The effects of silvicultural thinning on trees regenerating in strip clear-cuts in the Peruvian Amazon

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Abstract

Common logging practices in tropical rainforest are often not sustainable and can degrade the forest. The Palcazú Forest Management system (strip clear-cutting) has been proposed as one sustainable alternative. However, low growth rates of commercial tree species during early regeneration indicate that strip-cutting may not be sustainable. To test whether a silvicultural treatment enhances the growth, survival, recruitment or richness of regenerating trees, we carried out an experimental thinning in 1996 within two strips cleared in 1989 at Jenaro Herrera, Peru, then censussed and remeasured trees on thinned and control plots in 2000. In addition, for strip 2, we compared tree regeneration on two felling treatments, clear-cutting and deferment-cutting.

Thinning significantly enhanced annual growth increment (AGI) for stems of all regeneration categories (recruits, stump sprouts, and advance regeneration) of commercial species in strip 1, and for all categories of recruits and stump sprouts in strip 2. In most cases, mean increment in the thinned treatment was approximately twice that of the control. Recruitment, survival and richness, however, demonstrated little response to thinning. Although growth tended to be higher in clear-cut portions, significant differences in increment for felling treatment were detected for only two of seven categories on strip 2, and there was no effect of felling treatment on survival, recruitment or richness. Thinning is likely to raise the value of the second harvest on the strips by enhancing the growth rates of regenerating trees, so thinning should be included in the strip clear-cutting system. This system should not, however, be considered sustainable unless growth rates are sufficient to ensure the value of successive harvests.

1. Introduction

Several methods of natural forest management have been proposed as sustainable and implemented in tropical rainforests. Assessment of sustainability how-ever, is often lacking or incomplete at the time a system is adopted (Dawkins and Philip, 1998; South-gate, 1998).

One system of natural forest management that requires more complete assessment of sustainability is the Palcazú Forest Management model. In this system, upland forest is clear-cut in 30–40 m wide strips, with length dependent on topography (Hartshorn, 1989,

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1990; Tosi, 1982). Different strips in a production unit are cleared each year over the first 30–40 years, after which time the second rotation begins. To maximize value, all trees within each strip are harvested and utilized as sawnwood, preserved roundwood, or charcoal. Animal traction is used to minimize soil compaction. Depending on the productivity of the system, silvicultural treatments may be carried out during regeneration. Stump sprouts may be reduced to one per stump, lianas may be cut if they are inhibiting the growth of commercially valuable species, and thinning of less valuable species may occur after canopy formation (Hartshorn, 1990; INADE, 1990).

Assessments of this strip-cutting system have raised concerns about its sustainability (Southgate, 1998). Simeone (1990) observed that outside technical assistance would be necessary at the onset of management to make the system practical for local people. Cornejo and Gorchov (1993) found labor and fuel costs to be higher than gross value in one strip and only slightly lower than gross value in their second strip. Gorchov et al. (1993) found that the composition early in regeneration was heavily dominated by pioneer species of low commercial value, countering the claim that pioneer species will not regenerate well in this system because the strips are too narrow to allow sufficient sunlight (Tosi, 1982).

Since the strip-cutting system is relatively new, studies that address the question of sustainability from a long-term perspective are needed. In addition, the effects of silvicultural treatments on thinning of pioneer species need to be evaluated. Other studies have shown that treatments such as liberation thinning can dramatically improve the yield of valuable species (Guariguata, 1999; De Graaf et al., 1999).

We investigated the effect of silvicultural thinning on the regeneration of trees in previously established clear-cut strips in Amazonian Peru. This treatment was applied in response to the observed low growth rates of commercially valuable trees. We compared tree growth, survival, recruitment and species richness on treated versus control plots. An additional objective was to determine the effect on regeneration of a deferment-cut carried out in 1989, in comparison to regeneration in a clear-cut.

2. Methods

2.1. Study site

Research was carried out at the Centro de Investigaciones Jenaro Herrera (CIJH) ($73°45'$W–$4°55'$S), approximately 140 km south of Iquitos Peru, and 2.5 km east of the Ucayali river (Fig. 1). 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, however rainfall is highly variable each month of the year (Ascorra et al., 1993). Soils are sandy-loam and the vegetation is considered lowland tropical rainforest on high terrace (Spichiger et al., 1989).

2.2. Stand history

Two 30 m × 150 m strips were clear-cut in 1989 in primary, high terrace tropical rainforest. The area had been selectively logged 15–20 years prior, but maintained an intact canopy. Lianas and shrubs were cut in advance of tree felling. The long axis of each strip was oriented north–south and strip 1 was approximately 150 m from strip 2. Strip 1 was cleared in April–May 1989 and strip 2 was cleared in October–November 1989. Trees ≥5 cm in diameter at breast height (dbh) were felled in each strip, except a few large trees leaning out of the strips. Directional felling was used to ensure that cut trees landed in the strip (Gorchov et al., 1993). Fifty-six medium-sized trees (5–28 cm dbh) were left standing in the south half of strip 2 as an experimental deferment-cut to determine its effect on regeneration (Cornejo and Gorchov, 1993).

Large felled trees (≥30 cm dbh) of commercial taxa were sawn into boards on site. Some additional trees were harvested as roundwood. The remaining wood >2.5 cm diameter was carried off the site, while slash (<2.5 cm) was left on site (Cornejo and Gorchov, 1993). Most stems <5 cm dbh snapped during felling and subsequently died or resprouted.

A complete survey of the trees ≥5 cm dbh was made prior to the 1989 felling for both strips, resulting in 248 taxa in strip 1 and 212 taxa in strip 2 (Cornejo and Gorchov, 1993). Each taxon was collected and is represented by vouchers at the CIJH herbarium and Herbario Amazonense (AMAZ) in Iquitos.
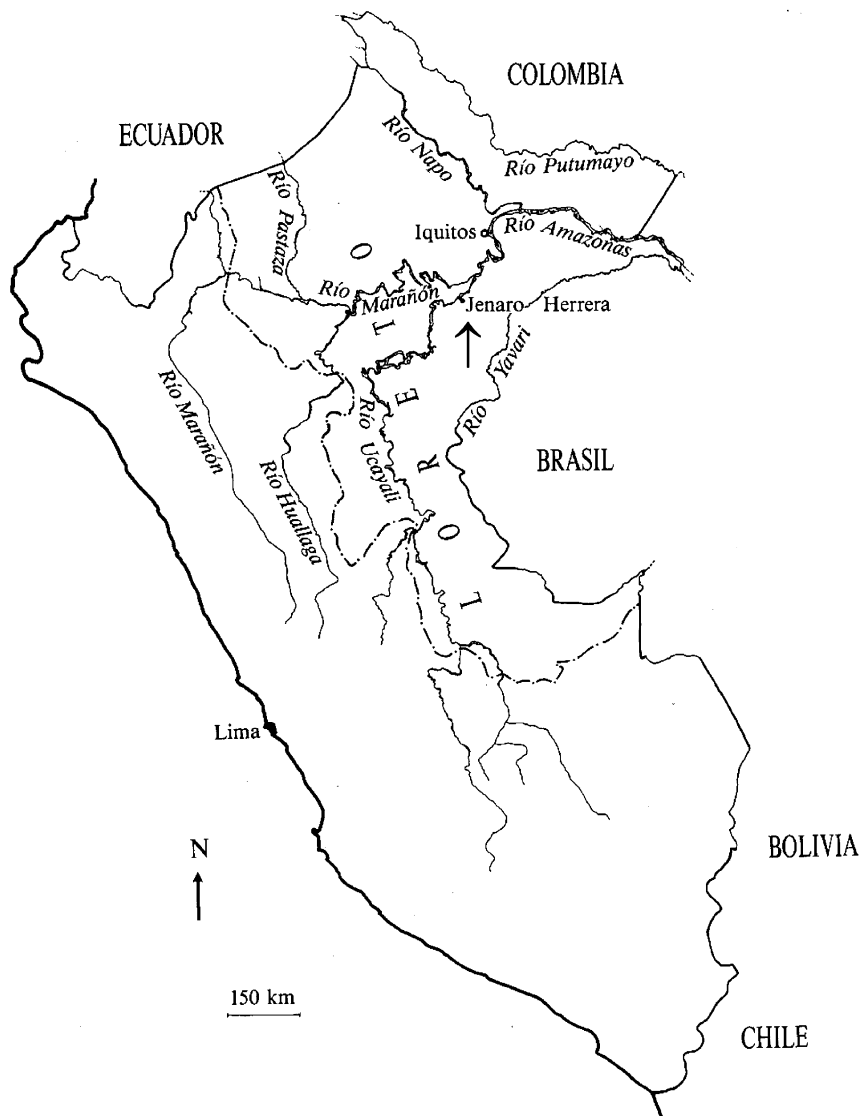
Fig. 1. Map of Peru, showing the study site, Centro de Investigaciones Jenaro Herrera, near the village of Jenaro Herrera. Adapted from Spichiger et al. (1990).

Each strip was divided into 20, 15 m × 15 m plots (Fig. 2). Stump sprouts and advance regeneration (saplings <5 cm) were identified and tagged in all 20 plots, with censuses occurring approximately once per year 1990–1994 and 1996 in strip 2, and 1990–1994 in strip 1. On 8 of the 20 plots in each strip (Fig. 2), we monitored recruitment: new seedlings reaching 2 m were identified, tagged and censused regularly from 1990 to 1994 and 1996.

2.3. Silvicultural treatment

Due to the dominance of pioneer species and slow growth of commercial stems after 5 years of regeneration (Gorchov and Cornejo, 2000), a silvicultural treatment was implemented in March of 1996. Pioneer trees (all *Cecropia*, and trees <10 tall of the genus *Alchornea* and family Melastomataceae) were girdled by machete on two 30 m × 45 m blocks in each
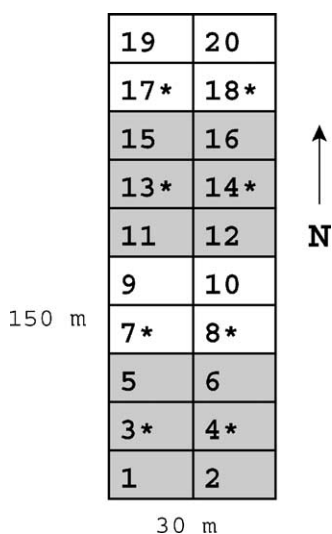
Fig. 2. Numbering of 15 m × 15 m plots within each strip at Centro de Investigaciones Jenaro Herrera, Peru. Plots thinned in 1996 are shaded. Plots with asterisk (✸) were censused regularly for all saplings ≥2 m. Advance regeneration and stump sprouts were censused throughout the strip.

strip. These blocks were placed so that the eight plots where all recruitment was monitored were equally divided between treatments (thinned, control) and each was bordered to the north by the same treatment (Fig. 2). This last constraint was to minimize edge effects; in the southern hemisphere the light environment experienced by trees will be more affected by the canopy to its north than that to its south.

2.4. 2000 census

From 9 June to 16 July 2000, tagged trees were located, verified, and measured, and new recruits >2 m tall were added to the census. The height of trees <15 m was determined using a 15 m telescoping pole. For trees >15 m, height was estimated to the nearest 0.5 m. Trees not previously identified and new recruits that could not be positively identified in the field, were collected. When possible, collection was made in triplicate, with one replicate remaining at CIJH, one at the Herbario Amazonense (AMAZ) at the Universidad Nacional de la Amazonía, in Iquitos, and one in the Willard Sherman Turrell Herbarium (MU) at Miami University, Oxford, OH, USA. Identification was carried out in the field using Gentry

(1993) and Spichiger et al. (1989). Additional work was done at AMAZ, MU, and the Missouri Botanical Garden.

3. Data analysis

Tree taxa were classified into groups of commercial species, pioneer species, and "others" (Table 1). Commercial taxa represent species valued for sawnwood at local markets during the 1989 cutting based on Pinedo-Vásquez et al. (1990), Peters et al. (1989) and the advice of CIJH professional staff (Table 1). These do not include species valued for roundwood or non-timber forest products. Very few pioneers were present among stump sprouts and advance regeneration, so these were included with "others".

Analysis of tree data from strip 1 was based solely on comparisons between the thinned portions and nonthinned portions of the strip (thinning treatment). Because strip 2 contained the deferment-cut in the south half, analyses in that strip included clear-cut versus deferment-cut (felling treatment), as well as thinning treatment.

The question of whether thinning affected tree regeneration in the strips was approached by analyzing survival, growth, and recruitment. In addition, species richness was determined as a simple measure of the community response to thinning. All the analyses were carried out using Minitab, version 13.1 for Windows, with $\alpha = 0.05$.

Survival was defined as the proportion of individuals from the previous census (in most cases 1996) that were alive in 2000. For each strip, the effect of thinning was tested with a 2×2 χ^2-test of independence. For strip 2, the effect of felling treatment was tested with a 2×2 table, and a 4×2 contingency table, to compare survival in each combination of thinning treatment × felling treatment.

Growth was defined as the change in dbh from one census to the next and expressed as annual growth increment (AGI; hereafter "increment"), the change in dbh divided by the number of years elapsed between censuses. Since diameter measurements were subject to error, and many trees experienced very little growth increment, AGI of many smaller trees was slightly negative. Larger negative values were attributed to mis-coding and were excluded from analyses

Table 1
Tree genera at CIJH classified as commercial (for sawnwood) and pioneer

Commercial	Source	Pioneer
Annonaceae		Cecropiaceae
Duguetia	1	*Cecropia*
Guatteria	1	Euphorbiaceae
Xylopia	1	*Alchornea*
Apocynaceae		Melastomataceae (all genera)
Aspidosperma	1	
Macoubea	1	
Caryocaraceae		
Caryocar	1	
Clusiaceae		
Calophyllum	1	
Combretaceae		
Terminalia	1	
Fabaceae		
Dialium	1	
Diplotropis	3	
Hymenaea	1	
Ormosia	3	
Parkia	1	
Swartzia	1	
Lauraceae		
Aniba	1, 2	
Cryptocarya	2	
Endlicheria	1, 2	
Licaria	2	
Mezilaurus	1	
Nectandra	2	
Ocotea	1, 2	
Persea	2	
Lecythidaceae		
Cariniana	1	
Eschweilera	1	
Meliaceae		
Carapa	2	
Cedrela	2	
Guarea	1, 2	
Trichilia	1	
Moraceae		
Brosimum	1	
Clarisia	2	
Myristicaceae		
Iryanthera	1, 2	
Osteophloeum	1	
Otoba	2	
Virola	1, 2	

Table 1 (*Continued*)

Commercial	Source	Pioneer
Olacaceae		
Heisteria	1	
Rutaceae		
Dictyoloma	2	
Sapotaceae		
Chrysophyllum	1	
Manilkara	1	
Pouteria	1	
Simaroubaceae		
Simarouba	2	
Sterculiaceae		
Guazuma	2	
Tiliaceae		
Apeiba	2	
Vochysiaceae		
Qualea	3	

Genera not appearing in either of these groups were considered "others". Sources for commercial classification were: (1) Peters et al., 1989; (2) Pinedo-Vásquez et al., 1990; (3) Arostegui, 1975.

(Dolanc, 2002). Diagnostic analyses revealed right-skewed distributions of AGI for each stem category, so AGI was logarithmically transformed using $\log(\text{AGI} + 1.0)$ prior to analyses.

Treatment effects on $\log(\text{AGI} + 1.0)$ were analyzed by analysis of variance (ANOVA), using the general linear model (GLM) in Minitab, treating each tree as an observation. For stems in strip 1, a one-way ANOVA was used and for stems in strip 2, a two-way ANOVA with interaction was used. Plot was originally nested within treatment in each ANOVA, but was not significant in any ANOVA model and was therefore removed from each.

Species richness was analyzed by comparing the numbers of taxa per plot for thinning treatment in both strips, and felling treatment in strip 2. These analyses were carried out using the GLM ANOVA, with one factor (thinning treatment) in strip 1 and two factors (thinning treatment, felling treatment) plus interaction in strip 2, and plots as replicates. Many trees not identified to species were recognized as distinct taxa from identified species and tallied as such (Dolanc, 2002), but this assignment was generally conservative.

Recruitment was defined as the number of new stems reaching 2 m in the 2000 census. Number of recruits per plot was analyzed using the GLM ANOVA, with one factor for strip 1 and two factors plus interaction for strip 2, as with richness.

For both richness and recruitment, sample variances were unequal, so Kruskal–Wallis tests were carried out to examine differences between treatments. These tests produced results qualitatively similar to those of ANOVA, and are therefore not reported.

4. Results

Survival was high for every category of stems in both strips (Table 2). Thinning had no significant effect on the survival of any stem category in either

Table 2
Survival of different categories of stems in thinned versus non-thinned plots in each strip

Stem category and treatment	Strip 1		Strip 2	
	Alive 1996/1994	Survival	Alive 1996	Survival
Commercial recruits				
Thinned	102	0.91	86	0.86
Non-thinned	102	0.93	91	0.90
Other recruits				
Thinned	298	0.86	292	0.79
Non-thinned	361	0.83	305	0.82
Commercial stump sprouts				
Thinned	45	0.87	64	0.86
Non-thinned	24	0.79	45	0.78
Other stump sprouts				
Thinned	42	0.81	60	0.85
Non-thinned	16	0.81	45	0.80
Commercial advance regeneration				
Thinned	73	0.93	37	0.92
Non-thinned	34	0.97	38	0.92
Other advance regeneration				
Thinned	130	0.85	55	0.86
Non-thinned	53	0.85	47	0.87

In strip 1, stump sprouts and advance regeneration were not censused in 1996, so survival for that category is based on 1994–2000, but survival of recruits in strip 1 is based on 1996–2000. All categories of strip 2 were censused in 1996. Entries in the "Alive 1996/1994" and "Alive 1996" columns are the numbers of stems alive in 1996 and 1994, respectively. For each category, the effect of treatment was not significant (χ^2-test, d.f. = 1, $P > 0.05$).

strip. Furthermore, there was no general trend for the effect of thinning on survival; survival was higher in the thinned treatment for about as many stem categories as it was lower.

Similarly, survival in the deferment-cut half was not significantly different than the clear-cut half (no felling treatment effect) in strip 2 for any of the stem categories. However, in strip 2, a marginal difference was observed ($P = 0.061$) for "others" recruits, where survival was higher in the clear-cut half (84% versus 78%). Considering felling and thinning treatments in this strip together, there was a marginally significant ($P = 0.057$) trend for the "others" stumps, where thinning enhanced survival in the deferment-cut (96% versus 77%) but reduced survival in the clear-cut (81% versus 91%). Mean survival of commercial species was higher than "others" for all three categories of stems in strip 1 and two of three categories in strip 2 (Table 2).

Annual growth increment was higher in thinned plots for nearly all stem categories in each strip. In strip 1, increment was significantly higher in thinned plots than in non-thinned plots for three of the seven stem categories (commercial recruits, $F = 5.79$, $P = 0.017$; commercial stump spouts, $F = 4.34$, $P = 0.042$; commercial advance regeneration, $F = 10.5$, $P = 0.002$) (Fig. 3). Three other categories showed the same trend, but the differences were only marginally significant (pioneer recruits, $F = 2.73$; "others" stump sprouts, $F = 4.01$; "others" advance regeneration, $F = 3.13$). The remaining category ("others" recruits, $F = 1.98$) was not significant. Mean increment of stems on thinned plots was approximately twice that of stems on non-thinned plots in three of the seven categories, and nearly three times that of stems on non-thinned plots for commercial advance regeneration (Fig. 3).

In strip 2, annual growth increment was significantly higher in thinned than in non-thinned plots in all three categories of recruits (commercial, $F = 8.87$, $P = 0.003$; "others", $F = 28.25$, $P < 0.0005$; pioneer, $F = 21.91$, $P \leq 0.0005$), and "other" stump sprouts ($F = 4.39$, $P = 0.039$) (Fig. 4). For commercial stump sprouts both thinning ($F = 5.53$, $P = 0.021$) and the interaction of thinning treatment and felling ($F = 5.37$, $P = 0.023$) affected the growth; sprouts in thinned/clear-cut plots averaged twice the growth of the other treatment combinations (Fig. 4). No significant effect was found for either advance regeneration category (commercial, $F = 0.02$; "others", $F = 0.24$). As in
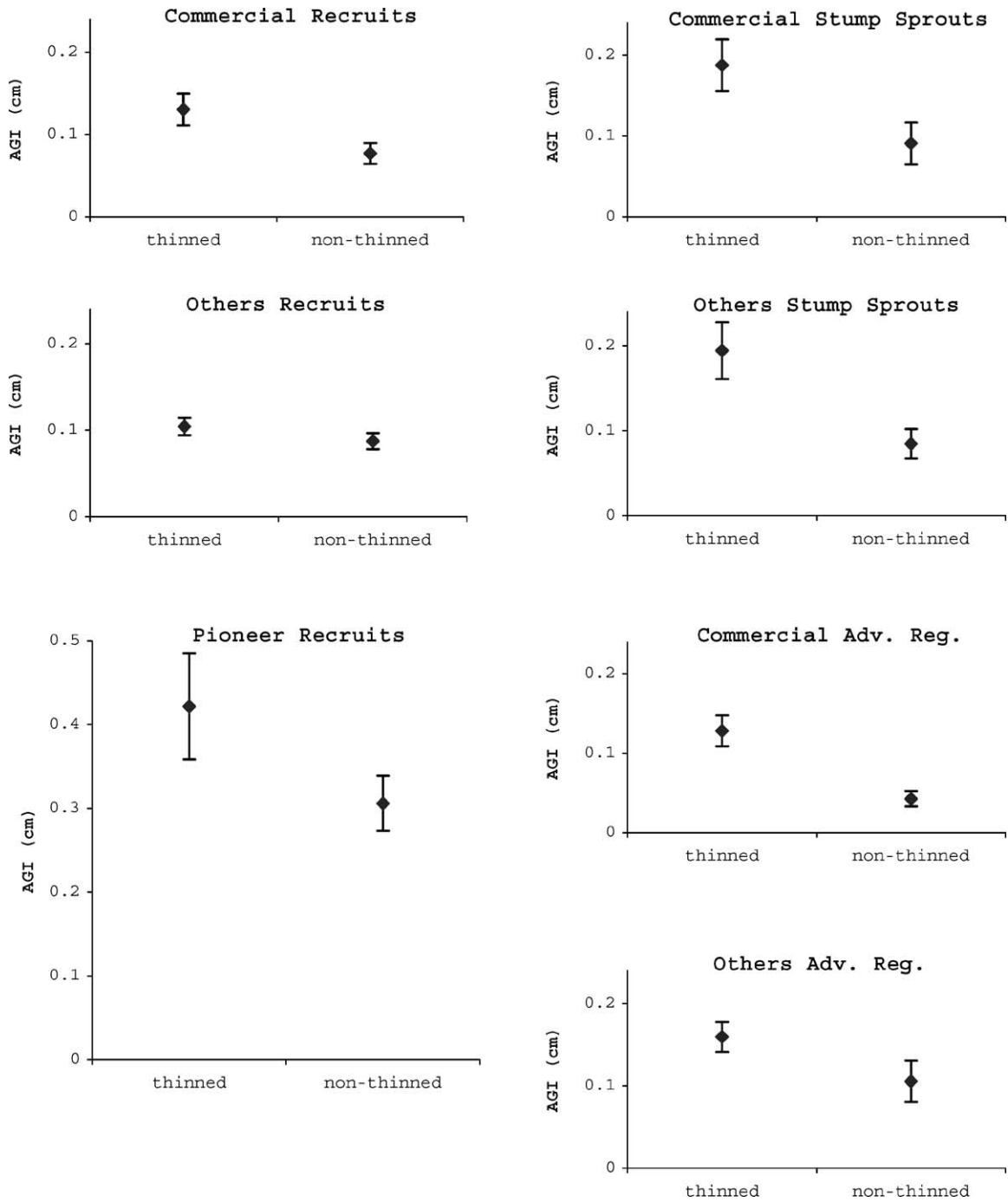
Fig. 3. Mean (±S.E.) annual growth increment (AGI) 1996–2000 of trees in each regeneration category in strip 1, Centro de Investigaciones Jenaro Herrera, Peru. Growth was significantly higher in thinned plots for commercial recruits, commercial stump sprouts and commercial advance regeneration.
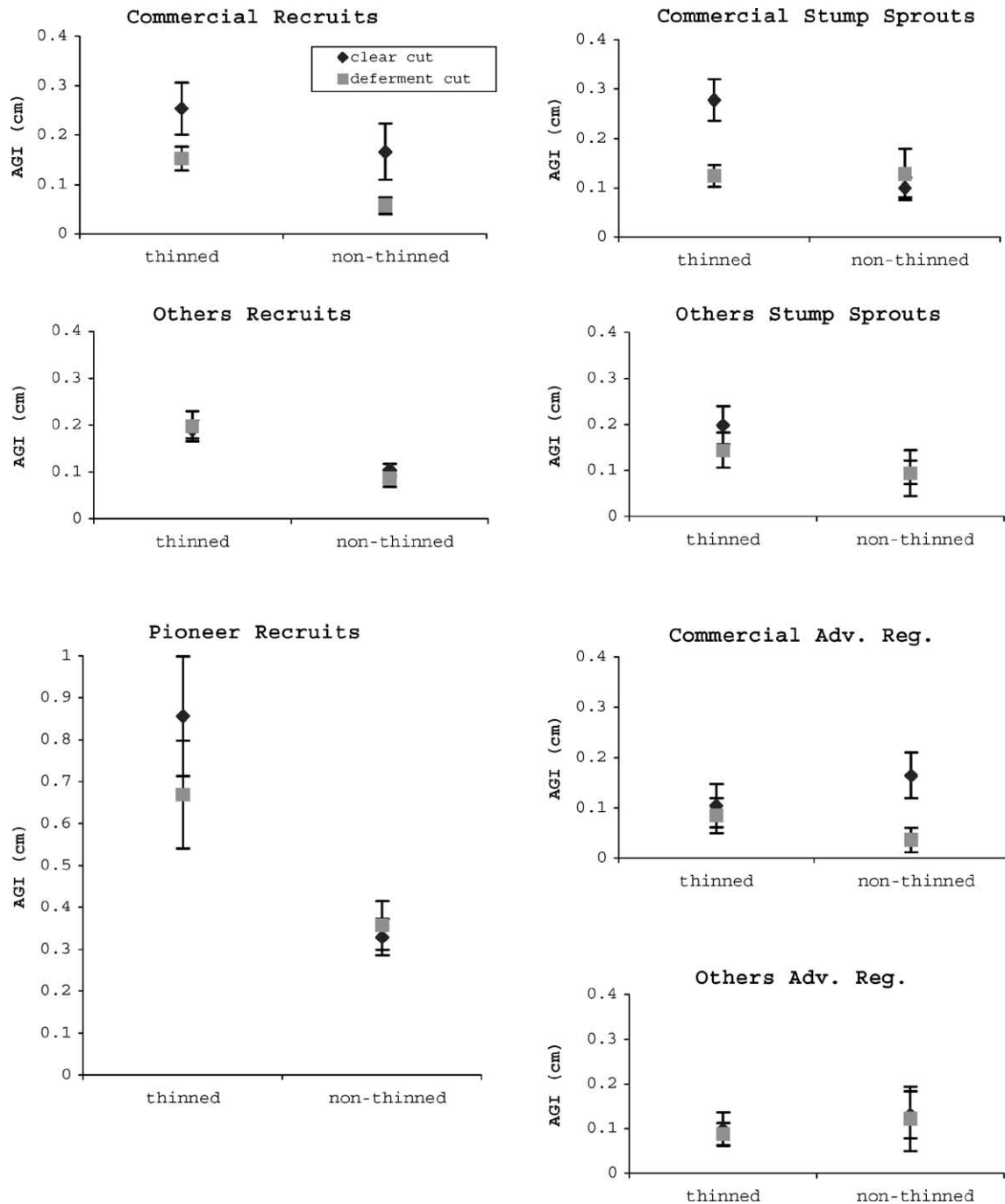
Fig. 4. Mean (±S.E.) annual growth increment (AGI) 1996–2000 of trees in each regeneration category in strip 2, Centro de Investigaciones Jenaro Herrera, Peru. For thinning treatment, growth was significantly higher in thinned plots for commercial recruits, "others" recruits, pioneer recruits, commercial stump sprouts, and others stump sprouts. For felling treatment, growth was significantly higher in clear-cut plots for commercial recruits and commercial advance regeneration. There was a significant interaction of thinning treatment and felling treatment only for commercial stump sprouts.
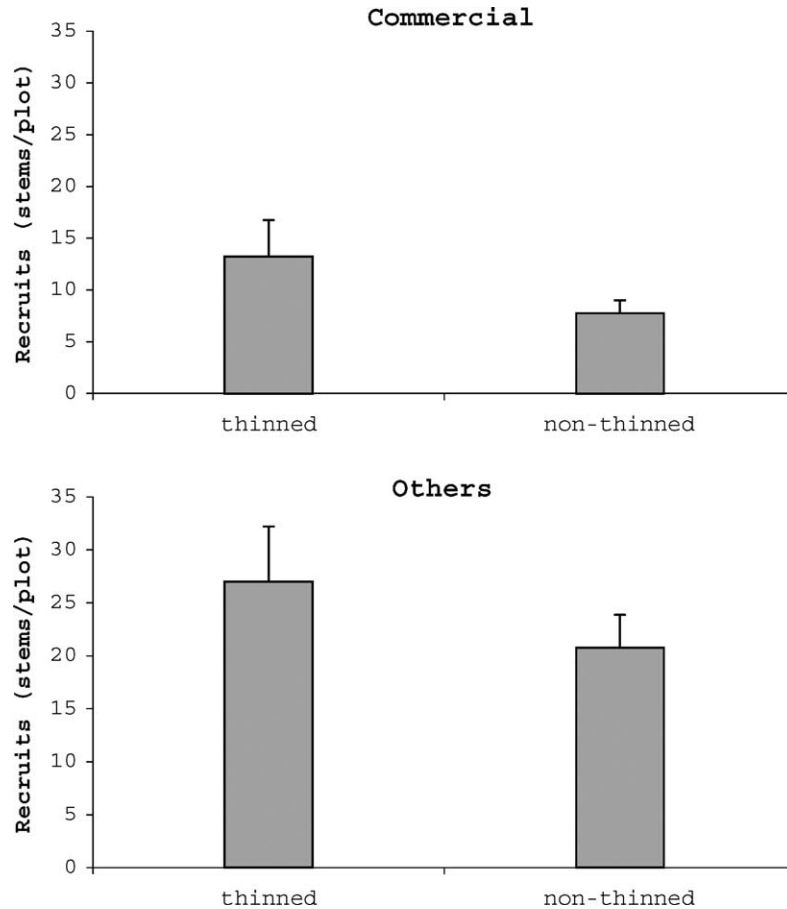
Fig. 5. Mean (±S.E.) numbers of new recruits per 15 m × 15 m plot in strip 1, Centro de Investigaciones Jenaro Herrera, Peru.

strip 1, growth in these thinned plots was nearly twice that of non-thinned plots in five of the seven categories.

Annual growth increment was significantly higher in the clear-cut portion than the deferment-cut portion for commercial recruits ($F = 6.77$, $P = 0.01$) and commercial advance regeneration ($F = 4.08$, $P = 0.048$) (Fig. 4). For the other stem categories, there was no significant effect of felling treatment on growth ("others" recruits, $F = 1.02$; pioneer recruits, $F = 0.40$; commercial stump sprouts, $F = 2.75$; "others" stump sprouts, $F = 0.81$, "others" advance regeneration, $F = 0.20$).

Recruitment from 1996 to 2000 tended to be higher in thinned plots in each strip but was only significantly higher for the "others" ($F = 33.8$, $P = 0.004$) in strip

2 (Figs. 5 and 6). The remaining three categories were not significant (strip 1 commercial, $F = 2.19$; strip 1 "others", $F = 1.06$; strip 2 commercial, $F = 1.91$). For strip 2, no significant effects of felling treatment (commercial, $F < 0.005$; "others", $F = 0.01$) or thinning × felling treatment interaction were found.

Altogether, 352 species were found in strip 1 and 341 species in strip 2. Although richness tended to be higher in thinned plots than non-thinned plots in each strip, these differences were not statistically significant in either strip (strip 1, $F = 0.31$; strip 2, $F = 2.76$) (Figs. 7 and 8). Likewise, richness was not significantly different between the deferment-cut half and clear-cut half of strip 2 ($F = 0.85$), and there was no significant interaction between thinning treatment and felling treatment.
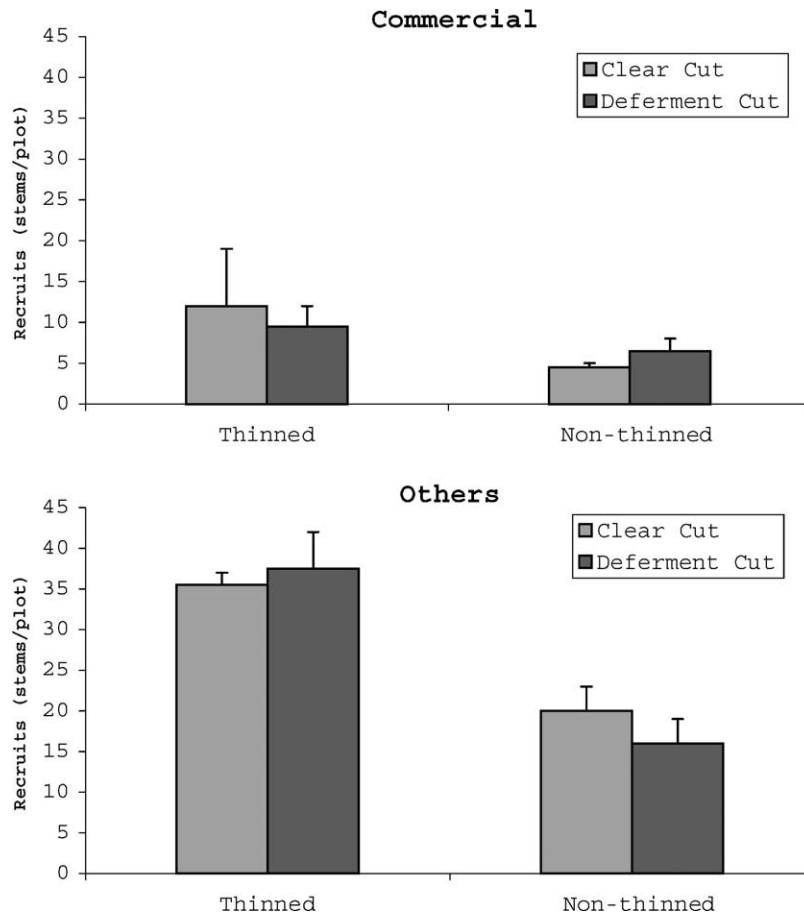
Fig. 6. Mean (±S.E.) numbers of new recruits per 15 m × 15 m plot in strip 2, Centro de Investigaciones Jenaro Herrera, Peru. Recruitment was significantly higher in thinned plots than non-thinned plots for ''others''.
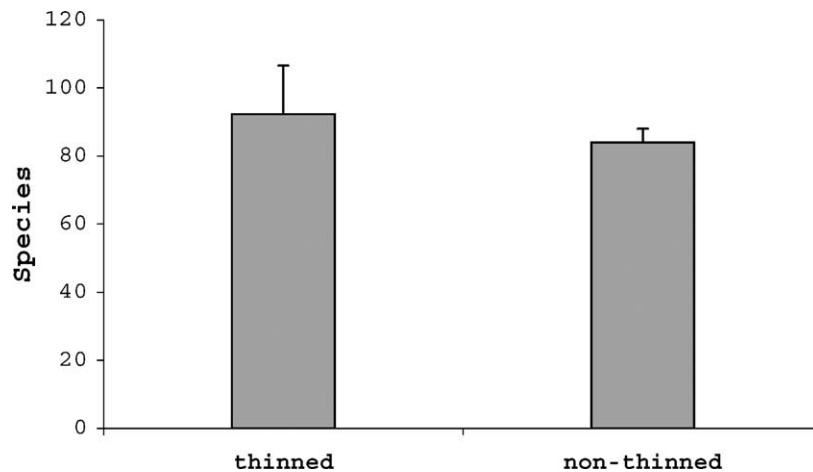

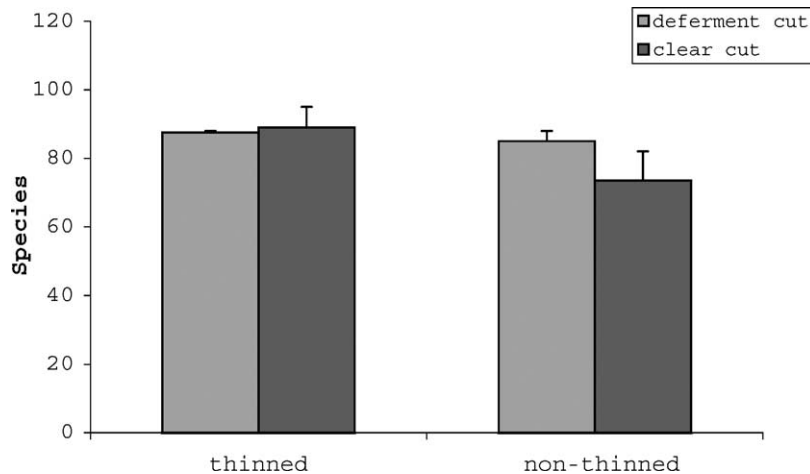Fig. 7. Mean (±S.E.) species richness per 15 m × 15 m plot in strip 1, Centro de Investigaciones Jenaro Herrera, Peru.

Fig. 8. Mean (±S.E.) species richness per 15 m × 15 m plot in strip, Centro de Investigaciones Jenaro Herrera, Peru.

5. Discussion

Thinning pioneer trees a few years after logging increased the diameter growth of regenerating trees and moderately increased recruitment. Of all the parameters measured in this study, annual diameter growth increment was influenced most substantially by thinning. Nearly all (12 of 14) stem categories in the two strips exhibited increased increment in thinned plots. Furthermore, higher growth was demonstrated for at least one data set in each of the three value categories (commercial, pioneer, and ''others'') and each of the three regeneration categories (recruits, stump sprouts, and advance regeneration).

Thinning affected the growth of commercial species more than other species. Thinning significantly enhanced growth for four of six sets of commercial stems, and for a fifth set (stump sprouts in strip 2), it enhanced growth in clear-cut but not deferment-cut plots. This finding is important for the assessment of thinning in this management system, but it is not clear why commercial species showed a stronger response than the other two groups. Denslow (1987) remarked that most tropical species have some degree of shade tolerance, but will still respond positively to openings in the canopy. She also noted that many commercial timber species are considered ''small gap species''; they germinate in the understory or in small gaps, and require some opening for substantial growth and reproduction. Thus, commercial species would be

expected to respond to openings, but, pioneers and ''others'' should as well. Conceivably, commercial species respond more to the small openings created by thinning than ''others''. Few other trends for thinning effects across all stem categories were apparent. Growth increment of pioneers was higher than non-pioneers, but the relative difference in increment in treated versus control plots was similar for both pioneers and non-pioneers.

Of the regeneration categories, stump sprouts responded most consistently to thinning. Many of the stump sprouts may still have been supported by a larger root system in 1996 than recruits or advance regeneration; perhaps this aided their ability to grow quickly when above-ground competition was reduced. Advance regeneration demonstrated the weakest response to thinning, with only one of four groups showing significantly higher growth in thinned plots. This weak response could be due to the greater height of advance regeneration when the thinning was carried out (strip 2, advance regeneration = 6.8 m, stump sprouts = 4.1 m, recruits = 3.9 m), giving these stems greater access to light regardless of thinning.

As with thinning, felling treatment had a greater effect on growth increment than on survival, recruitment or richness. Growth was lower in the deferment-cut, significantly so for commercial recruits and commercial advance regeneration. However, the effect of felling treatment was smaller than the effect of thinning. Felling and thinning treatments had an

additive effect on stem growth only for commercial recruits.

Although one might predict the effects of felling to be most apparent in the first few years after clearing (1989), survival from 1991 to 1993 was approximately 81% in each half. However, the density of commercial stems in the clear-cut half was nearly twice (489 ha^{-1}) that of the deferment-cut half (256 ha^{-1}) 3 years after felling (Gorchov and Cornejo, unpublished data), indicating that deferment-cutting depressed the initial stocking of commercial seedlings relative to clear-cutting. Although deferment-cutting had few negative effects on regeneration, survival from 1989 to 2000 of the 56 sub-canopy trees spared in the felling, was moderate ($\geq$79%). This finding makes it difficult to infer the overall impact of deferment-cutting on commercial tree volume of the second harvest.

It is noteworthy that growth, but not survival, of non-pioneers was enhanced by thinning. Trees of many species can endure years of suppressed growth, where growth increment is minimal, but the tree does not die. Swaine et al. (1987a) concluded that as long as trees are growing, they are more likely to survive. During the 4-year period between censuses (1996–2000), many trees in our strips exhibited this pattern of minimal growth. Survival may be affected by thinning or felling, but trees may not manifest this effect unless they endure several years of treatments (more than the 4 years of our study).

Other tree regeneration studies in tropical forests similarly found increased growth, but no change in survival/mortality, in response to liberation from competition (Mesquita, 2000; De Graaf et al., 1999; Guariguata, 1999). Mesquita (2000) simulated canopy openings from 0 to 100% canopy removal in 10-year-old secondary Amazonian forest. She reported no significant difference in mortality, but greater growth in more open plots. Guariguata (1999) thinned around target commercial trees in young secondary forest in Costa Rica. The treatment increased diameter growth of target trees 1 and 2 years after thinning, but survival was not measured. De Graaf et al. (1999) thinned non-commercial species in successive treatments in a regenerating logged forest in Surinam. They reported that mortality of commercial species was variable with no general trend among treatments, but that one thinning treatment applied to a lightly exploited forest had a positive effect on growth increment and recruitment.

Furthermore, De Graaf et al. (1999) commented that wind-throw and rot influence mortality, and argued that this could explain why mortality usually occurs at similar rates in all size classes. While we did not incorporate size classes into analyses, it seems likely that greater susceptibility and wind-throw balanced any positive effect on survival by thinning or clear-cutting in our strips.

Nearly all of the results of this study can be understood within the context of the light environment within the strips. Gaps increase the duration and intensity of sunlight in the lower strata of the forest (Chazdon and Fetcher, 1984), where saplings are growing. Guariguata (1999) and Clark and Clark (1999) reported that changes in diameter growth of trees mirrored changes in crown illumination conditions. Mesquita (2000) found that tree height increment after 2 years closely mirrored increases in photosynthetically active radiation. Denslow et al. (1990) showed that relative stem growth rates were highest where sunlight was highest (gap center), and lowest where sunlight was lowest (understory). While other microsite variables likely affect growth (Everham et al., 1996), most studies that have looked at effects of different environmental factors on demographic variables have concluded that growth is most closely tied to light availability (Swaine et al., 1987b). Although we did not measure light in this study, trees below the canopy undoubtedly received more light if they were in thinned plots.

6. Conclusions

The results of this study, combined with those of others that quantified the effect of thinning on trees regenerating after logging, demonstrate that thinning enhances growth increment. Furthermore, commercial species, as a group, more consistently benefited from thinning than ''others'' and were the only group significantly affected by felling treatment. Silvicultural thinning should be considered as an amendment to the strip-cutting system to enhance the value of the regenerating stand. However, growth increment declines after an initial increase in 1 or 2 years after logging (De Graaf et al., 1999; Guariguata, 1999; Silva et al., 1995), and therefore may similarly decline in thinned plots. If so, subsequent thinning may enhance growth and periodic (e.g. every 4–5 years)

thinning would be advisable when growth rates decline.

To ascertain whether the augmented growth that we observed due to thinning, and/or the deferred felling of sub-canopy trees, could be enough make the system sustainable in the long-term, requires additional data beyond the scope of this study. Ecologically, this management system appears to be quite sustainable; species richness is high and regeneration occurred rapidly. However, economic sustainability of this system is questionable, as growth rates of commercial stems, even in thinned plots, were quite low (<0.3 cm per year for all categories). Unless growth rates increase dramatically over the next 30 years (rotations are supposed to be 30–40 years), few trees will reach marketable size.

Acknowledgements

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