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Harvesting intensity affects forest structure and composition in an upland Amazonian forest

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Abstract

Forest structure and floristic composition were studied in a series of 0.5 ha natural forest plots at four sites near Porto Trombetas in Pará State, Brazil, 11–12 years after being subjected to differing levels of above-ground biomass harvest and removal. In addition to undisturbed control plots, experimental treatments included: removal of most trees ≥45 cm DBH (low intensity harvest); removal of trees <20 and ≥60 cm DBH (moderate intensity harvest); clear-cutting (100% above-ground biomass removal). Post-harvest basal area growth generally increased with harvest intensity, and total basal areas for trees ≥5 cm DBH were, at the time of our study, 60% (in the clear-cut) to about 80% of those in the control plots. Biomass harvests stimulated recruitment and growth of residual trees, particularly in the smaller diameter classes, but had little effect on species richness for small trees, seedlings, vine, herbs, and grasses. Species richness for trees ≥15 cm DBH was greater in the control and low-intensity (74–75 species) than in the moderate intensity (47 species) and clear-cut (26 species) treatment plots. While the tree flora within all harvest treatments was broadly similar to the undisturbed (control) plots and included similar numbers of species of the major plant families typical of the surrounding forests, the more intensive harvest treatments, especially the clear-cut, were dominated by a higher proportion of short-lived, early successional tree species.

Keywords: Brazil; Floristic diversity; Forest management; Productivity; Regeneration

1. Introduction

The impact of logging and biomass harvesting on the future structure, biological diversity and ecological function of tropical forests is a topic of continuing debate. In many tropical regions, including the Brazilian Amazon, natural forests are less often "managed" than "mined" for selected high-value timber species or fuel wood. Loggers rarely follow harvesting practices proven elsewhere and give little consideration to long- or even short-term environmental impacts (Uhl et al., 1991; Fredericksen, 1998). If the capacity of these forested lands to produce economic, social and environmental goods and services is to be sustained for future generations, improved management techniques, based on a better scientific understanding of natural forest dynamics and disturbance ecology, are required (Hartshorn, 1989; Martins et al., 1997; Dawkins and Philips, 1998; Kammesheidt, 1998; De Graaf et al., 1999; Finegan

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and Camacho, 1999; Finegan et al., 1999; Mostacedo and Fredericksen, 1999).

Ongoing work in many tropical countries on the assessment of reduced-impact logging techniques is a promising development, one that is increasing our understanding of the critical disturbance factors (and operational methods) affecting post-harvest forest productivity and community structure (Hammond et al., 2000; Pinard et al., 2000b; Sist, 2000). For example, recent studies in this field have shown that soil compaction associated with the use of heavy machinery in forest harvest operations can have persistent negative effects on natural regeneration, and that minimizing the area used for access roads, skid trails and decking sites greatly diminishes the overall negative impact of logging on future stand productivity (Van Gardingen et al., 1998; Pinard et al., 2000a).

While it is generally accepted that most tropical forests that are selectively logged or cleared for short-term (shifting) agricultural production eventually regenerate both structurally and functionally (Brown and Lugo, 1990; Attiwill, 1994; Lugo, 1995; Fredericksen, 1998), the rates of recovery of biomass, structural complexity and biodiversity are highly variable. Biophysical factors such as site productivity, susceptibility of the local flora and fauna to natural disturbances, and landscape-level biotic interactions, all influence, post-disturbance forest recovery (Uhl, 1987; Gorchov et al., 1993; Fredericksen, 1998; Liu et al., 1999).

Superimposed on these biophysical factors and processes are the human impacts associated directly with logging or other forest disturbances, and those that often occur after the event (such as post-harvest forest clearance and increased susceptibility to fire). Like the biophysical factors influencing post-disturbance forest dynamics, these impacts are site-specific, varying in their intensity, duration, and thus their influence on natural forest recovery.

In the present study, we focus on the impacts of above-ground biomass harvests on forest structure and floristic diversity in upland (*terra firme*) forests in the Brazilian Amazon. Through this study, we sought to determine if and how increasing levels of biomass extraction affected subsequent rates of tree biomass (or basal area) development and floristic diversity, which we view as important indicators of sustainability. The experimental treatments in this study differ from earlier ones conducted in the region (and elsewhere in moist tropical forest areas) in that they were non-selective as to the species harvested. In this respect, the experiment reflects tropical forest harvesting that occur in many parts of the world for a combination wood fuel and mixed-species timber production, rather than selective logging operations focusing on a small number of large-diameter trees of a limited number of species.

2. Site description and methods

The study site is located in the Saracá-Taquera National Forest at an elevation of 180 m, 65 km northwest of the town of Oriximiná and 30 km south of the Trombetas river in western Pará State, Brazil (1°40′S, 56°27′W). Mean annual rainfall at the nearby town of Porto Trombetas (1970–1994) is 2185 ± 64 mm (SE) with distinctly dry (winter) and wet (summer) seasons; mean monthly rainfall exceeds 100 mm in all months except July–October. The mean annual temperature in this area is 24.8 °C, with mean monthly maximum and minimum temperatures of 34.6 and 19.9 °C, respectively. The terrain in the area of the study sites is gently undulating; soils are sandy with a thick (about 8 cm) litter and humus layer interwoven with tree roots.

In November 1985, in collaboration with Florestas Rio Doce, an experiment was established by Mineração Rio do Norte (MRN) to evaluate the feasibility of managing natural forest stands for sustainable production of wood as an alternative energy source for drying bauxite ore at MRN's Porto Trombetas processing facilities (Jesus et al., 1985). The old-growth forests chosen for study are broadly representative of the upland forests of the region with respect to their structure and species composition; for a more complete description of the forests of this region, see Knowles and Parrotta (1995, 1997). Experimental forest plots were established using a randomized complete block design at each of four sites, located between 200 and 1500 m from the road linking Porto Trombetas to the Saracá Plateau, at 5 km (Block 1), 7 km (Block 2) and 24 km (Blocks 3 and 4). Each block included 0.5 ha $(100 \times 50\,\text{m}^2)$ plots of the following four treatments, with each plot separated from its neighbors by a 50 m wide buffer strip of undisturbed forest:

1. *Control*, in which no harvesting was done.
2. *Low-intensity harvest*, in which all trees $\geq$45 cm DBH (diameter at breast height: 1.37 m) were removed ($201 \pm 15\,m^3$), but retaining a minimum of two trees per plot as seed-bearing trees.
3. *Moderate intensity harvest*, in which all trees $\leq$20 and $\geq$60 cm were removed ($219 \pm 26\,m^3$), but retaining a minimum of two trees in each plot as seed bearers, plus subsequent removal of all trees damaged by initial harvest as well as trees deemed to have poor stem form.
4. *Clear-cutting*, in which all above-ground biomass ($373 \pm 52\,m^3$) was removed.

Chainsaws were used to fell and cut the trees and all harvest biomass was manually removed from the plots. In treatments 2, 3 and 4, saplings and small diameter stems (<10 cm DBH) were manually cut prior to felling of larger trees to facilitate harvest operations. No tractors or other heavy machinery were employed, deliberately avoiding soil compaction and minimizing other potentially damaging site impacts.

Complete (full 0.5 ha plot area) inventories of all trees $\geq$10 cm DBH and palms were made prior to, and immediately after, treatment in late 1985. At the time of the initial inventories, individual tree stems were not mapped; data available to the present authors from these early surveys consisted of species-wise tabulations of the numbers of individuals in each 0.5 ha plot in each of the following stem diameter classes: 10.0–19.9, 20.0–34.9, 35.0–54.9, 55.0–79.9 and $\geq$80.0 cm (Jesus et al., 1985). Two years later (in April 1988), residual tree growth was assessed and inventories made of seedlings and trees <10 cm DBH (Mineração Rio do Norte, 1988).

In 1996–1997, approximately 11 years after the experimental plots were established and treated, we revisited these plots to evaluate their structural and floristic development. To minimize edge effects, we chose not to include the full 0.5 m plot area in our analyses, but rather to exclude the outermost 15 m wide strip of each plot bordering the surrounding undisturbed forest. Within the central $20 \times 70\,m^2$ zone of each ($50 \times 100\,m^2$) plot, all trees $\geq$15 cm DBH (including palms) were identified and their DBHs and heights recorded. In the clear-cut plots only, stems arising from post-harvest coppice regrowth were distinguished from those regenerating from seed to evaluate the relative importance of vegetative reproduction in the recovery of these stands. For surveys of smaller trees (including palms), vines, herbs and grasses, and measurements of canopy closure and forest floor characteristics, 10 m diameter (78.5 m^2) circular plots were established within the central 1400 m^2 zone of each plot; four such plots were established in the control and clear-cut plots, and two in each of the other two intermediate harvest-intensity plots.

Within these circular plots, a complete floristic (higher plants) inventory was made, and the total numbers of individuals (or clumps, for grasses) of each species were recorded. For trees and shrubs (including palms), height and stem diameters (DBH) for trees $\geq$2 m in height were also measured. Canopy closure was estimated as the mean percentage crown cover measured with a spherical crown densiometer at 1 m from ground level at four points located 3 m from plot centers (N, S, E, and W compass bearings). Litter and humus depths were measured at these same four points within each plot, with plot means for each horizon used for subsequent analyses.

The numbers of individuals per square meter and basal area (for trees $\geq$5 cm DBH) for all species in each treatment were calculated. Species richness for each floristic category in each plot was expressed simply as the number of species. Kulezinski's index of similarity (K), the number of species common to two sample plots divided by the total number of species occurring in both plots, was calculated for each floristic category (grasses, herbs, vines, tree seedlings, saplings, pole-size trees, and trees $\geq$15 cm DBH) for comparisons of species composition between undisturbed (control) and harvest treatment plots. Mean canopy closure, canopy height, tree stem diameter, basal area, litter and humus depth, plant density, species richness, and compositional similarity (K) were compared among treatments with unpaired two-group t-tests.

3. Results and discussion

3.1. Harvest impacts on forest structure

Tree harvests in the three stand manipulation treatments greatly reduced both stem basal area and

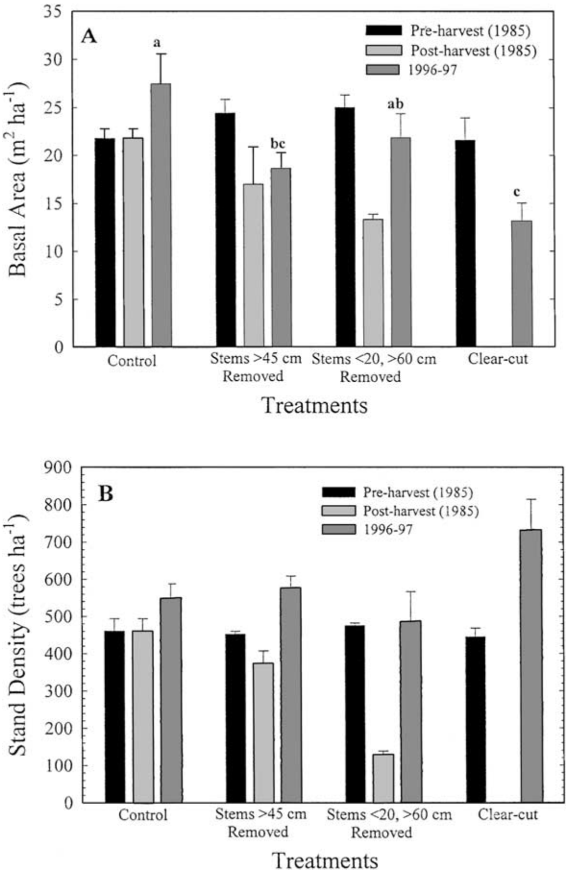

Fig. 1. Structural characteristics of experimental forest stands prior to, immediately following, and approximately 11.5 years after harvest treatments: (A) stand basal area ($m^2\,ha^{-1}$), trees ≥ 10 cm DBH; (B) stand density (stems ha^{-1}), trees ≥ 10 cm. Error bars indicate standard errors of means ($n = 4$). Different letters above 1996–1997 bars in A indicate that means were significantly different ($p < 0.05$; LSD, t-test).

stem density (Fig. 1). Prior to cutting basal areas and stem densities (for trees ≥ 10 cm DBH, including palms) in all treatments ranged from approximately 20–25 $m^2\,ha^{-1}$ (Fig. 1A) and 440–470 trees ha^{-1} (Fig. 1B) among sites, with no significant differences among treatments or sites for either parameter (ANOVA, $p < 0.05$). In the low-intensity harvest treatment, a total wood volume of $201 \pm 15\,m^3$ was removed, leaving 70% of the original basal area ($17.0 \pm 3.9\,m^2\,ha^{-1}$) and 83% of the original stem density (373 ± 34 trees ha^{-1}). In the moderate intensity harvest treatment, $219 \pm 26\,m^3$ was removed, leaving 53% of the original basal area ($13.3 \pm 0.6\,m^2\,ha^{-1}$) and 27% of the original stem density (128 ± 10 trees ha^{-1}). In the clear-cut plots, a total wood volume of $373 \pm 52\,m^3$ was removed, reducing both basal area and stem density to zero (Jesus et al., 1985).

Approximately 11 years after the harvest treatments were applied, stand basal areas for trees ≥ 10 cm DBH were approximately 50% lower ($13.2 \pm 1.9\,m^2\,ha^{-1}$) in the clear-cut treatment than in the control plots ($27.5 \pm 3.1\,m^2\,ha^{-1}$); basal areas in the moderate intensity and low-intensity treatments were 18.7 ± 1.6 and $21.9 \pm 2.5\,m^2\,ha^{-1}$, respectively (Fig. 1A). During this interval, total basal area in the control plots had risen by 26% (5.7 $m^2\,ha^{-1}$), with increases across all diameter classes (Fig. 2A). In the low-intensity harvest treatment (removal of stems ≥ 45 cm), stand basal area increased only by an average of 1.7 $m^2\,ha^{-1}$; this included significant increases in the smaller diameter classes (<35 cm), and reductions in the larger (≥ 55 cm) classes (Fig. 2B). This reduction resulted from post-harvest mortality of large residual trees in this treatment, probably due to physiological stress associated with the sudden exposure of the crowns and upper stems to full open sunlight, leading to necrosis of bark tissue (Knowles, personal observation), and/or increased susceptibility to pests and diseases (De Graaf et al., 1999). In the moderate-intensity harvest treatment (removal of stems ≤ 20 and ≥ 60 cm), there was an increase (8.6 $m^2\,ha^{-1}$) in total basal area, this increase occurring mainly in the 10–20 and 35–55 cm diameter classes (Fig. 2C). The clear-cut stands recovered about 60% ($13.2\,m^2\,ha^{-1}$) of their original basal area, predominantly in the smallest diameter (<20 cm) class (Fig. 2D).

Rates of basal area development during this period were generally related to harvest intensity, with annual increments averaging 0.15, 0.75, and 1.15 $m^2\,ha^{-1}$ in the low-, medium-, and high-intensity (i.e., clear-cut) treatments, respectively, as compared with 0.50 $m^2\,ha^{-1}$ in the control stands. While higher basal area increments in the medium-intensity harvest and clear-cut treatments were expected relative to the control as a result of competitive release, the very low basal area increment in the low-intensity harvest treatment was not expected. Despite rapid basal area development in the smaller tree classes (stems <35 cm DBH) in this treatment, post-harvest basal area reductions in the larger stem classes (trees >55 cm DBH that

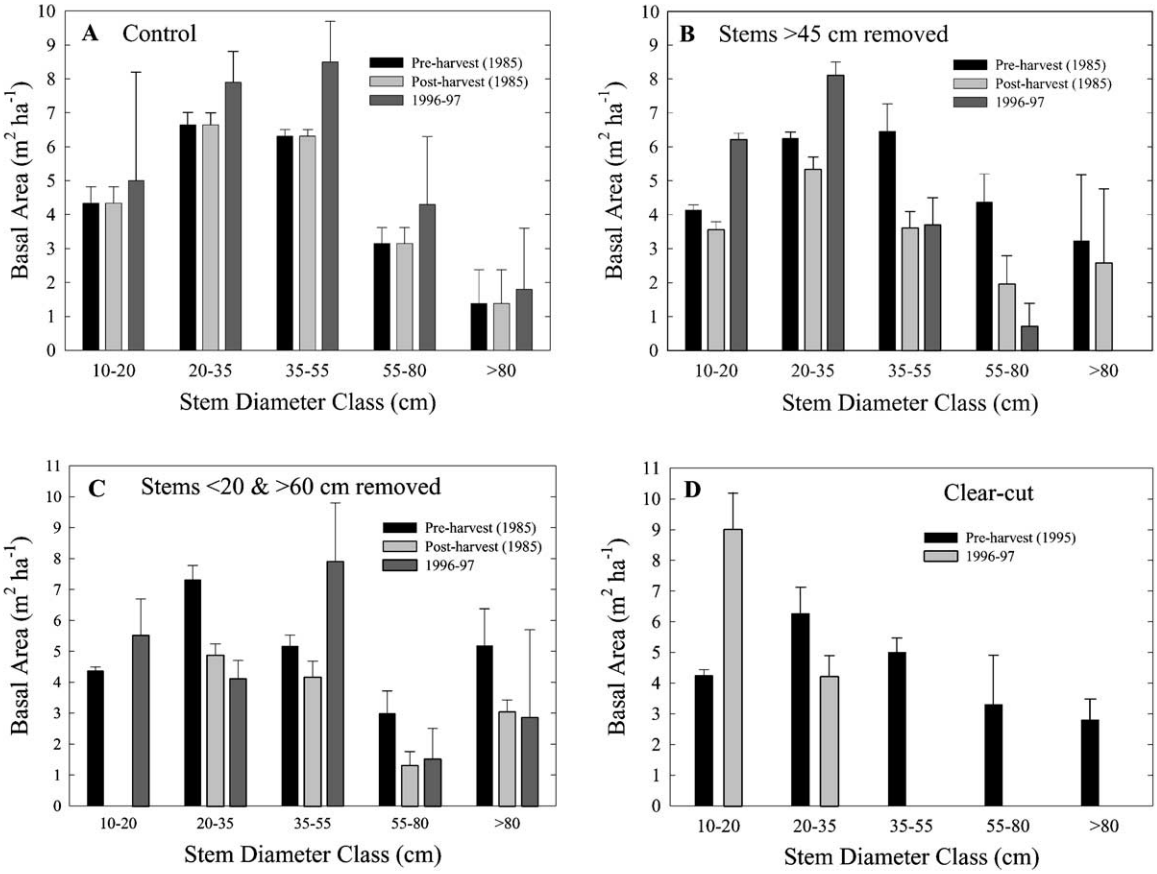

Fig. 2. Basal area distributions of experimental forest stands prior to, immediately following, and approximately 11.5 years after harvest treatments: (A) control (no harvest) treatment; (B) low-intensity harvest treatment; (C) moderate intensity harvest treatment; (D) clear-cut treatment.

had been retained on the site as seed-bearers), offset these gains.

Post-harvest changes in stand density (for trees $\geq$10 cm DBH) followed expected trends and were, as with basal area development, broadly related to harvest intensity (Fig. 1B). The largest post-treatment increases occurred in the clear-cut plots (731 trees ha^{-1}), followed by the moderate intensity harvest treatment (486 trees ha^{-1}), somewhat smaller increases in the low-intensity harvest treatment (205 trees ha^{-1}), and the smallest increase in the control plots (88 treesha^{-1}).

By 1996–1997, the density of trees $\geq$15 cm DBH was similar (296–339 trees ha^{-1}) in all but the moderate intensity harvest treatment (163 trees ha^{-1}), in which trees of this size were significantly less abundant ($p > 0.05$; LSD, t-test; Table 1). Relative to the control plots, ingrowth into the pole-size tree class (5–14.9 cm DBH) was greater, though not significantly so, in all harvest treatments (1720–1975 stems ha^{-1}) than in the control (1115 stems ha^{-1}). Saplings (trees $\geq$2 m tall, <5 cm DBH) were significantly more abundant in all harvest treatments (0.58–1.08 stems m^{-2}) than in the control (0.31 stems m^{-2}), particularly in the moderate intensity harvest treatment ($p > 0.05$; LSD, t-test). Tree seedlings (<2 m tall), while abundant in the harvest treatments (2.8–3.4 m^{-2}), were significantly less than in the control (5.8 m^{-2}), possibly due to the higher density of trees in the 5–15 cm DBH class within the harvest treatment plots and their shading effects on understory seedlings. Also, compared to the harvested plots, the structural integrity of the canopy at all levels in the

Table 1
Structural characteristics of old-growth forest plots near Porto Trombetas, Pará, Brazil, approximately 11 years after biomass harvests (all values are means of four replicates per treatment)[a]

Parameter	Control	Stems >45 cm removed	Stems <20, >60 cm removed	Clear-cut	ANOVA
Crown cover (%)	78.6	77.4	78.1	74.6	NS[b]
Litter depth (cm)	3.9	4.3	3.9	4.5	NS
Humus depth (cm)	3.3	3.2	3.1	3.3	NS
Mean height, trees ≥15 cm DBH (m)	25.5 ab	22.7 bc	27.8 a	20.9 c	*
Mean DBH, trees ≥15 cm DBH (cm)	26.6 b	23.4 bc	33.1 a	19.1 c	***
Basal area (m^2 ha^{-1})					
Stems ≥15 cm DBH	25.1 a	16.2 b	17.3 b	8.7 c	***
Stems 5–15 cm DBH	5.5	7.7	8.9	9.9	NS
All stems ≥5 cm DBH	30.7 a	24.0 bc	26.1 ab	18.6 c	*
Density (No. ha^{-1})					
Trees ≥15 cm DBH	323 a	339 a	164 b	296 a	**
Trees 5–15 cm DBH	1115	1720	1863	1975	NS
Trees <5 cm DBH, ≥2 m tall	3130 c	5772 b	10844 a	5970 b	***
Trees <2 m tall	58206 a	33576 b	34045 b	28155 b	*
Vines	17468	8758	11147	9268	NS
Herbs	1210	1131	1401	1417	NS
Grasses	334	223	270	6362	NS

[a] Similar letters within a row indicate that means were similar ($p < 0.05$; LSD, t-test); $n = 4$ for all means.
[b] Treatment effect not significant.
* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

control plots remained intact, and probably provided greater niche space for a larger number and greater variety of seed-dispersing birds, bats and arboreal mammals.

Vegetative regeneration (i.e., resprouting from cut stumps and root suckers), while important, contributed somewhat less than regeneration from seed to both stand density and basal area in the clear-cut treatment plots. In these stands, 78 of the 136 tree species present were found to regenerate by resprouting, of which 28 species had regenerated exclusively by this means. Recent studies in Brazil (Martini et al., 1994), Venezuela (Kammesheidt, 1999), and Mexico (Negreros-Castillo and Hall, 2000) also reported high rates of resprouting for a large proportion of tree species following logging in moist tropical forests. In our study, vegetative reproduction accounted for approximately 47% of all stems >2 m tall, and an average of 19% of the total stand basal area in the clear-cut treatment. Assuming that these results from the clear-cut treatment are indicative of regeneration patterns in the remaining harvest treatments, it appears that post-harvest regeneration from seed—arising from either the soil seed bank or seed inputs from the surrounding forests—is of greater importance than vegetative regrowth to floristic diversity and basal area development.

No significant differences among treatments were noted for other stand structural characteristics, including percentage crown cover (averaging 79% in the untreated control plots and 75–78% in the three harvest treatments), litter depth (3.9–4.5 cm among all treatments), or humus depth (3.1–3.3 among treatments; Table 1). Similarly, the densities of vines and herbs were not significantly affected by treatment, with mean values among treatments ranging from 0.88 to 1.75 m^{-2} (for vines) and 0.11–0.14 m^{-2} (for herbs). Grasses were, on average, 20–30 times more abundant in the clear-cut plots (0.64 clumps m^{-2} vs. 0.022–0.033 m^{-2} in the other treatments), although treatment differences were not significant due to very high spatial variability.

Despite the comparatively high rates of basal area reduction in our experimental treatments, our results on stand structural changes following tree harvests are broadly similar to those reported in studies of (less intensive) selective harvest impacts in the region. At an upland forest site in the nearby Tapajós National Forest, Silva et al. (1995) reported modest increases in tree density, an increased dominance of light demanding over shade-tolerant tree species, and an annual basal area increment (for all stems >5 cm DBH) of approximately 0.5 m^2 ha^{-1}, and recovery of 76% of the initial stand basal area, between 2 and 13 years after removal of 75 m^3 ha^{-1} of commercial species >45 cm DBH (or 38–50% of total stand volume).

3.2. Harvest impacts on floristic diversity and canopy dominance

Harvest treatments appeared to have little impact on species richness for ground flora (herbs, grasses, and tree seedlings <2 m tall) and vines after 11 years (Table 2). The mean numbers of species per 78.5 m^2 circular plot among treatments ranged from 0.50 to 0.75 for grasses, 2.0 to 3.0 for herbs, 12.2 to 12.9 for vines, and 52.6 to 60.1 for seedlings <2 m tall, with no significant treatment differences ($p < 0.05$; ANOVA).

Overall tree species richness (all size classes) was not significantly different among treatments (range of means: 64–72 species/78.5 m^2 plot). However, treatment effects on species richness were apparent within the sapling, pole-size, and larger tree size classes. Mean species richness for saplings and pole-size trees (stems up to 15 cm DBH) was significantly greater in the three harvest treatments than in the control plots ($p < 0.05$; LSD, *t*-test; Table 2). Differences in tree species richness in these smaller tree size classes paralleled differences in stem densities among

Table 2
Floristic composition indices of old-growth forest plots near Porto Trombetas, Pará, Brazil, approximately 11 years after biomass harvests (all values are means of four replicates per treatment)[a]

Parameter	Control	Stems >45 cm removed	Stems <20, >60 cm removed	Clear-cut	ANOVA
Species richness/plot[b]					
Trees ≥15 cm DBH	19.8 b	20.0 b	12.5 ab	7.0 a	**
Trees 5–15 cm DBH	9.3 a	17.5 b	15.8 b	15.5 b	*
Trees <5 cm DBH, ≥2 m tall	16.1 a	25.1 bc	29.5 c	21.7 b	***
Trees <2 m tall	60.1	56.8	58.4	52.6	NS[c]
Vines	12.9	12.6	12.3	12.2	NS
Herbs	3.0	2.0	2.3	2.9	NS
Grasses	0.63	0.50	0.63	0.75	NS
Compositional similarity (*K*)					
Trees ≥15 cm DBH		0.11	0.11	0.04	NS
Trees 5–15 cm DBH		0.17	0.13	0.14	NS
Trees <5 cm DBH, ≥2 m tall		0.24 b	0.19 a	0.24 b	*
Trees <2 m tall		0.48	0.46	0.53	NS
Vines		0.52	0.48	0.48	NS
Herbs		0.44	0.52	0.43	NS
Grasses		0	0	0.08	NS
Species/stems ratio					
Trees ≥15 cm DBH	0.63 ab	0.67 a	0.45 bc	0.41 c	*
Trees 5–15 cm DBH	0.60 a	0.66 a	0.54 a	0.39 b	**

[a] Similar letters within a row indicate that means were similar ($p < 0.05$; LSD, *t*-test); $n = 4$ for all means.

[b] Plot area: 78.5 m^2 for vines, herbs, grasses, seedlings <2 m tall and saplings ≥2 m, <5 cm DBH; 157 m^2 for trees 5–14 cm DBH; 1400 m^2 for trees ≥15 cm DBH.

[c] Treatment effect not significant.

* $p < 0.05$.

** $p < 0.01$.

*** $p < 0.001$.

treatments, as discussed earlier. For larger trees ($\geq$15 cm DBH), mean species richness was significantly greater ($p < 0.05$; LSD, t-test) in the control and low-intensity harvest treatments (19.8–20.0 species/ 1400 m^2 plot) than in the clear-cut treatment (7.0 species/plot), with intermediate species richness in the moderate intensity harvest treatment (12.3 species/ plot).

While these comparisons are useful for examining patterns of tree species diversity at a very small spatial scale, it is perhaps more instructive to compare treatment effects on a somewhat larger scale by combining our data from all sample plots in each treatment. These aggregated data are presented in the species–area relationships for each of the four tree size classes in Fig. 3. For seedlings (Fig. 3A), the species–area relationships are virtually identical for all except the moderate intensity harvest treatment, in which there are approximately 10–15% fewer species present than in the control or other harvest treatments within a total sampling area of 628 m^2. Although differences in total sampling area among treatments for the sapling (Fig. 3B) and pole-size (Fig. 3C) tree classes makes similar comparisons more difficult, there is a trend towards lower species richness in the control treatment than in the harvest treatments that reinforces the smaller-scale, plot-based findings presented above. In the case of larger trees ($\geq$15 cm DBH; Fig. 3D), species richness in the control and low-intensity harvest treatments are quite similar (80–84 species per 0.56 ha total sampling area) and consistently greater than in the moderate intensity (50 species) or

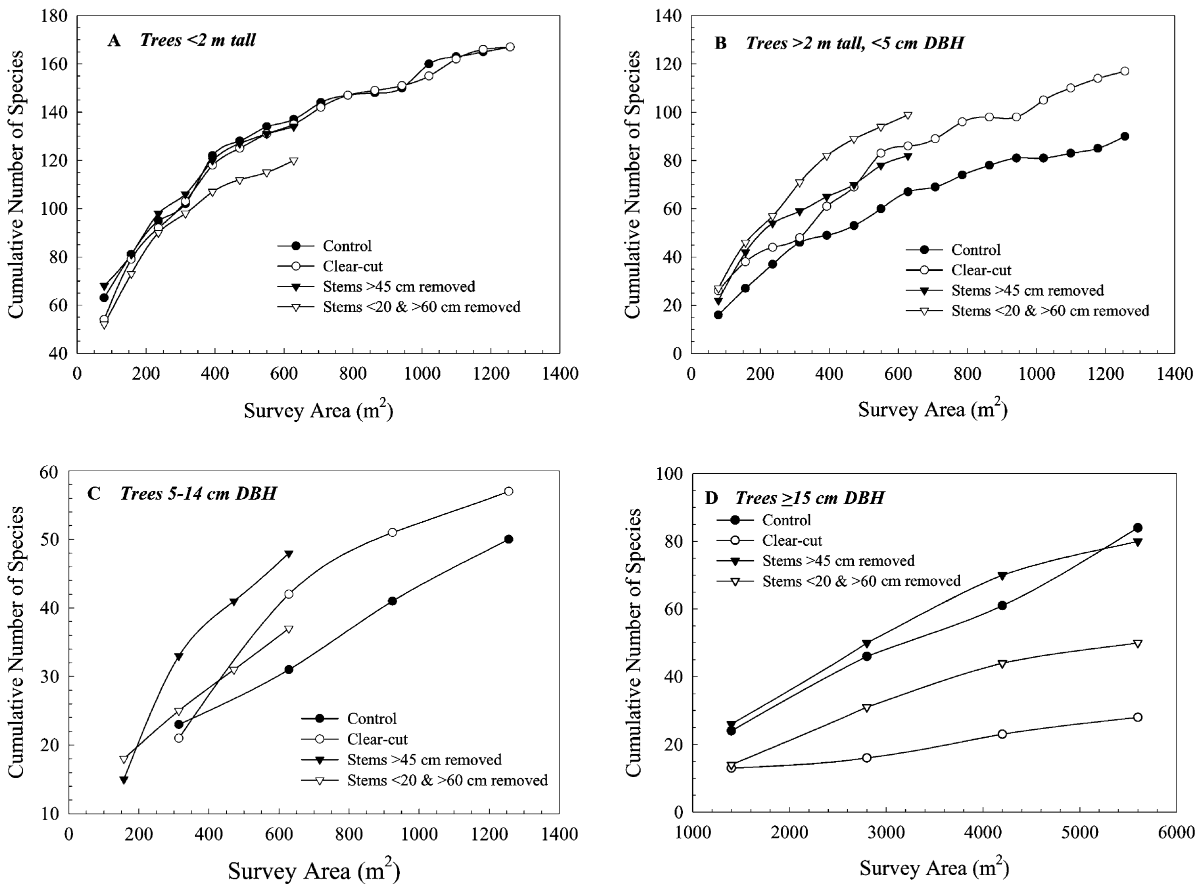

Fig. 3. Species–area relationships for tree species in undisturbed (control) and harvest treatment plots: (A) seedlings: individuals <2 m tall; (B) saplings: stems $\geq$2 m tall and <5 cm DBH; (C) pole-size stems: 5–14 cm DBH; (D) larger stems: $\geq$15 cm DBH.

Table 3
Number of tree species by family and size class in undisturbed lowland forest (control) harvest treatment plots 11 years after plot establishment and biomass removal (treatments: CT, control; CC, clear-cut; $R > 45$, stems >45 cm DBH removed; RSL, stems <20 and >60 cm DBH removed)

Family	Seedlings (<2 m tall)[a]				Saplings (<5 cm DBH)[a]				Pole-size stems[a]				Stems >15 cm DBH[b]			
	CT	$R > 45$	RSL	CC	CT	$R > 45$	RSL	CC	CT	$R > 45$	RSL	CC	CT	$R > 45$	RSL	CC
Anacardiaceae	3	3	3	5	3	2	3	5	0	1	0	1	2	2	1	1
Annonaceae	6	7	6	7	6	5	4	4	2	3	1	4	2	3	1	1
Apocynaceae	5	3	3	5	3	1	3	4	0	0	0	1	2	2	0	0
Arecaceae	11	12	10	11	4	3	1	2	5	4	6	7	1	1	1	1
Bignoniaceae	1	0	0	0	0	1	0	0	0	0	1	0	0	1	1	1
Boraginaceae	1	1	1	1	1	1	0	1	1	0	0	0	1	0	0	0
Burseraceae	5	5	5	6	4	4	6	5	4	4	4	4	4	4	1	0
Caryocaraceae	0	0	0	1	0	1	0	1	0	0	0	2	0	0	0	0
Celastraceae	1	1	0	2	0	1	1	1	0	1	1	1	1	0	0	0
Chrysobalanaceae	6	7	7	7	6	6	4	6	3	1	0	1	1	5	4	0
Combretaceae	2	1	1	2	1	0	1	1	0	0	0	0	1	1	1	0
Connaraceae	2	1	1	2	0	0	1	1	0	0	0	0	0	0	0	0
Ebenaceae	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Elaeocarpaceae	1	1	1	1	1	0	1	1	1	1	0	1	0	0	0	0
Euphorbiaceae	1	1	1	4	0	0	0	1	0	0	0	1	0	1	0	1
Flacourtiaceae	2	1	1	4	2	2	1	3	0	1	1	1	0	0	1	0
Guttiferae	4	3	2	5	3	2	2	3	1	3	3	2	0	2	2	2
Humiriaceae	3	3	3	3	1	2	2	2	1	0	0	0	3	3	2	0
Lauraceae	14	10	10	12	7	6	9	9	5	3	2	2	6	5	1	2
Lecythidaceae	2	2	1	4	1	3	2	3	1	0	0	0	3	4	3	0
Leguminosae–Caesalpinioideae	6	7	4	6	3	1	1	4	1	1	1	1	3	2	2	1
Leguminosae–Mimosoideae	15	9	9	13	3	6	10	7	4	5	7	8	6	4	5	7
Leguminosae–Papilionoideae	10	4	6	11	3	2	4	3	1	1	0	1	3	4	4	0
Malpighiaceae	0	1	0	0	1	1	1	0	0	0	1	0	0	0	1	1
Melastomataceae	5	4	3	4	3	3	5	1	0	2	2	3	1	1	1	1
Meliaceae	3	3	3	3	2	3	4	3	2	2	1	1	1	3	0	0
Monimiaceae	1	1	0	1	1	1	1	1	0	1	0	0	0	0	0	0
Moraceae	10	7	8	8	5	5	3	7	1	2	2	2	7	6	5	4
Myristicaceae	3	3	3	3	3	2	2	2	1	0	2	2	3	3	0	0
Myrtaceae	2	2	3	3	2	1	3	3	1	1	0	0	2	1	2	0
Nyctaginaceae	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Olacaceae	3	2	2	1	0	0	2	2	0	0	0	0	0	0	0	0
Rubiaceae	3	2	2	2	1	2	2	3	1	0	0	1	1	1	0	0
Rutaceae	1	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1
Sapindaceae	1	1	1	1	1	1	1	2	1	0	0	0	0	0	0	0
Sapotaceae	17	12	11	15	12	11	11	13	9	9	0	6	14	11	8	0
Simarubiaceae	1	1	0	1	1	0	0	0	0	0	0	1	0	1	0	1
Solanaceae	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sterculiaceae	1	1	1	1	1	1	1	1	2	2	0	1	0	1	0	1
Tiliaceae	1	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0
Verbenaceae	0	1	0	1	0	0	0	1	0	1	0	0	1	0	0	0
Violaceae	2	2	3	2	2	2	2	2	2	1	1	1	1	0	0	0
Vochysiaceae	2	1	2	2	0	0	2	1	0	0	0	0	3	1	1	0
Unidentified families	8	6	5	9	5	2	3	6	2	1	0	1	0	0	1	0
Total number of species	165	134	123	170	92	84	100	116	52	51	36	58	73	75	49	26

[a] Data for four replicate plots of each treatment combined; total sampling area: 1256 m^2 for control (CT) and clear-cut (CC) treatments, 628 m^2 for remaining treatments ($R > 45$, RSL).

[b] Data for four replicate plots of each treatment combined; total sampling area: 0.56 ha for all treatments.

clear-cut (28 species) treatments. These results mirror those obtained at the individual plot level.

Despite the broad similarities in species richness among treatments, compositional similarities between the harvest treatment and control plots were generally low (Table 2). The percentage of species common to the treatment and control plots at each site (Kulezinski index values: *K*) ranged from 43 to 53% for herbs, vines and tree seedlings, 19 to 24% for saplings, 13 to 17% for pole-size trees, and only 4 to 11% for larger trees.

Table 4
Tree species comprising 50% of total stand basal area in experimental plots 11 years after application of harvest treatments, trees ≥15 cm DBH

Treatment	Dominant tree species	Family	Common name	Basal area (m^2 ha^{-1})
Control	*Vatairea sericea*	Fabaceae (Caesalpinioideae)	Fava amargosa	1.86
	Lucuma dissepala	Sapotaceae	Abiurana barriguda	1.61
	Chrysophyllum prieurii	Sapotaceae	Abiurana vermelha	1.36
	Micropholis guianensis	Sapotaceae	Abiurana rosadinha	1.20
	Unidentified	Sapotaceae	Abiurana ajará	1.15
	Eschweilera sp.	Lecythidaceae	Matamatá branca	0.98
	Endopleura uchi	Humiriaceae	Uchí pucú	0.86
	Swartzia sp.	Fabaceae (Papilionoideae)	Gombeira amarela	0.78
	Parahancornia amapa	Apocynaceae	Amapá amargosa	0.69
	Oenocarpus bacaba	Arecaceae	Bacaba palm	0.61
	Brosimum rubescens	Moraceae	Muirapiranga	0.61
	Virola multicostata	Myristicaceae	Ucuuba preta	0.59
	Guarea sp.	Meliaceae	Jatoá vermelha	0.56
	61 Other species			11.96
Trees >45 cm DBH removed	*Lucuma dissepala*	Sapotaceae	Abiurana barriguda	2.03
	Micropholis guianensis	Sapotaceae	Abiurana rosadinha	0.91
	Unidentified	Sapotaceae	Abiurana ajará	0.73
	Mezilaurus sp.	Lauraceae	Itaúba	0.72
	Oenocarpus bacaba	Arecaceae	Bacaba palm	0.67
	Geissospermum sericeum	Apocynaceae	Quinarana	0.60
	Chrysophyllum prieurii	Sapotaceae	Abiurana vermelha	0.39
	Tetragastris panamensis	Burseraceae	Breu preto	0.38
	Mouriri plasschaerti	Melastomataceae	Muirauba	0.34
	Ormosia discolor	Fabaceae (Papilionoideae)	Tento	0.33
	Noyera mollis	Moraceae	Muiratinga preta	0.33
	Licania sp.	Chrysobalanaceae	Caraipê açu	0.33
	Tapirira guianensis	Anacardiaceae	Tatapiririca	0.32
	62 Other species			7.84
Trees <20 and >60 cm DBH removed	*Dinizia excelsa*	Fabaceae (Mimosoideae)	Angelim pedra	2.84
	Micropholis guianensis	Sapotaceae	Abiurana rosadinha	1.92
	Lucuma dissepala	Sapotaceae	Abiurana barriguda	1.21
	Inga sp.	Fabaceae (Mimosoideae)	Ingá vermelha	1.08
	Radlkofarella macrocarpa	Sapotaceae	Abiurana cutite	0.56
	Manilkara amazonica	Sapotaceae	Maparajuba	0.52
	Pithecellobium racemosum	Fabaceae (Mimosoideae)	Angelim rajado	0.49
	40 other species			8.63
Clear-cut	*Inga alba*	Fabaceae (Mimosoideae)	Ingá branca	1.81
	Cecropia sp.	Moraceae	Imbauba branca	1.39
	Cecropia sp.	Moraceae	Imbauba vermelha	0.79
	Vismia sp.	Clusiaceae	Lacre vermelho	0.62
	22 Other species			3.93

Given the high floristic diversity of these forests and the typically dispersed distribution patterns of individuals of most tree species, the floristic dissimilarities between treatment and control plots is not surprising given the fairly small sampling areas involved for these comparisons.

However, when we consider the family-wise distribution of tree species in the different size classes (Table 3), we see very similar numbers of species in most of the dominant families among treatments, at least in the smaller tree size classes (<15 cm DBH). For seedlings, saplings and pole-size stems, the dominant tree families such as Fabaceae, Lauraceae, Sapotaceae, Arecaceae and Moraceae are well represented in all treatments, and the total number of families represented in each of the harvest treatments are very similar when compared to the control treatment. For larger trees ($\geq$15 cm DBH), the number of families (and species) present in the clear-cut and moderate intensity harvest treatments was lower than in either the control or low-intensity harvest treatments. These results echo those of Cannon et al. (1998), who reported significant structural changes but no reduction in total tree species diversity 8 years after removal of 43% of the total stand basal area in selectively logged lowland dipterocarp forests in Borneo.

Eleven years after forest harvest treatments were applied, the relative dominance of tree species (stems $\geq$15 cm DBH) comprising the intermediate and upper canopy strata was distinctly dissimilar among treatments (Table 4). In both the control and low-intensity harvest treatment plots, 13 mostly long-lived tree species comprised 50% of the total basal area, with an additional 61–62 species comprising the remaining basal area. In both the cases, the dominant species include several representatives of the families that are characteristic of old-growth forests in this region—Sapotaceae, Fabaceae, Apocynaceae, Moraceae, and Arecaceae. In contrast, the moderate- and high-intensity (clear-cut) treatment plots were dominated by a smaller number of species, and while both treatments included individuals of the ‘‘typical’’ mature forest species found in the control plots, the overall numbers of species $\geq$15 cm DBH were markedly lower than in the control or low-intensity harvest treatments. In the moderate intensity harvest treatment, seven of the 48 species present—all species of either Fabaceae or Sapotaceae—comprised 50% of the basal area. In the clear-cut treatment, the four dominant species were all early successional—*Inga alba*, two *Cecropia* species and one species of *Vismia*; another 22 species comprised the remaining 50% of the basal area in these plots.

The predominance of short-lived successional tree species in the higher intensity harvest treatments strongly suggests that the fairly high rates of stand basal area recovery reported earlier are not likely to continue indefinitely as these trees senesce, die, and are replaced in the canopy by slower-growing, shade-tolerant, species. Therefore, our results must be treated with caution when attempting to project future patterns of stand dominance and, particularly, growth rates. This is particularly true for the subset of species in these forests considered to be of commercial value under current market conditions; studies by Silva et al. (1995) in Brazil and Kammesheidt (1998) in Venezuela have shown that these species, as a group, respond less favorably than the less valuable, faster-growing species to logging interventions. As a result, the recovery of ‘‘commercial’’ basal area in these forests is expected to occur a great many years after total basal area has reached, or surpassed, pre-logging levels. These authors, among others, suggest that a 30-year harvest cycle is probably too far short for sustained production of commercial timber species in moist neotropical forests.

4. Conclusion

The results of this study show that tree removal and associated disturbances in all of the harvest treatments does not precluded in any significant way the regrowth of these forests. With the exception of the low-intensity harvest treatment, in which stands recovered only about 25% of the basal area removed (vs. 60–75% in the more intensive harvest treatments), the rates of basal area recovery during the 11–12 years after harvest were fairly rapid and occurred mainly in the smaller stem diameter classes. Post-harvest mortality of large trees (>55 cm DBH) was an important factor contributing to the relatively slow rate of stand basal area development in the low-intensity harvest treatment. Although there was a marked decrease in seedling densities associated with increased densities of saplings and pole-sized trees in the harvest treatments relative to the undisturbed control, tree species diversity was not affected at the plot level except for larger stem classes ($\geq$15 cm DBH) and actually increased significantly in the sapling and pole-size classes. While the plot sizes used in this study were inadequate for detailed treatment comparisons of species composition for the larger, dominant trees in this forest, our data do strongly suggest that species richness (for ground flora and vines, as well as tree flora) was not negatively affected by harvest interventions applied 11–12 years earlier. While plots subjected to biomass harvests, particularly in the clear-cut treatment, tended to have upper canopy strata dominated by a fewer number of early- and mid-successional tree species, the abundant and species-rich regeneration of seedlings, saplings and pole-sized trees in all the harvest treatment plots strongly suggests that these stands will recover both their original structure and full complement of tree species in all strata.

For the purposes of biomass (as opposed to timber) production, which this experiment was established to evaluate, our data suggest that a system of clear-cutting (the harvest treatment yielding the most rapid recovery of stand basal area, though markedly less rapid than in intensively managed tropical plantations) might be preferable to harvest strategies that remove only a portion of the trees in a natural forest stand. However, since these clear-cut stands are, at this early stage of development, dominated by short-lived species, we consider it unlikely that the high rates of basal area development will continue indefinitely and that they could decline significantly before pre-harvest stand basal area (and biomass) levels are attained. Furthermore, while an estimated 60% of the original stand basal area was recovered within 12 years of the initial harvest without an apparent loss in floristic diversity, we caution that our results do not shed any light on the question of how subsequent repeated harvests would affect biomass productivity, stand structural development or biodiversity. Although our data provide a fairly detailed picture of stand structure and composition a decade after harvest interventions, we consider these forests to be in a very dynamic developmental phase that precludes extrapolation of our results to predict the age at which these stands will attain their original tree biomass. Continued monitoring of these and other previously studied logged stands in the region is required over a longer period before reasonably reliable predictions of long-term stand (and individual species) growth can be made to guide sustainable management practices (Alder and Silva, 2000).

Given the very important role of the adjacent old-growth forests in post-harvest regeneration processes, particularly as high-diversity reservoirs of seeds and habitat for their dispersal agents (predominantly birds and mammals in this region), our findings suggest that the long-term productivity and floristic diversity of these forests would in all likelihood be jeopardized if they were managed for biomass energy production on an extensive scale. Alternative management approaches involving selective harvests in small (<10 ha) blocks, or narrow (<100 m wide) strip clear-cuts covering larger areas but located within a much larger natural forest matrix, would appear far more conducive to the maintenance of long-term structural integrity and local biodiversity in these forests (Hartshorn, 1989; Ocana-Vidal, 1992; Fredericksen, 1998).

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References

Alder, D., Silva, J.N.M., 2000. An empirical cohort model for management of *terra firme* forests in the Brazilian Amazon. For. Ecol. Manage. 130, 141–157.

Attiwill, P.M., 1994. The disturbance of forest ecosystems: the ecological basis for conservation management. For. Ecol. Manage. 63, 247–300.

Brown, S., Lugo, A.E., 1990. Tropical secondary forests. J. Trop. Ecol. 6, 1–32.

Cannon, C.H., Peart, D.R., Leighton, M., 1998. Tree species diversity in commercial logged Bornean rainforest. Science 281, 1366–1368.

Dawkins, H.C., Philips, M.S., 1998. Tropical Moist Forest Silviculture and Management: A History of Success and Failure. CAB International, Wallingford, UK.

De Graaf, N.R., Poels, R.L.H., van Rompaey, R.S.A.R., 1999. Effect of silvicultural treatment on growth and mortality of rainforest in Surinam over long periods. For. Ecol. Manage. 124, 123–135.

Finegan, B., Camacho, M., 1999. Stand dynamics in a logged and silviculturally treated Costa Rican rain forest. For. Ecol. Manage. 121, 177–189.

Finegan, B., Camacho, M., Zamora, N., 1999. Diameter increment patterns among 106 tree species in a logged and silviculturally treated Costa Rican rain forest. For. Ecol. Manage. 121, 159–176.

Fredericksen, T.S., 1998. Limitations of low-intensity selection and selective logging for sustainable tropical forestry. Commonw. For. Rev. 77, 262–266.

Gorchov, D.L., Cornejo, F., Ascorra, C., Jaramillo, M., 1993. The role of seed dispersal in the natural reproduction of rain forest after strip-cutting in the Peruvian Amazon. Vegetatio 107–108, 339–349.

Hammond, D.S., van den Hout, P., Zagt, R., Marshall, G., Evans, J., Cassells, D., 2000. Benefits, bottlenecks and uncertainties in the pantropical implementation of reduced impact logging techniques. Int. For. Rev. 2, 45–53.

Hartshorn, G.S., 1989. Application of gap theory to tropical forest management: natural regeneration in strip clearcuts in the Peruvian Amazon. Ecology 70, 567–569.

Jesus, R.M., Menandro, M.S., Chichorro, J.F., 1985. Produção sustenada em floresta do medio Amazonas, Mineração Rio do Norte, Porto Trombetas, Pará. Tropical Forests Department, Florestas Rio Doce S.A., Linhares, Espírito Santo, Brazil, 129 pp., Unpublished report.

Kammesheidt, L., 1998. Stand structure and spatial patterns of commercial species in logged and unlogged Venezualan forest. For. Ecol. Manage. 109, 163–167.

Kammesheidt, L., 1999. Forest recovery by root suckers and above-ground sprouts after slash-and-burn agriculture, fire and logging in Paraguay and Venezuela. J. Trop. Ecol. 15, 143–157.

Knowles, O.H., Parrotta, J.A., 1995. Amazonian forest restoration: an innovative system for native species selection based on phenological data and performance indices. Commonw. For. Rev. 74, 230–243.

Knowles, O.H., Parrotta, J.A., 1997. Phenological observations and tree seed characteristics in an equatorial moist forest at Trombetas, Pará State, Brazil. In: Lieth, H., Schwartz, M.D. (Eds.), Phenology in Seasonal Climates I. Backhuys Publishers, Leiden, The Netherlands, pp. 67–84.

Liu, J., Ashton, P.S., Liu, J.G., 1999. Simulating effects of landscape context and timber harvest on tree species diversity. Ecol. Appl. 9, 186–201.

Lugo, A.E., 1995. Management of tropical biodiversity. Ecol. Appl. 5, 956–961.

Martini, A.M.Z., de Rosa, N.A., Uhl, C., 1994. An attempt to predict which Amazonian tree species may be threatened by logging activities. Environ. Conserv. 21, 152–162.

Martins, E.P., Oliveira, A.D., Scolforo, J.R.S., 1997. Avaliação dos danos causados pela exploração florestal a vegetação remanescente em florestas naturais. Cerne 3, 14–24.

Mineração Rio do Norte, 1988. Produção sustenada em floresta primitiva do medio Amazonas, Avaliação do remanescente e da regeneração natural. Planning and Research Department, Florestas Rio Doce S.A., Linhares, Epírito Santo, Brazil, 50 pp., Unpublished report.

Mostacedo, C.B., Fredericksen, T.S., 1999. Regeneration status of important tropical forest tree species in Bolivia: assessment and recommendations. For. Ecol. Manage. 124, 263–273.

Negreros-Castillo, P., Hall, R.B., 2000. Sprouting capability of 17 tropical tree species after overstory removal in Quintana Roo, Mexico. For. Ecol. Manage. 126, 399–403.

Ocana-Vidal, J., 1992. Natural forest management with strip clear-cutting. Unasylva 43, 24–27.

Pinard, M.A., Barker, M.G., Tay, J., 2000a. Soil disturbance and post-logging forest recovery on bulldozer paths in Sabah, Malaysia. For. Ecol. Manage. 130, 213–225.

Pinard, M.A., Putz, F.E., Tay, J., 2000b. Lessons learned from the implementation of reduced-impact logging in hilly terrain in Sabah, Malaysia. Int. For. Rev. 2, 33–39.

Silva, J.N.M., de Carvalho, J.O.P., Lopes, J.C.A., de Almeida, B.F., Costa, D.H.M., de Oliveira, L.C., Vanclay, J.K., Skovsgaard, J.P., 1995. Growth and yield of a tropical rain forest in the Brazilian Amazon 13 years after logging. For. Ecol. Manage. 71, 267–274.

Sist, P., 2000. Reduced-impact logging in the tropics: objectives, principles and impacts. Int. For. Rev. 2, 3–10.

Uhl, C., 1987. Factors controlling succession following slash-and-burn agriculture in Amazonia. J. Ecol. 75, 377–407.

Uhl, C., Verissimo, A., Mattos, M.M., Brandino, Z., Vieira, I.C.G., 1991. Social, economic, and ecological consequences of selective logging in an Amazon frontier: the case of Tailandia. For. Ecol. Manage. 46, 243–273.

Van Gardingen, P.R., Clearwater, M.J., Nifinluri, T., Rusmantoro, W., Noor, M., Mason, P.A., Ingleby, K., Munro, R.C., 1998. Impacts of logging on the regeneration of lowland dipterocarp forest in Indonesia. Commonw. For. Rev. 77, 71–82.