* sp. and *Inga* sp. ranked 3rd. *Bixa arborea* was present in the stand, but was not as prevalent as in the present study.

Generally, plots increased in basal area, volume and number of trees during the 11 year period (Table 2). The stand basal area in 1992 was about 76% of an unlogged area in the Tapajós Forest, which on average, is about 36 m²ha⁻¹ (Silva et al. 1985). Eight dominant species lost trees, but only one

species (the *Miquartia* sp.) declined in basal area and volume. For the remaining species, growth compensated the loss of individuals through death. *Manilkara huberi* (Sapotaceae) had no ingrowth at 5 cm dbh during the 11 year period, reflecting its slow growth when young.

Diameter increment

Periodic annual diameter increment (PAI_{dbh}) was calculated for all 195 species and for the 32 commercial species over three periods, 1981-1987, 1987-1992 and 1981-1992. Increment in both groups declined considerably following canopy closure. The average PAI_{dbh} for all species decreased by about 50%, while the commercial PAI_{dbh} declined by about 40% (Table 3). During the 11 year observation period, PAI_{dbh} of all species and of the commercial group averaged 0.3 and 0.4 cm yr^{-1} , respectively. In another research plot in the same forest, growth rates were reported to be 0.4 cm yr^{-1} eight years after logging and 0.2 cm yr^{-1} in the unlogged stand (Carvalho 1992). Increments in the present study approach those of an unlogged forest, and it appears that the stimulus of logging on growth lasted for only 3 years, consistent with results elsewhere (e.g. Primack *et al.* 1985). Thus "log and leave" regimes will require cutting cycles longer than other silvicultural regimes which include periodic treatments to stimulate growth.

There is a strong correlation between crown illumination class and tree growth (Table 3), consistent with other findings (e.g., Wyatt-Smith and Vincent 1962; Bryan 1981; Alder and Synnott 1992). In the present study, nearly 66% of commercial trees which received full or some overhead light. Releasing the partially shaded trees (Crown illumination class 2) would stimulate the growth of these trees and enhance timber production. Crown illumination is thus an important guide in decisions concerning the need for and timing of silvicultural treatments. In this region, monitoring of crown status for timely silvicultural treatment is possible because of cost-effective labour and rapid growth rates. Therefore this should be considered in operational forest management.

In tropical forests, diameter increments in any class of trees (e.g. classified both by diameter and site) may vary greatly (e.g., Mervart 1972; Primack *et al.* 1989; Silva 1989). This may be attributed in part to environmental conditions and intrinsic factors such as specific growth habits and genotypes. The coefficients of variation in PAI_{dbh} are high in all dbh classes, but tend to decrease with increasing tree size (Table 4). Eleven years after the first assessment, some trees still exhibited growth too small to measure, and no response to logging can be expected in these trees. The largest increments occurred in the medium-sized and larger trees, but some of these trees also exhibited very slow growth rates.

Ingrowth and mortality

After logging, the ingrowth of new recruits into diameter classes larger than 5 cm increased substantially during the first eight years. During the next five years, there was a sharp decrease, both in absolute and in relative terms for all species as well as for the commercial group (Table 5). Several years after logging, light conditions in the forest understorey no longer promote fast growth of the seedlings and saplings. Elsewhere in the Tapajós Forest, the percentage of ingrowth increased 8 years after logging (Carvalho 1992), but it seems that a greater timber harvest ($90 \text{ m}^3\text{ha}^{-1}$) provided more light in the understorey and so stimulated ingrowth.

In the present study, mortality increased slightly between the first and second observations while ingrowth decreased (Table 5). In the first period ingrowth was higher than mortality but in the second period the balance was reversed. However, over the whole period, the stand increased in tree numbers and stand basal area (Table 1).

The ingrowth found in this study is similar to results reported for comparable forest types in Costa Rica (Lieberman *et al.* 1985, Lieberman and Lieberman 1987), Puerto Rico (Weaver 1979), and Ghana (Swaine *et al.* 1987a; Swaine 1990). Mortality was comparatively high (cf. Swaine *et al.* 1987b;

Vanclay 1991), but lower than in logged dipterocarp forests in Malaysia (Thang and Yong 1989). In all these cases, mortality was balanced or nearly balanced by ingrowth. Unbalanced figures for ingrowth and mortality (9 and 5% respectively) during a five year period have been reported for a virgin tropical rainforest near Manaus, Brazil (Higuchi *et al.* 1993). However, a five year period may be too short to provide reliable estimates of ingrowth and mortality, as year-to-year variability may be considerable in this region (e.g., Borchert 1992).

Volume increment

The total volume of all species increased by 38% between 1981 and 1992 (Table 6), and a similar increase (37%) was observed for the commercial species. As expected, the periodic annual increment in volume followed the general declining trend observed for the PAI_{dbh} .

In 1992, there were only 6 trees and 18 m³ per ha larger than 45 cm dbh (the commercial size according to the Brazilian forestry regulations) represented on the 1979 commercial species list, and only a few smaller trees of these species appeared to be candidates for the next harvest. However, since the forest was logged, many additional species have been accepted by the timber market, and a revision of the species

list revealed a further 29 species that could be designated commercial.

These additional 29 species boost the commercial volume in 1992 to 54 m³ha⁻¹ in 15 trees per hectare, and more than double the annual increment including ingrowth (Table 6). This is comparable with other silvicultural systems in Suriname (Jonkers and Schmidt 1984) and in Malaysian dipterocarp forest (Thang and Yong 1989). Even though the initial logging was considered heavy by regional standards, growth to date suggests that a second cut of similar intensity may be possible after 30–35 years. Remeasurements of the permanent sample plots should continue on a regular basis for the next 30 years or more, to confirm this assertion and to provide a better basis for forest management prescriptions.

CONCLUSIONS

Logging and the resulting changes in canopy structure altered the composition of the stand, reducing the number of shade tolerant species and stimulating light demanding species. There has been a nett increase in stem numbers and stand basal area during the 11 year observation period, and this trend has been echoed by most of the individual species. The stand basal area 13 years after logging was about 75% of that in a comparable unlogged primary forest. Logging stimulated growth, but this effect was short-lived, lasting

only about 3 years, and current growth rates are similar to those in unlogged primary forest. Tree growth and timber production may be enhanced by periodic silvicultural treatment to release trees from competition and this should be considered as a mechanism to reduce the cutting cycles in the Brazilian Amazon.

The recognition of 29 additional species of commercial importance raised the commercial volume increment to $1.8 \text{ m}^3\text{ha}^{-1}\text{yr}^{-1}$, but further work will be necessary to confirm that this production can be sustained on a 30–35 year cutting cycle.

Results from the experiment reported here and in related works, provide the first quantitative information for management planning in the Tapajós Forest. These data will provide a useful guide for choosing the cutting cycle and setting the annual allowable cut. It has highlighted the need to consider silvicultural treatment to stimulate growth rates in forest areas zoned for timber production. However, we caution that these findings are drawn from observations over an 11-year period, and extrapolations to a 30–35 year cutting cycle must be interpreted with caution. Periodic remeasurement and analysis of these plots over the next 30 years or more is necessary to confirm these preliminary findings.

This case study has demonstrated just one possible application of successive inventories. Additional remeasurements on these and other permanent sample plots in Amazonian *terra firme* forest will provide a suitable database for more detailed studies. Such studies may range from the ecological to the commercial, from simple analyses of changes between measures to dynamic growth models linked to management systems.

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REFERENCES

- Alder, D. and Synnott, T.J., 1992. Permanent sample plot techniques for mixed tropical forest. Oxford Forestry Institute, Tropical Forestry Papers No 25. 124 p.
- Borchert, R., 1992. Computer simulation of tree growth periodicity and climatic hydroperiodicity in tropical trees. *Biotropica* 24:385-395.
- Bryan, M.B., 1981. Studies of timber growth and mortality in the mixed dipterocarp forest in Sarawak. FAO FO:MAL/76/008 Field Document 11. 56 p.
- Carvalho, J.O.P. de, 1992. Structure and dynamics of a logged over Brazilian Amazonian rain forest. D.Phil Thesis, University of Oxford.
- Dawkins, H.C., 1958. The management of natural tropical forest with special reference to Uganda. Imperial Forestry Institute Paper 34.
- Higuchi, N., 1987. Short-term growth of an undisturbed tropical moist forest in the Brazilian Amazon. Ph.D. Thesis, Michigan State University.
- Higuchi, N., Freitas, J.V. de and Coic, A., 1993. Experimental forest management on a sustained yield basis at ZF-2 (Manaus, Amazon, Brazil). Paper to Workshop on "Silviculture in Natural Tropical Rainforest", Kourou, French Guyana, 2-5 March 1993 (unpublished).

- Hutchinson, I.D., 1982. Field enumeration of permanent sample plots in the mixed dipterocarp forest of Sarawak. FAO FO:MAL/76/008 Field Document 16. 136 p.
- Johnson, N. and Cabarle, B., 1993. Surviving the cut: natural forest management in the humid tropics. World Resources Institute, Washington. 71 p.
- Jonkers, W.B.J. and Schmidt, P., 1984. Ecology and timber production in tropical rainforest in Suriname. *Interciencia* 9:290-297.
- Lamprecht, H., 1989. *Silviculture in the Tropics*. GTZ, Eschborn, Germany. 296 p.
- Lieberman, D. and Lieberman, M., 1987. Forest tree growth and dynamics at La Selva, Costa Rica (1969-1982). *Journal of Tropical Ecology* 3:347-358.
- Lieberman, D., Lieberman, M., Peralta, R. and Hartshorn, G.S., 1985. Mortality patterns and stand turnover rates in a wet tropical forest in Costa Rica. *Journal of Ecology* 73:915-924.
- Mervart, J., 1972. Growth and mortality rates in the natural high forest of western Nigeria. *Nigeria Forestry Information Bulletin* No 22. 28 p.
- Moraes, V.H.F., 1970. Periodicidade de crescimento do tronco em árvores da floresta amazônica. *Pesquisa Agropecuária Brasileira* 5:315-320.
- Pires, J.M., 1978. The forest ecosystems of the Brazilian Amazon: description, functioning and research needs. In: *Tropical Forest Ecosystems. A state-of-knowledge report*

prepared by UNESCO/UNEP/FAO, UNESCO-UNEP, France: pp. 607-627.

Primack, R.B., Ashton, P.S., Chai, P. and Lee H.S., 1985.

Growth rates and population structure of Moraceae trees in Sarawak, East Malaysia. *Ecology* 66:577-588.

Primack, R.B., Chai, E.O.K., Tan S.S. and Lee H.S., 1989.

Relative performance of dipterocarp trees in natural forest, managed forest, logged forest and plantations throughout Sarawak, East Malaysia. In: Wan Razali Wan Mohd, H.T. Chan and S. Appanah (Editors). *Growth and Yield in Tropical Mixed/Moist Forests*. Proceedings of the Seminar, held in Kuala Lumpur, 20-24 June 1988. Forest Research Institute Malaysia: pp. 161-175.

Poore, P., Burgess, P., Palmer, J., Rietbergen, S. and

Synnott, T., 1989. *No Timber without Trees: sustainability in the tropical forest*. Earthscan, London. 252 p.

Silva, J.N.M., 1989. *The behaviour of the tropical rainforest of the Brazilian Amazon after logging*. D.Phil Thesis, University of Oxford.

Silva, J.N.M., Lopes, J. do C.A. and Carvalho, J.O.P. de, 1985. Inventário florestal de uma área experimental na Floresta Nacional do Tapajós. *Boletim de Pesquisa Florestal*, 10/11:38-110.

Silva, J.N.M., Carvalho, J.O.P. de, Lopes, J. do C.A., 1989.

Growth of a logged-over tropical rain forest of the Brazilian Amazon. In: Wan Razali Wan Mohd, H.T. Chan and S. Appanah (Editors). *Growth and Yield in Tropical*

- Mixed/Moist Forests. Proceedings of the Seminar, held in Kuala Lumpur, 20-24 June 1988. Forest Research Institute Malaysia: pp. 117-136.
- Swaine, M.D., 1990. Population dynamics of moist tropical forest at Kade, Ghana. In: Atelier sur l'Aménagement et la Conservation de l'Ecosystème Forestier Tropical Humide, held in Cayenne, French Guyana, 12-16 Mars 1990. MAB/UNESCO, MAB/France, IUFRO.FAO. p. 40-61.
- Swaine, M.D., Hall, J.B. and Alexander, I.U., 1987a. Tree population dynamics at Kade, Ghana (1968-1982). *Journal of Tropical Ecology* 3: 331-345.
- Swaine, M.D., Lieberman, D. and Putz, F.E., 1987b. The dynamics of tree populations in tropical forest: a review. *Journal of Tropical Ecology* 3:359-366.
- Thang H.C. and Yong T.K., 1989. Status of growth and yield studies in Peninsular Malaysia. In: Wan Razali Wan Mohd, H.T. Chan and S. Appanah (Editors). *Growth and Yield in Tropical Mixed/Moist Forests. Proceedings of the Seminar, held in Kuala Lumpur, 20-24 June 1988. Forest Research Institute Malaysia: pp. 137-148.*
- Vanclay, J.K., 1981. Mortality functions for north Queensland rainforests. *Journal of Tropical Forest Science* 4:15-36.
- Weaver, P.L., 1979. Tree growth in several tropical forests in Puerto Rico. USDA Forest Service, Research Paper SO-152. 15 p.
- Wyatt-Smith, J. and Vincent, A.J., 1962. The swing from qualitative to quantitative assessment of individual tree

crown parameters in the Malayan Forest Service. *Malayan Forester* 25:276-291.

Yared, J.A.G., 1990. A atividade florestal na Amazônia: diagnóstico e perspectivas. Presented at the Seminar "Futuro Econômico da Amazônia: Agricultura", Brasilia, 23-24 May 1990, 23 p. (unpublished).

TABLE 1: Stem identity and crown illumination classes used in the Tapajós Forest. The stem identity class is a 2-digit code. The first digit indicates the tree status, the second stem status.

Crown Illumination		Tree Status	Stem Status
1	Full overhead light	1 Alive, standing	1 Complete trunk
2	Partial shade or some overhead light	2 Alive, fallen	2 Broken stem
3	Side light only or complete shade	3 Dead, standing	3 Broken stump
		4 Dead, fallen	4 Cut stump
			9 Not found

TABLE 2: Changes in stand basal area, volume, numbers of stems in experiment RP012 in the Tapajós Forest between 1981-1992.

Species	1981.....			1992.....			1981-1992.....			Balance		
	BA†	V	N	BA	V	N	Ingrowth N	Mortality N	N	BA/V	EC‡	
<i>Rinorea guianensis</i> (Aubl) Schum	1.26	8.3	51.0	1.16	7.9	43.1	2.6	10.5	-	-	ST	
<i>Pouteria</i> sp.	1.18	8.0	51.9	1.25	9.6	46.8	4.1	9.2	-	+	ST	
<i>Bixa arborea</i> Huber	0.98	7.6	39.7	1.71	14.0	64.4	36.0	11.3	+	+	LD	
<i>Protium apiculatum</i> Swartz	0.95	4.6	58.8	1.16	7.0	62.2	13.2	9.8	+	+	ST	
<i>Couratari oblongifolia</i> Ducke	0.86	9.1	18.7	0.92	9.9	17.7	1.1	2.1	-	+	ST	
<i>Carapa guianensis</i> Aubl	0.79	7.4	18.8	1.12	11.8	18.4	1.8	2.2	-	+	ST	
<i>Ocotea</i> sp.	0.64	4.5	29.2	0.71	5.5	29.4	6.8	6.6	+	+	ST	
<i>Sloanea froesii</i> C.E. Smith	0.55	2.9	78.0	0.79	3.8	69.0	38.7	47.7	-	+	LD	
<i>Inga</i> sp.	0.51	2.1	59.8	1.39	6.7	90.1	52.7	22.4	+	+	LD	
<i>Eschweilera blanchetiana</i> Miers	0.46	3.7	13.4	0.46	3.8	12.6	0.7	1.5	-	+	ST	
<i>Hevea</i> sp.	0.42	4.6	5.9	0.47	5.1	6.7	1.1	0.3	+	+	ST	
<i>Virola melinonii</i> (R. Ben.) A.C. Smith	0.41	3.8	10.9	0.52	5.0	16.0	6.2	1.1	+	+	ST	
<i>Eschweilera amara</i> Ndz.	0.39	3.4	12.2	0.44	4.1	12.2	1.0	1.0	+	+	ST	
<i>Eperua bifuga</i> Mart. ex Bth.	0.31	2.3	16.1	0.33	3.0	12.4	0.9	4.6	-	+	ST	
<i>Swartzia corrugata</i> Benth	0.31	3.7	2.2	0.29	3.5	2.3	0.6	0.5	+	+	ST	
<i>Sclerolobium chrysophyllum</i> Poepp. & Endl	0.26	2.3	9.1	0.61	6.7	13.2	6.8	2.7	+	+	LD	
<i>Goupia glabra</i> Aub.	0.24	2.9	1.4	0.22	2.7	1.6	0.4	0.2	+	+	LD	
<i>Jacaranda copaia</i> (Aubl) D. Don	0.23	2.1	9.0	0.47	4.0	17.1	10.3	2.2	+	+	LD	
<i>Licaria canella</i> (Meissn.) Kostermos	0.22	1.8	8.4	0.27	2.4	9.7	2.5	1.2	+	+	ST	
<i>Manilkara huberi</i> Stanley	0.21	2.3	3.3	0.24	2.8	2.8	-	0.5	-	+	ST	
<i>Cordia bicolor</i> D.C.	0.19	1.5	9.2	0.28	1.8	18.9	11.2	1.5	+	+	LD	
<i>Cecropia sciadophylla</i> Mart	0.15	0.7	19.8	1.35	12.2	28.2	13.3	4.9	+	+	LD	
Remaining Species	8.77	71.2	404.8	9.76	79.5	455.1	152.9	80.9	+	+	-	
Total	20.30	160.8	931.6	25.92	212.8	1050.1	364.9	224.9	+	+		

† BA = Basal area (m²ha⁻¹) for trees ≥5 cm dbh; V = Volume (m³ha⁻¹) of trees ≥20 cm dbh; N = Number of trees per ha ≥5 cm dbh.

‡ EC = Ecological group: ST= Shade tolerant, LD= Light demanding.

TABLE 3: Periodic annual diameter increment (cm yr⁻¹) by crown illumination class and species group. Class means differ significantly (P<0.05).

Crown illumination	1981-87	1987-92	Average
Emergent or full overhead light	0.7	0.6	0.6
Partial shade or some overhead light	0.5	0.3	0.4
Side light or complete shade	0.3	0.2	0.3
Average, all species	0.4	0.2	0.3
Average, commercial species	0.5	0.3	0.4

TABLE 4: Periodic annual diameter increment (cm yr⁻¹) by diameter classes during 1981-1992 (rounded to approximate values).

Dbh Class	N	Min	Max	Mean	SD	CV
5-14	2919	0.0	0.9	0.2	0.2	100
15-24	1189	0.0	1.8	0.5	0.4	80
25-34	576	0.0	2.6	0.8	0.7	90
35-44	254	0.0	3.3	0.8	0.7	90
45-54	149	0.1	2.2	0.8	0.5	60
55-64	40	0.1	2.6	0.7	0.5	70
65-74	27	0.1	3.5	1.1	0.9	80
75-84	9	0.1	3.3	1.1	1.1	100
85-94	3	0.9	2.0	1.3	0.6	50
≥95	7	0.2	1.0	0.7	0.3	40

N= number of observations in each class; SD= standard deviation; CV= coefficient of variation in percent

TABLE 5: Ingrowth and mortality.

Period & Species Group	Annual Rate (%) †	
	Ingrowth at 5 cm dbh	Mortality
<u>1981-87</u>		
All species	5.2	2.4
Commercials	5.4	1.2
<u>1987-92</u>		
All species	1.8	2.6
Commercials	1.3	1.5
<u>1981-92</u>		
All species	3.1	2.2‡
Commercials	3.2	1.3

† Proportion of trees which were new recruits or dead at the end of the observation period, in relation to the initial number of trees, divided by the number of years of the period.

‡ Not a simple average of 1981-87 and 1987-92; the initial number of trees in 1981 and 1987 differed.

TABLE 6: Relative and periodic annual increment in volume of trees over 20 cm dbh.

Species Increment (%) Group	1981-92	PAI _{vol} (m ³ ha ⁻¹ yr ⁻¹)		
		1981-87	1987-92	1981-92
All species	38.4	6.1	4.2	5.2
Commercial				
Old List	37.0	0.9	0.7	0.8
Updated List	31.8	2.0	1.7	1.8

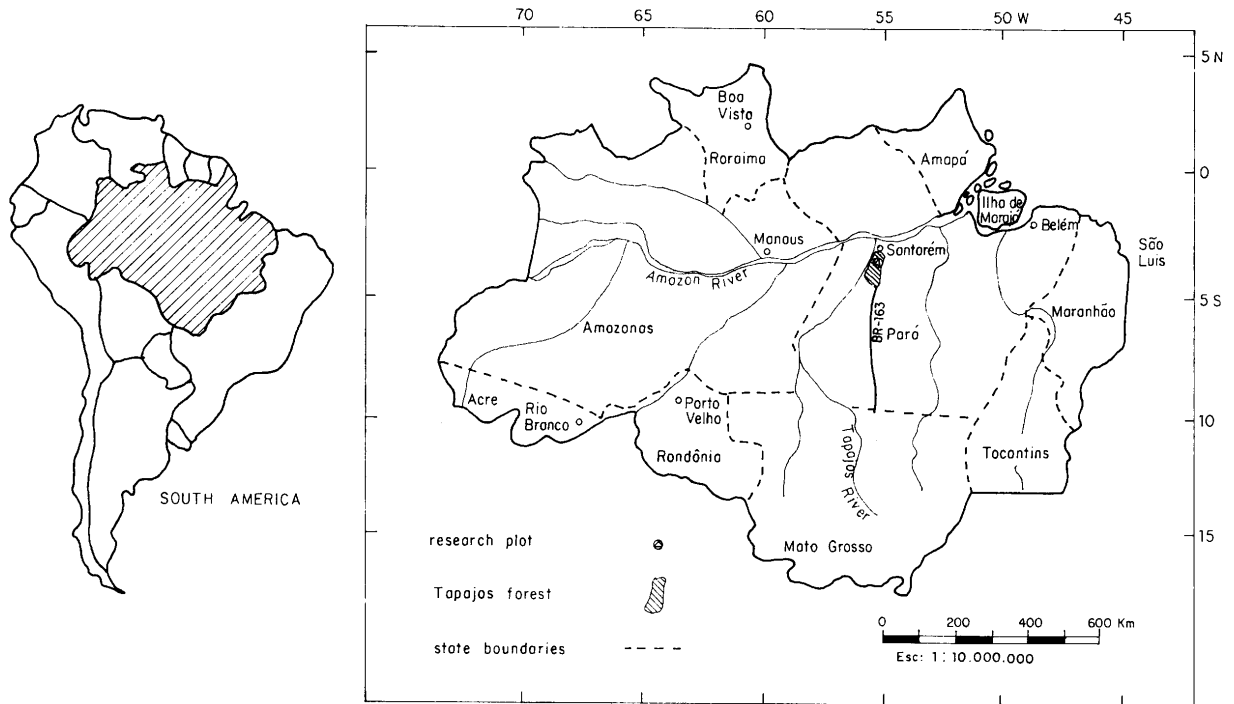


FIGURE 1: Location of the research plot in the Tapajós National Forest, Pará. Hatched area on map of South America is the Legal Amazon region of Brazil.