Plant Ecol (2009) 201:23–37
DOI 10.1007/s11258-008-9479-x

Tree species richness and composition 15 years after strip clear-cutting in the Peruvian Amazon

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Received: 17 November 2007 / Accepted: 21 July 2008 / Published online: 19 August 2008

Abstract Although strip clear-cutting has a long history of use in the temperate zone, it was only recently introduced for timber extraction in tropical rain forests, where it is known as the Palcazú Forest Management System. In this system heterogeneous tropical forests are managed for native gap-dependent timber species by simulating gap dynamics through clear-cutting long, narrow strips every 40 years. As part of an assessment of the sustainability of this system, we evaluated the recovery of tree basal area, species richness, and composition after 15 years of regeneration on two strips (30 × 150 m) clear-cut in 1989 in Jenaro Herrera, Peru. Timber stocking and the effects of silvicultural thinning were assessed in both strips. The strips recovered 58–73% of their original basal area and 45–68% of their original tree species richness. Although both strips recovered more than 50% of their original composition, commercial species had lower basal areas and lower densities than in the forest before the clearing. Pioneer species with high basal areas remained dominant 15 years after the cutting. Silvicultural thinning in 1996 reduced the abundance of pioneer species in both strips, and increased the abundance of commercial species in one of the strips. Half of one strip was harvested by deferment-cut (only commercial trees >30 cm dbh and “other” species >5 cm dbh were cut); regeneration here had greater abundance of commercial species and lower abundance of pioneer species. The low stocking of commercial trees challenges the sustainability claims for this forest management system.

Keywords Natural forest management · Palcazú forest management model · Rarefaction · Sustainable management · Tropical rain forest

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Introduction

Strip-clear cutting has extensively been used in the temperate zone for forest management (Thornton 1957; Smith 1986; Heitzman et al. 1999; Allison et al. 2003); Tosi (1982) and Hartshorn (1989a, 1995) introduced this system to manage tropical rainforests for timber extraction. The first implementation was in the Palcazú Valley in Peru, as part of a joint United States Agency for International Development (AID) and Peru Instituto Nacional de Desarrollo (INADE) development project (Tosi 1982; Hartshorn 1989a). As a result, Tosi’s (1982) and Hartshorn’s (1989a, 1995) strip clear-cutting system is also known as the Palcazú Forest Management System. In the Palcazú Forest Management System heterogeneous tropical forests are managed for native gap-dependent timber species by simulating gap dynamics through clear-cutting long, narrow strips (Hartshorn 1989a, 1995). In this system, upland forest is clear-cut into 30–40 m wide strips with a rotation of 30 to 40 years. The length of the strip varies and depends upon topography (Hartshorn 1989a).

In the Palcazú system, timber, regardless of species, is harvested and used locally (sawnwood, preserved roundwood, and charcoal) or sold to attain maximum value from the strips (Hartshorn 1989a; Gorchov et al. 1993). Animal traction is used to reduce soil compaction (Hartshorn 1989a; Gorchov et al. 1993). Natural regeneration of seeds and stump sprouts is permitted (Gorchov et al. 1993). Silvicultural treatments may also be applied in the regenerating strips to promote growth of desired species (Dolanc et al. 2003).

Initially, the Palcazú system was thought to be a sustainable alternative for timber extraction compared to uncontrolled logging or selective logging. Tosi (1982) and Hartshorn (1989a) predicted that non-commercial pioneer species would not regenerate well in this system because the strips were too narrow to allow sufficient sunlight, and commercial species would be well represented in the regeneration. Many tropical timber species are gap-dependent (Swaine and Whitmore 1988), and such gap-dependent species have rapid height and diameter growth (Lieberman et al. 1985).

Several studies, however, have questioned the sustainability of the Palcazú system (Simeone 1990; Cornejo and Gorchov 1993; Gram 1997; Southgate 1998). Rapid early regeneration with high tree species richness suggested that this system is ecologically sustainable (Hartshorn 1989a), but Gorchov et al. (1993) found that after one year of regeneration the composition of strips was mainly dominated by pioneer species of low commercial value. Thinning enhanced the growth rates of commercial stems 11 years after the cutting, but they still averaged <0.3 cm/year in diameter growth (Dolanc et al. 2003). Clearly, data are still needed for later stages of regeneration.

We studied tree regeneration after 15 years on two strips clear-cut in 1989 in the Peruvian Amazon in order to generate the first assessment of the ecological sustainability of the strip clear-cutting system. To assess the ecological sustainability of a forest management system one ought to assess the structural characteristics of a developing forest (basal area and biomass), community characteristics (species richness and composition), and functional characteristics (nutrient cycling and primary productivity). In this study, we focused on the recovery of tree basal area, species richness, and species composition 15 years after the cutting with values prior to the cutting. The criterion used to assess the ecological sustainability of this system was to evaluate whether these community descriptors had recovered to approximate pre-clearing levels. This criterion is based on the assumptions of sustainability for natural forest management; i.e., sustained timber yields can be produced while maintaining a high diversity (Bawa and Seidler 1998). A second objective was to determine stocking of commercial species in the strips 15 years after the cutting to assess timber regeneration in this system. A third objective was to determine if silvicultural thinning and harvesting by deferment-cut improved the recovery of structural and community descriptors in the strips.

Clear-cutting is the least severe anthropogenic disturbance when compared to cutting and burning for pasture or plantation establishment, and bulldozing for road building or development (Uhl et al. 1982). Thus, clear-cut stands tend to have a rapid increase in species richness a few years after logging (Hartshorn 1989a; Faber-Landgendoen 1992) and a faster richness recovery than stands cut and burned for pasture or bulldozed (Uhl et al. 1982). However, composition usually takes longer to recover (Finegan 1996; Guariguata and Ostetarg 2001). Thus, we expected greater recovery of basal area and species richness than of species composition. We also expected silvicultural thinning and deferment-cutting in the strips to improve the recovery of all of these structural and community descriptors.

Methods

Study site

This study took place at the Centro de Investigaciones Jenaro Herrera (CIJH S 4°53.95′ W 73°39.04′), 200 km south of Iquitos, Loreto, Peru. Mean annual temperature is 26.5°C and mean annual precipitation is 2521 mm (Spichiger et al. 1989). A relatively dry period occurs from June to August, but rainfall highly varies each month of the year (Ascorra et al. 1993; Rondon 2008). Soils are sandy-loam and the vegetation is considered lowland tropical rainforest on high terrace

(Spichiger et al. 1989). The families with highest densities on high terrace at CIJH are Sapotaceae, Leguminosae, Lecythidaceae, Chrysobalanaceae, Lauraceae, and Myristicaceae (Spichiger et al. 1996).

History of clear-cut strips in CIJH

Two 30 × 150 m strips (Fig. 1), 150 m apart, were clear-cut in 1989 in primary high terrace tropical rain forest at CIJH. The area had been selectively logged

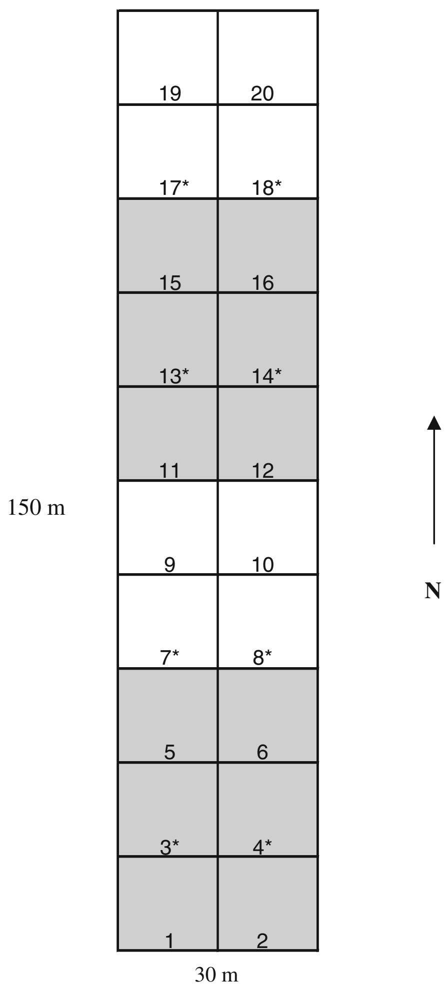

Fig. 1 Schematic of each of the two strips (30 × 150 m) at Centro de Investigaciones Jenaro Herrera, Peru. Twenty plots were marked in each strip (15 × 15 m). Plots thinned in 1996 are shaded. Plots with asterisk (*) were censused regularly for all saplings ≥2 m. Advanced regeneration and stump sprouts were censused throughout the strip. In strip 2, in the south half (plots 1 to 10), 56 commercial tree species (5–28 cm dbh) were left uncut as part of a deferment-cut treatment. Figure modified from Dolanc et al. (2003)

15–20 years prior, but the forest maintained an intact canopy. The long axis of each strip was oriented north–south. Strip 1 was cleared in April–May, 1989 and strip 2 in October–November, 1989. Lianas and shrubs were cut before tree felling. Most trees >5 cm in diameter at breast height (dbh) were felled in each strip using directional felling to ensure that the trees cut landed in the strips (Gorchov et al. 1993). A few large trees (>28 cm dbh, $N = 5$ in strip 1 and $N = 13$ in strip 2) leaning out of the strips were not cut to avoid damage to the surrounding forest (Cornejo and Gorchov 1993). An experimental deferment-cut treatment cut was implemented in the south half of strip 2 (plots 1–10). In the deferment-cut treatment, only commercial trees ≥30 cm dbh and "other" species >5 cm dbh were harvested in 1989; the smaller trees of commercial species were left uncut ($n = 56$, 5–28 cm dbh) to grow for the next harvest (Cornejo and Gorchov 1993). All timber harvested was locally used or carried off site. A complete survey of the trees (≥5 cm dbh) was made during the 1989 felling for both strips (Cornejo and Gorchov 1993).

Each strip was divided into 20 15 × 15 m plots (Fig. 1), in which all stump sprouts and survivors (saplings not cut <5 cm dbh in 1989) were identified and tagged. Recruits (trees >2-m tall) were identified and censused on 8 out of the 20 plots in each strip. Censuses took place once a year during 1990–1994, 1996, and 2000. In addition, an experimental silvicultural thinning treatment took place in March 1996; pioneer trees (all *Cecropia* and trees <10-m tall of the genus *Alchornea* and the family Melastomataceae) were girdled by machete in portions of each strip (Fig. 1). Censuses carried out May–June, 2004 in strip 1 and June–July, 2005 in strip 2 provide the 'post-clearing' data analyzed here.

Tree identification

Tree identification was done in the field using Gentry (1993) and Spichiger et al. (1989, 1990). Voucher specimens were deposited at the CIJH herbarium, AMAZ, and MU. Voucher specimens of difficult taxa were brought for comparison to Missouri Botanical Garden (MOBOT). Several taxa were not identified to the species level in the pre-clearing (1989) period; identification for these taxa was only done to genus or family level. For analysis purposes, trees identified to the same genus or family, without species determination, were considered as one morphospecies. Some *Cecropia* species were difficult to identify to the species level, and they were grouped as one morphospecies for all richness comparisons.

Data analysis

Comparisons of tree basal area (BA), species richness, composition, and timber stocking were evaluated in strip 1 in 1989 (prior to cutting) vs. 2004, 15 years after cutting, and in strip 2, in 1989 (prior to the cutting) vs. 2005, 15 ½ years after cutting. In strip 2, all comparisons of community descriptors between the pre- and post-clearing period were carried out separately for the clear-cut and deferment-cut portions. We are aware that forests are not stable and community descriptors vary over time. In this study, we used the pre-clearing level (1989) as a reference of mature growth. All tree species richness and composition comparisons were done for trees >7.5 cm dbh since both strips had complete datasets per plot for these trees. Additional comparisons of richness and composition of trees ≥5 cm dbh between the post- and pre-clearing censuses were carried out for strip 2 (Rondon 2008), but these did not differ qualitatively from trees >7.5 cm dbh.

The effect of thinning and deferment-cut on structural and community descriptors

Before comparing structural and community descriptors in the pre- versus the post-clearing period, we tested the effect of silvicultural thinning in the post-clearing period in order to determine whether it was appropriate to pool thinned and unthinned plots. In strip 1, we used SAS proc GLM with thinning as a fixed factor and plots as replicates. For strip 2, we used a two-way ANOVA with two fixed factors, thinning and felling treatment (clear-cut versus deferment-cut), and their interaction. All analysis were done using SAS version 9.1, with $\alpha = 0.05$; ANOVA tables are reported in Rondon (2008). Statistical findings should be interpreted with caution since the 15 × 15 m plots within each strip were not independent.

Structural and community descriptors

Basal area (BA, m^2/ha) was calculated for trees >10 cm dbh for each strip at pre-clearing, one year after the clearing (1990), and 15 years post-clearing. The effect of thinning and deferment-cut was tested on per plot BA (m^2/plot). Calculations of BA are in Rondon (2008).

To compare tree species richness between the pre- and post-clearing censuses at equal sample sizes, sample-based rarefaction curves were obtained from EstimateS 7.5 (Colwell 2005). The 15 × 15 m plots were used as subsamples in each strip. Separate rarefaction curves were constructed for the clear-cut and deferment-cut portions in strip 2. Before constructing the rarefactions for the two different censuses, the effect of thinning and deferment-cut on tree species density (no. of species/plot) was tested using the post-clearing censuses of the strips.

Tree composition comparisons were done at the genus level because species identification may not have been consistent between censuses. Since the classic Sorensen index is sensitive to sample size and assemblages with numerous rare species (Chao et al. 2005), the abundance-based Sorensen index (L) was used to assess compositional similarity between censuses in the strips. Using EstimateS 7.5 (Colwell 2005), we calculated L, $L = 2UV/(U+V)$, where U and V are the total relative abundances of the shared species in samples 1 and 2 (Chao et al. 2005).

After determining if thinning and deferment-cut had an effect on L calculated between pre- and post-clearing censuses for each 15 × 15 m plots in the strips, we pooled the data for each strip (keeping clear-cut and deferment-cut halves of strip 2 separate) to assess the compositional change of the strips between censuses. In strip 1, L was recalculated for the entire strip between pre- and post- censuses ($N = 1$). In strip 2, L was recalculated separately for the deferment-cut ($N = 1$) and clear-cut ($N = 1$) portions of the strip. These values were compared with L between two mature forest stands: strip 1 and strip 2, both before the clearing (1989).

To calculate the relative abundances and basal area of commercial and pioneer species, trees >7.5 cm dbh in the strips were classified as commercial, pioneer, and "other" species (Table 1). Commercial species were those in genera valued for sawnwood at international and local markets based on data from the International Tropical Timber Organization (ITTO) from 1997 to 2005 (ITTO 1997–2005) and studies in the Peruvian Amazon (Peters et al. 1989; Pinedo-Vasquez et al. 1990). The list did not include species valued for roundwood or non-timber forest products.

Table 1 Commercial and pioneer taxa occurring in censused plots at CIJH with sources for commercial taxa

Commercial	Source	Commercial	Source
Annonaceae		Meliaceae	
Duguetia	2	Guarea	2, 3
Guatteria	2	Trichilia	2
Xylopia	2	Moraceae	
Apocynaceae		Brosimum	1, 2
Aspidosperma	1, 2	Clarisia	3
Macoubea	2	Myristicaceae	
Boraginaceae		Iryanthera	1, 2, 3
Cordia	1	Osteophloeum	2
Bignoniaceae		Virola	1, 2, 3
Tabebuia	1	Olacaceae	
Caryocaraceae		Heisteria	2
Caryocar	2	Sapotaceae	
Clusiaceae		Chrysophyllum	2
Calophyllum	2	Manilkara	1, 2
Combretaceae		Pouteria	2
Terminalia	1, 2	Simaroubaceae	
Fabaceae		Simarouba	1, 3
Dialium	2	Vochysiaceae	
Diplotropis	1	Vochysia	1
Hymenaea	1, 2	Erisma	1
Ormosia	1	*Pioneer*	
Parkia	2	Cecropiaceae	
Swartzia	2	Cecropia	
Lauraceae		Euphorbiaceae	
Aniba	2, 3	Alchornea	
Endlicheria	2, 3	Melastomataceae	
Licaria	3	All genera	
Mezilaurus	2		
Nectandra	1, 3		
Ocotea	1, 2, 3		
Persea	3		
Lecythidaceae			
Cariniana	1, 2		
Eschweilera	2		

Source: (1) ITTO 1997–2005; (2) Peters et al. 1989; (3) Pinedo-Vasquez et al. 1990

Taxa not appearing in commercial or pioneers were considered "others". This table was modified from Dolanc et al. (2003)

We classified those taxa that made up the vast majority of pioneers in this system as "pioneer" species: the genera *Cecropia* (Cecropiaceae), *Alchornea* (Euphorbiaceae), and all genera in the Melastomataceae family (Dolanc et al. 2003). "Other" species were taxa that were not classified into one of the other two groups and taxa that were only identified to the family level ($N = 3$ morphospecies in strip 1 and $N = 8$ morphospecies in strip 2, both in 1989). "Other" species were a combination of fast growing species (e.g., *Inga*), successional species (e.g., *Protium*), and old growth species (e.g., *Mabea*). Since "other" species, grouped taxa of several life histories, this group was not statistically analyzed.

The relative abundance of commercial and pioneer species was calculated for each 15 × 15 m plot in both strips in the pre- and post-clearing censuses. The effect of thinning and deferment-cut was tested on the relative abundance of commercial species and pioneer species in the strips. Due to unequal variance of samples in testing the effect of thinning on commercial species in strip 1, additional analysis was done using Kruskal–Wallis test, a non-parametric test. This test did not differ qualitatively from the parametric analysis; thus, only the latter was reported here. For each strip, we used paired *t*-tests to determine whether the relative abundance of commercial and pioneer species for 15 × 15 m plots differed between censuses. We also calculated basal area of commercial, pioneer, and "other" species in both strips in the pre- and post-clearing censuses of each strip.

Stocking (no. of trees/ha) of commercial species was calculated for (1) small trees between 5 to 10 cm dbh, and (2) large trees >10 cm dbh, in the post- and pre-clearing censuses of each strip. We tested the effect of thinning and deferment-cut on the number of commercial stems per plot for each size class in the strips. To make timber stocking comparisons between censuses, for each size class the total number of stems/ha in the post-clearing period was calculated and compared to the pre-clearing period of each strip.

Results

After 15 years of regeneration, the advance regeneration (trees that survived the clearing in 1989) comprised 16 and 18% of the total tree regeneration (trees >5 cm dbh) of strips 1 and 2, respectively; stump sprouts comprised 3 to 6%, and recruits (apparently regenerating from seed) 81 to 76% (Table 2).

Table 2 Number of trees ≥5 cm dbh censused in both strips before the clearing (from Cornejo and Gorchov 1993) and after the clearing in 2004 for strip 1 and 2005 for strip 2 at CIJH, Peru

Categories	Strip 1	Strip 2
Pre-clearing (1989)		
No. of trees	662	619
No. of morphospecies	*248*	*228*
Post-clearing (2004–2005)		
Trees >5 cm dbh and not cut in 1989	3	52
Survivors (<5 cm dbh but >2 m tall in 1989)	131	108
Sprouts from stumps of trees ≥5 cm dbh in 1989	25	36
Recruits ≥5 cm dbh in 2004/2005	662	457
Total	821	653
No. of not identified taxa in the post-clearing	*1*	*2*
No. of species	*172*	*176*

Number of taxa is given in italics

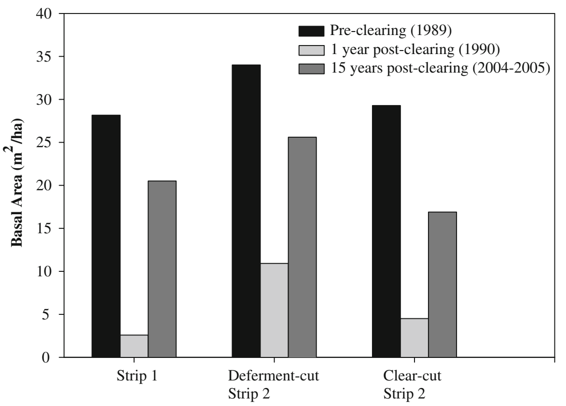

Fig. 2 Stand basal area (m^2/ha) of strip 1 and strip 2 before the clearing (1989), a year after the clearing (1990), and 15 years (2004) after the clearing (strip 1—2004, strip 2—2005)

Stand basal area

After 15 years of the first cutting, strip 1 and strip 2 recovered 73% (21 m^2/ha) and 58% (17 m^2/ha) of their original BA (Fig. 2), whereas the deferment-cut portion of strip 2 recovered 75% (26 m^2/ha) of its pre-clearing BA (Fig. 2). Silvicultural thinning did not affect 2004/2005 BA of trees >10 cm dbh in the strips (in strip 1, $F_{1,18} = 3.44$, $P = 0.080$, and in strip 2: $F_{1,16} = 0.55$, $P = 0.467$). In strip 2, neither felling (deferment-cut versus clear-cut, $F_{1,16} = 2.97$, $P = 0.104$) nor the interaction of thinning and felling ($F_{1,16} = 0.57$, $P = 0.461$) affected 2005 BA.

Tree species richness

Before clearing (1989), strip 1 had 422 trees >7.5 cm dbh, comprising 187 morphospecies (not all trees were identified to the species level in the pre-clearing censuses), whereas in 2004 there were 494 trees and 97 species. For strip 2, in 1989 there were 391 trees comprising 192 morphospecies compared to 410 trees and 109 species in 2005. Total number of trees and species ≥5 cm dbh found in 1989 and in the post-clearing censuses (2004/2005) of each strip are reported in Table 2.

In both strips silvicultural thinning did not affect the 2004/2005 tree species density (strip 1: $F_{1,18} = 1.85$, $P = 0.191$; strip 2: $F_{1,16} = 0.01$, $P = 0.926$); similarly, neither felling ($F_{1,16} = 0.32$, $P = 0.580$), nor the interaction of thinning and felling ($F_{1,16} = 0.08$, $P = 0.781$) affected the 2005 species density in strip 2. Fifteen years into the second rotation, strip 1 and the clear-cut portion of strip 2 recovered 47 and 45% of their pre-clearing richness, at equal sample sizes. The deferment-cut portions of strip 2 recovered 68% of its pre-clearing richness. Rarefaction curves for strip 1 and the clear-cut portion of strip 2 showed that species

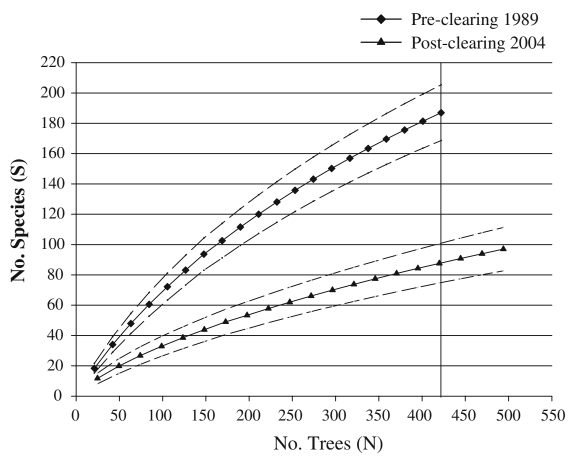

Fig. 3 Sample based rarefaction curves for 1989 ($N = 417$) and 2004 ($N = 494$) for trees >7.5 cm dbh in strip 1. Dotted lines are 95% CI. Number of samples was rescaled to number of individuals. Vertical line indicates species richness at equal sample sizes

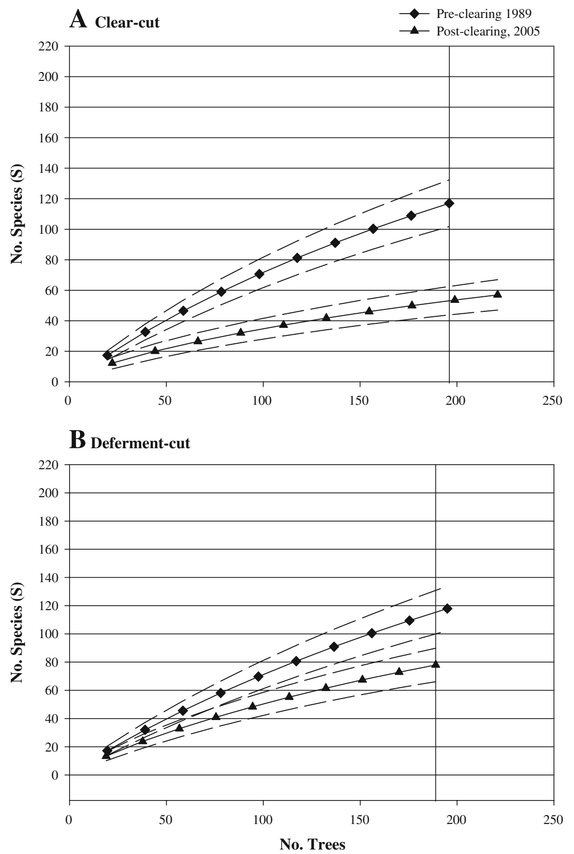

Fig. 4 Sample based rarefaction curves for the (**a**) clear-cut portion and (**b**) deferment-cut portion of strip 2 in 1989 and 2005 for trees >7.5 cm dbh. In the clear-cut portion, there were 196 trees in 1989 and 221 trees in 2005. In the deferment-cut portion, there were 195 trees in 1989 and 189 trees in 2005. Dotted lines are 95% CI. Number of samples was rescaled to number of individuals. Vertical line indicates species richness at equal sample sizes

richness was significantly lower in 2004/2005 than in 1989, as these curves diverged clearly and confidence intervals did not overlap (Figs. 3, 4a). In the deferment-cut portion of strip 2, rarefaction curves showed overlapping confidence intervals of species richness at smaller sample sizes ($N < 75$, Fig. 4b), but clearly diverged at greater sample sizes. Thus, species richness in the deferment-cut portion was also lower in 2005.

Tree composition

In 2004/2005, the strips had recovered more than 50% of the compositional similarity with the pre-clearing censuses. In strip 1, compositional similarity of 1989 vs. 2004 ($L = 0.828$) was slightly lower than compositional similarity of two mature stands ($L = 0.855$, Fig. 5). In strip 2, compositional similarity of 1989 vs. 2005 in the clear-cut ($L = 0.592$) and the deferment-cut portion ($L = 0.656$) was lower than the compositional similarity of two mature stands (Fig. 5). Thinning did not affect the compositional similarity of trees >7.5 cm dbh between 1989 and 2004 in strip 1 ($F_{1,18} = 3.78$, $P = 0.068$) or in strip 2 ($F_{1,16} = 0.39$, $P = 0.542$). In strip 2, neither felling treatment ($F_{1,16} = 1.03$, $P = 0.324$) nor the interaction of felling and thinning ($F_{1,16} = 0.72$, $P = 0.408$) significantly affected the compositional similarity between 1989 and 2005.

Commercial species

The relative abundance of commercial species was lower in 2004/2005 than in 1989 in strip 1 (thinned plots: $t = 6.44$, $P < 0.01$; unthinned plots: $t = 7.99$, $P < 0.01$), the clear-cut portions of strip 2 ($t = 5.83$, $P < 0.001$), and deferment-cut portions of strip 2 ($t = 3.56$, $P < 0.01$) (Fig. 6a). Strip 1 and the clear-cut portion of strip 2 recovered 25 and 43%, respectively, of the relative abundance of commercial species in the pre-clearing censuses, whereas the deferment cut portions of strip 2 recovered 67%.

Silvicultural thinning tripled the relative abundance of commercial species in one of the strips in 2004 ($F_{1,18} = 6.29$, $P = 0.022$). However, thinning did not significantly affect the relative abundance of commercial species in strip 2 ($F_{1,16} = 2.52$, $P = 0.132$). In strip 2, deferment-cut plots almost doubled the relative abundance of commercial species found in clear-cut plots ($F_{1,16} = 6.52$, $P = 0.021$), but the interaction of thinning and felling treatment ($F_{1,16} = 0.40$, $P = 0.534$) did not have an effect. In 1989, the BA of commercial species in strip 1 and the clear-cut portion of strip 2 were both about 14 m^2/ha, and in the deferment-cut portion of strip 2 was 18 m^2/ha. In 2004/2005 the BA of commercial species was 2 m^2/ha in strip 1 and 3 m^2/ha in the clear-cut portion of strip 2, 14 to 21% of their 1989 BA, whereas in the deferment-cut portion of strip 2 BA for these species was 6 m^2/ha, 33% of its 1989 BA (Fig. 7).

Pioneer species

Pioneer species were still abundant in 2004/2005, 65 and 62% of all trees (>7.5 cm dbh) belonged to

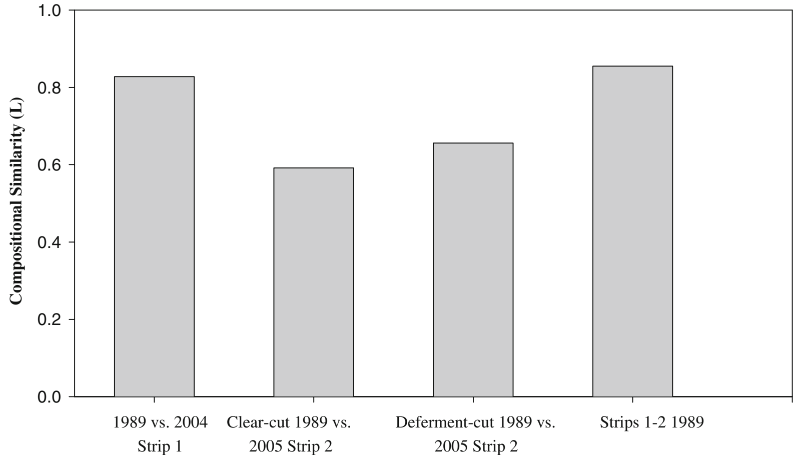

Fig. 5 Compositional similarity (L) of strip 1 between 1989 and 2004; clear-cut and deferment-cut halves of strip 2 between 1989 and 2005, and mature forest (strip 1 versus strip 2) in 1989 at the genus level, using the abundance-based Sorensen index

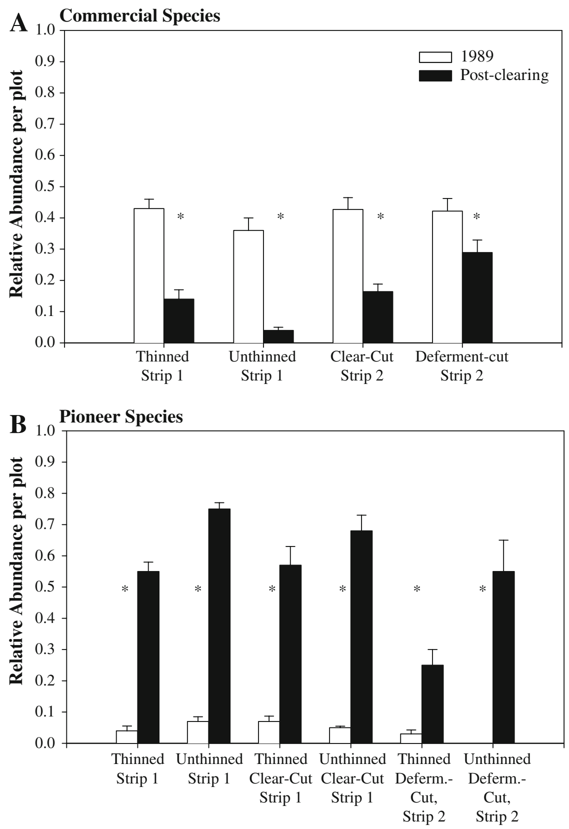

Fig. 6 (**a**) Mean (+SE) relative abundance of commercial species in thinned and unthinned 15 × 15 m plots of strip 1, and the clear-cut and deferment-cut plots of strip 2 in 1989 and post-clearing (2004, 2005) censuses. (**b**) Mean (+SE) relative abundance of pioneer species in thinned and unthinned plots of strip 1, and thinned and unthinned clear-cut, and deferment-cut plots of strip 2, in 1989 and post-clearing censuses. Asterisks (*) indicate significant difference between 1989 and post-clearing census

pioneer species in strip 1 and the clear-cut portion of strip 2, respectively. In the deferment-cut portion of strip 2 only 42% of the trees belonged to pioneer species. As expected the relative abundance of pioneer species was higher in 2004/2005 than in 1989 regardless of thinning treatment in strip 1 (thinned plots of strip 1: $t = 13.37$, $P < 0.001$; unthinned plots of strip 1: $t = 27.93$, $P < 0.001$), the clear-cut portion of strip 2 (thinned plots: $t = 8.32$, $P < 0.01$; unthinned: $t = 13.80$, $P < 0.01$), and the deferment-cut portion of strip 2 (thinned: $t = 3.45$, $P = 0.018$; unthinned: $t = 6.03$, $P < 0.01$, Fig. 6b). Silvicultural thinning and deferment-cutting both reduced the relative abundance of pioneer species. In 2004/2005 unthinned plots had 19 to 36% greater relative abundance of pioneer species than thinned plots in strip 1 and the clear-cut portion of strip 2; in the deferment-cut, unthinned plots doubled thinned plots in relative abundance of pioneer species (strip 1: $F_{1,18} = 21.10$, $P < 0.001$; strip 2: $F_{1,16} = 11.37$, $P < 0.01$). In strip 2, clear-cut plots had greater abundance of pioneers than the deferment-cut plots ($F_{1,16} = 10.41$, $P < 0.01$), and in some case doubled the amount of pioneers. However, the interaction of felling treatment and thinning ($F_{1,16} = 2.73$, $P = 0.118$) did not have an effect on pioneer species. In 1989 the BA of pioneer species in both strip 1 and the clear-cut portion of strip 2 were about 1 m^2/ha, compared to the deferment-cut portion of strip 2 which was about 0.2 m^2/ha. In 2004/2005, the BA of commercial species was 19 m^2/ha in strip 1 and 12 m^2/ha in the clear-cut portion of strip 2. The BA of commercial species of the

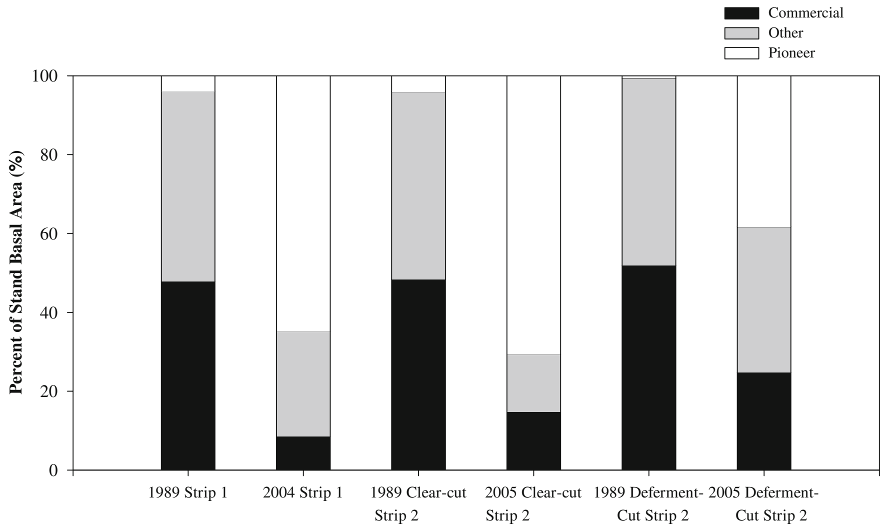

Fig. 7 Percent basal area of commercial, pioneer, and "other" species >7.5 cm dbh for strip 1 in 1989 and 2004, and in the clear-cut and deferment-cut portions of strip 2 in 1989 and 2005

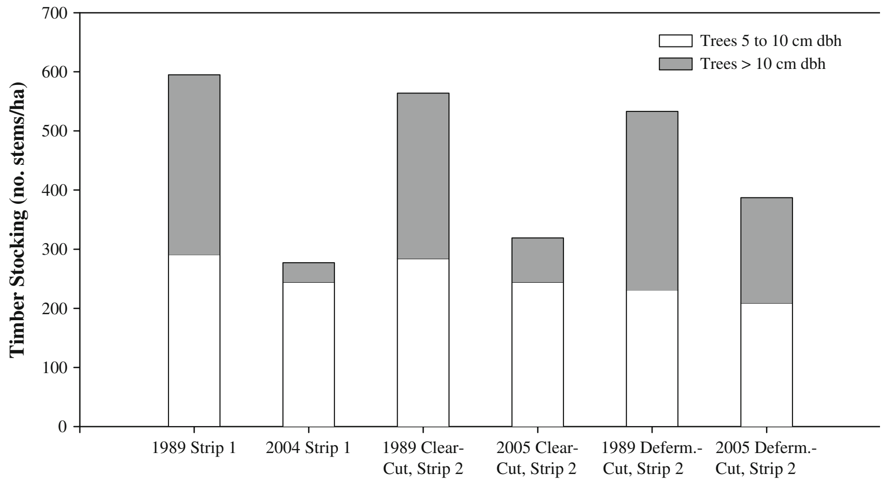

Fig. 8 Timber stocking (no. of commercial stems/ha) of small trees (5–10 cm dbh) and large trees (>10 cm dbh) in the pre-clearing (1989) and post-clearing period (2004/2005) for strip 1, and the deferment-cut and clear-cut portions of strip 2

deferment-cut portion of strip 2 was 10 m^2/ha in 2005. Figure 7 shows the percent BA of commercial, pioneer, and "other" species in 1989 and 2004/2005.

Stocking of commercial stems

In both strips, timber stocking of large stems (>10 cm dbh) was lower in 2004/2005 than in 1989 (Fig. 8). In strip 1, stocking of large commercial stems recovered 11% of its pre-clearing value (33 vs. 304 stems/ha). The clear-cut and deferment-cut portions of strip 2 recovered 27% (76 vs. 280 stems/ha) and 59% (178 vs. 302 stems/ha) of their pre-clearing stocking, respectively. Stocking of small stems (5 to 10 cm dbh) in 2004/2005 was similar to pre-clearing levels, and greater than stocking of large stems (Fig. 8). In both strips, the 1996 silvicultural thinning treatment did not affect the stocking of small (strip 1: $F_{1,18} = 2.50$, $P = 0.131$; strip 2: $F_{1,16} = 0.30$, $P = 0.590$) and large commercial stems (strip 1: $F_{1,18} = 1.68$, $P = 0.211$; strip 2: $F_{1,16} = 0.91$, $P = 0.355$) in 2004/2005. In 2005, the deferment-cut plots of strip 2 had greater than twice as much stocking of large commercial stems than the clear-cut plots ($F_{1,16} = 7.60$, $P = 0.014$), but similar stocking of small commercial stems ($F_{1,16} = 0.23$, $P = 0.637$, Fig. 8). The interaction of thinning and felling affected neither the stocking of small ($F_{1,16} = 0.80$, $P = 0.385$) nor large commercial stems ($F_{1,16} = 0.00$, $P = 0.961$).

Discussion

Basal area recovery

The recovery of a high percentage of stand BA 15 years after clear-cutting (73% in strip 1 and 58% in the clear-cut portion of strip 2) is consistent with rapid BA growth in the early years of secondary succession (Saldarriaga et al. 1988; Moran et al. 1996; Denslow and Guzman 2000), although this strongly depends on land use history and site productivity. BA of forest stands 12 to 18 years after clear-cutting for pulp in Colombia did not exceed 50% of old growth values (Faber-Landgendoen 1992). In Brazil, BA recovery 11 to 12 years after clear-cutting treatment was 50% of undisturbed forest and 60% of its pre-clearing value (Parrotta et al. 2002). Parrota et al. (2002) also compared BA recovery of different systems 11 to 12 years after harvesting. They found that high intensity harvesting or clear-cut (removal of 373 m^3, all above-ground biomass) had a lower BA recovery (50%) than moderate harvesting (trees ≤20 cm and ≥60 cm dbh for a total removal of 219 m^3) (68%), and low harvesting (trees ≥45 cm dbh for a total of 201 m^3) treatments (68%). Thus, the recovery of BA in this study was comparable to that reported for moderate harvest in Brazil (Parrotta et al. 2002) and somewhat higher than clear-cutting in Colombia (Faber-Landgendoen 1992).

Species richness recovery

The strips in the pre-clearing stage had high species richness: estimates reported in Table 2 underestimate the true richness since identification of some trees was done to morphospecies. Therefore, the extent to which species richness recovered after 15 years to pre-clearing values (47% in strip 1 and 45% in the clear-cut portion of strip 2) is probably slightly overestimated. Nevertheless, this was similar to the recovery 18 years after clear-cutting for pulp in Colombia, <50% of mature forest (trees ≥10 cm dbh, Faber-Landgendoen 1992). Less intensive harvesting systems, however, have greater species-richness recovery. Parrotta et al. (2002) reported lower species richness recovery of trees ≥15 cm dbh following clear-cut treatment (32%) versus moderate (59%) and low harvesting (94%) treatments after 11 to 12 years. In a dipterocarp forest in Borneo, Cannon et al. (1998) found that samples 8 years after selective logging (removal of 43% of stand BA) had as many tree species as unlogged forest.

Several studies have found that species richness tends to be more similar in secondary growth and old growth when smaller tree size classes are compared (Saldarriaga et al. 1988; Faber-Landgendoen 1992; Aide et al. 1996; Guariguata et al. 1997; Magnusson et al. 1999; Denslow and Guzman 2000; Parrotta et al. 2002; Peña-Claros 2003). We were not able to make such comparisons in our study due to incomplete pre-clearing datasets for smaller trees in both strips.

Composition recovery

While species richness increases in the early years of secondary succession, and takes only a few decades to reach old growth values when land use has not been severe and seed sources are close, composition of these forests remains different from old growth and may take longer to become similar to old growth stands (Finegan 1996; Guariguata and Ostetarg 2001). In our study, the strips recovered more than 50% of their pre-clearing composition at the genus level. If the analysis had been done at the species level, compositional similarities would have been lower, but genus-level analysis was conservative in the face of possible inconsistencies between censuses in some species identification, and is often done in studies of diverse tropical rainforests (e.g., Laurance et al. 2004). Despite this high composition recovery in the strips, the relative abundance and basal area of commercial and pioneer species were far from reaching pre-clearing levels.

Recruitment of commercial species after harvesting is difficult due to the different environmental conditions required by different species for regeneration. Although Swaine and Whitmore (1988) considered most commercial species gap-dependent, commercial seedlings have a broad range of shade-tolerances (Martini et al. 1994; Pinard et al. 1999). Out of 31 timber species (of high and low commercial value) studied by Pinard et al. (1999), 45% were shade intolerant and regenerated in forest edges and large gaps, 36% were shade-tolerant and regenerated in the understory, and 19% were in between the latter groups and regenerated under partial shade or small gaps. Similarly, Martini et al. (1994) classified timber species of the Brazilian Amazon.

Recruitment from seed was more important in our system than stump sprouts or advance regeneration. Sprouting of timber species in Amazonia is common; out of 305 timber species saplings, 87% of them produced sprouts following the breaking and crushing injuries associated with logging (Martini et al. 1994). In the strips, however, stump sprouts and the advance regeneration had a minor role in tree regeneration (Table 2) and the regeneration of commercial species. Although 41% of the stumps (>7.5 cm dbh) had one or more living sprouts, 10 months after cutting one of the strips (Gorchov et al. 1993), only four sprouting stumps in each strip (unpublished data) were of commercial value after 15 years. A high density of saplings (903/ha), belonging to mature forest trees, including many of commercial value, survived the clearing operation in 1989 (Gorchov et al. 1993), but 15 years later these only comprised a small percentage (16–18%) of the total regeneration in the strips, a little higher than the sprouting stumps.

Low seed input and/or high seed predation of commercial species could have lowered the recruitment of commercial species into the strips, resulting in low stocking and relative abundance of commercial trees in the strips 15 years later. Using seed traps aboveground, Gorchov et al. (1993) showed that very few large seeds, characteristic of timber species, were dispersed into the strips by birds or bats, one year after clear-cutting. Also, seeds of a valuable timber species, *Hymenaea courbaril*, were rarely moved by rodents into the interior of a strip, 10 to 30 months after the clearing (Gorchov et al. 2004). Predation of timber seeds (*Pouteria* sp.), was also greater in the strips than in the surrounding forest, 3 years after strip clear-cutting (Notman et al. 1996). Once established, commercial species compete for light with vines, lianas, and short-lived pioneer species that quickly colonize logged areas (Buschbacher 1990; Fredericksen and Mostacedo 2000; Pariona et al. 2003). As a result, growth and BA of commercial species often respond to logging less favorably than faster growing species of low commercial values (Silva et al. 1995; Kammesheidt 1998).

After 15 years of regeneration, timber stocking of small stems (5–10 cm dbh) in both strips was similar to pre-clearing levels. However, stocking of larger stems (>10 cm dbh) was low (33.3–75.5 stems/ha) and far from reaching pre-clearing levels (300 stems/ha, Fig. 8), and mature forest levels (233 stems/ha in Peters et al. (1989)), and lower than in a 50 year-old communal forest near Iquitos (125.5/ha for trees >25 cm dbh in Pinedo-Vasquez et al. 1990). This low stocking of large commercial stems in this system negatively affects the economic value projected for a potential second harvest after 25 years (Rondon 2008).

On the other hand, pioneers with large basal areas were still abundant in 2004/2005, 8 to 9 years after the thinning treatment. In the study of clear-cutting for pulp, pioneer species in a 12-year old forest comprised more than 50 to 60% of basal area and biomass (Faber-Landgendoen 1992); Parrotta et al. (2002) found that although tree floras within low, moderate, and intensive (clear-cut) harvesting treatments were broadly similar to those of undisturbed plots after 11 years; the clear-cut treatment was dominated by a higher proportion of short-lived early successional tree species, including *Cecropia* and *Vismia*.

One year after the clearing, the majority of the seedlings in the strip were a few bat (*Cecropia*)- and bird-dispersed (Melastomatace*ae* and *Alchornea triplinervia*) pioneer tree species (Gorchov et al. 1993). *Cecropia membranacea*, one of the species with the most seedlings in the strips, was also present in the seed bank; other tree seedlings, not represented in the seed bank, were attributed to the seed rain (Gorchov et al. 1993). Seeds from the seed bank as well as recently dispersed seeds contribute to the development of secondary forest. In a tropical forest of Mexico, all viable seeds of *Cecropia obtusifolia* were renewed from the soil almost every year; seed loss was mainly due to pathogen attack and high predation rates, but the seed bank was continually replenished by seed rain (Alvarez-Buylla and Martínez-Ramos 1990). It is very likely that the pioneer trees that currently dominate the strips depended on seed dispersal events that followed the clearing of the strips. One year after clearing one of the strips, bat- and wind-dispersed seeds accounted for more seed dispersal in the strip interior than bird-dispersed seeds, which arrived at high density within the forest or strip edge (Gorchov et al. 1993). Fifteen years after the felling, pioneer species comprised 65 and 62% of the trees in strip 1 and the clear-cut portion of strip 2, respectively.

Germination and establishment of short-lived pioneer species (such as *Cecropia*) can be reduced when residual vegetation and litter are present (Uhl et al. 1981; Putz 1983; Molofsky and Augspurger 1992). In this study, only slash <2.5 cm was left on site (Cornejo and Gorchov 1993). Although substantial, this amount of litter was apparently not sufficient to suppress germination and establishment of pioneer species.

In Jenaro Herrera, pioneer species such as *Cecropia*, *Alchornea, Miconia*, and *Vismia* spp. have been found to be dominant in 14 and 17-year old fallows (Baluarte Vásquez 1998). Dominance of few pioneers that established early in succession tends to "break up" within <25 years (Denslow and Guzman 2000). Senescence and mortality of these species will have a strong impact on the future biomass and stem density of secondary stands (Feldpausch et al. 2007). Thus, BA recovery in the strips is not likely to increase continuously over the next years unless there is higher growth of commercial and "other" species into larger size classes.

Silvicultural thinning

Liberation treatments such as thinning of lianas and pioneer species are commonly used to improve recruitment and tree growth (de Graaf et al. 1999; Guariguata 1999, 1997; Dolanc et al. 2003; Pariona et al. 2003). In this study, silvicultural thinning in 1996 was sufficient to significantly increase the 1996–2000 growth of commercial species (Dolanc et al. 2003), and to reduce 2004/2005 relative abundance of pioneer species of both strips, although pioneers were still abundant in the post-clearing censuses of both strips. Thinning also increased the relative abundance of commercial species significantly in one of the strips. However, thinning did not have an effect on basal area, compositional similarity, or timber stocking 8 to 9 years after the treatment application. The lack of effects of thinning on these community parameters might be because large *Alchornea* and melastomes that were not thinned, because some of the girdled pioneer trees did not die, and/or due to increased growth of the trees remaining in the thinned plots.

Deferment-cut

Deferment-cutting appeared to be more sustainable than clear-cutting. The deferment-cut portion of strip 2 had greater BA, species richness, and composition recovery than the clear-cut portion. The deferment-cut portion also had higher representation, stocking, and BA of commercial species, and a lower percentage of pioneers, than the clear-cut portion. This better recovery of the deferment-cut is consistent with the well documented role of remnant or residual vegetation in promoting recovery of species richness, tree density, and aboveground biomass (Guariguata and Ostetarg 2001; Parrotta et al. 2002; Chazdon 2003).

The Palcazú forest management system

Tosi (1982) and Hartshorn (1989a) proposed harvesting cycles of 30 to 40 years for the strip clear-cutting system. Tree regeneration in the two clear-cut strips, 15 years into the second harvesting, suggests that this system may not be ecologically sustainable, but this conclusion is tempered by replication constraints at the plot and site scale of this study.

Both strips showed some inherent variability in the pre- and the post-clearing censuses, especially in the recovery of commercial species. Predicting species richness and composition of the strips in the next 15 to 25 years would be difficult because this system would still be affected by variability in recruitment, growth, and mortality rates of commercial, pioneer, and "other" species due to biotic and abiotic factors. Thus far, 15 years into the regeneration, our results reveal that in this system regeneration of pioneer species exceed that of commercial species, even when the strips are surrounded by a matrix of old growth forest. In a forest managed by the strip clear-cutting system as it was originally proposed for the Palcazú, 44,000 ha would be under management for timber production (Hartshorn 1989b), and about half of the area would be cleared (Hartshorn 1989b); thus, eventually the surrounding matrix for many of the strips would be that of young growth. Therefore, the species that would thrive in these strips would be the ones that can reproduce within the cutting cycle of 30–40 year; i.e., pioneers. Contrary to predictions of Tosi (1982) and Hartshorn (1989a), pioneer species dominate the composition of the strips 15 years into the regeneration. Unless pioneer species have a high mortality rate in the coming years, and there is more recruitment of commercial and "other" species into the larger size classes, this system is not sustainable.

Two approaches could be taken to reduce the number of pioneer species in the strips. It is possible that cutting narrower strips (<30 m) in this system may reduce the amount of light entering the strip and thus, the germination and establishment of pioneer species. Periodic silvicultural thinning treatments may further reduce the abundance of pioneer species and further increase the establishment and growth of more commercial and "other" species in the strips.

We are aware that in the future high quality timber species will become scarce due to their high demand and strong extraction pressures. International markets will start accepting a broader range of lower quality timber species that are also gap-dependent, but this market will take some time to develop. In this study we were interested in studying the regeneration of timber species that already have an established market in order to assess the value of the strips in a potential second harvest.

From the economic perspective, composition in a forest management system has a great influence on the financial value of the next harvest. Relative abundance, stocking, and growth of commercial species will determine whether the second harvest (which is in the next 15–25 years) will be financially profitable. In order to fully assess the economic viability of this system, we have also investigated whether those few large commercial trees in the strips would reach marketable size in the next 25 years, in time for a second cutting (Rondon 2008).

Acknowledgements We thank Dr. Dennis del Castillo, Ing. Euridice Honorio, Ing. Gustavo Torres, and the Instituto de Investigaciones de la Amazonía Peruana (IIAP) for allowing us to conduct this study at Centro de Investigaciones Jenaro Herrera (CIJH). We thank the Instituto de Recursos Naturales (INRENA) for providing collecting and exportation permits as well as Zunilda Rondón for help in the application process. We also thank Italo Melendez and Margarita Jaramillo for assistance in the field. Identification was performed with the help of Rodolfo Vásquez at Missouri Botanical Garden (MOBOT), Nállaret Dávila at CIJH herbarium, and César Grandés at Herbario Amazonense (AMAZ). We thank Tom Crist, Hank Stevens, and anonymous reviewers for comments on earlier drafts of this manuscript. This study was funded by USAID Program in Science and Technology Cooperation, Grant no. 7228 to J. Terborgh, D. Gorchov and F. Cornejo and by Academic Challenge Grant (Botany, Miami University), Garden Club of Ohio, Sigma Xi, and Hispanic Scholarship Fund grants awarded to X. J. Rondon.

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