



Recruitment, growth and recovery of commercial tree species over 30 years following logging and thinning in a tropical rain forest



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ABSTRACT

Sustainable production of timber from commercial species across felling cycles is a core challenge for tropical silviculture. In this study, we analysed how the intensity and type (harvesting and thinning) of silvicultural interventions affect: (a) recruitment of small stems ($5 \text{ cm} \leq \text{DBH} < 15 \text{ cm}$), (b) increment of future crop trees ($15 \text{ cm} \leq \text{DBH} < 50 \text{ cm}$) and (c) recovery of harvestable growing stocks ($\text{DBH} \geq 50 \text{ cm}$) of 52 commercial timber species in the Tapajós National Forest, Brazil. Intervention intensities comprised logging (on average $61 \text{ m}^3 \text{ ha}^{-1}$) and associated damage to remaining trees (1982) and thinning (refinement) to reduce basal area at the stand level (1993/1994). These interventions together resulted in a gradient of reduction in basal-area from 19 to 53% relative to pre-logging stocks. Trees ($\text{DBH} \geq 5 \text{ cm}$) were measured on eight occasions in 41 permanent sample plots of 0.25 ha each. The dynamics were analysed at the stand level over 30 years and compared among treatments (including unlogged forest) and to pre-logging stands. Recruitment and growth temporarily increased following interventions and recovery of harvestable growing stock decreased with intervention intensity. Harvesting substantially increased recruitment of small stems relative to the unlogged forest, but recruitment rates decreased over time and did not increase following thinning. Gross increment of future crop trees was higher in logged than in unlogged forest and increased over time with high intensity of follow-up thinning, where it remained significantly higher than in control plots over time. Increased recruitment rates and volume increments were mainly driven by long-lived pioneer species, changing the composition of the growing stock. In 2012, recovery of harvestable growing stock of the 22 species harvested in 1982 varied between 19% and 57% in logged treatments relative to pre-logging levels. When considering an additional group of 30 species that were not harvested in the permanent sample plots but are now potentially commercial, relative recovery increased enough to support a second harvest under the present regulations (maximum harvest of $30 \text{ m}^3 \text{ ha}^{-1}$), except for treatment with high thinning intensity where stocks were still less than 30% relative to pre-harvest levels. In contrast, light and medium thinning intensity promoted recovery of harvestable growing stock. These findings indicate that intensive thinning should be avoided and silvicultural interventions oriented towards future crop trees of target species should be adopted. This may enhance recovery and reduce unintended changes in composition of the commercial growing stock.

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1. Introduction

Sustainable forest management for timber production demands that forest functions are maintained and the growing stock of commercial species recovers during each felling cycle to allow a continuous provision of ecosystem services and a sustainable yield of target species. A core challenge for tropical silviculture is to main-

tain adequate levels of growing stock and to facilitate regeneration of valuable, commercial timber species. In tropical forests, there is evidence that current felling cycles of around 30 years under poly-cyclic silvicultural systems may be insufficiently long to enable forest recovery (e.g., Bonnell et al., 2011; Chapman and Chapman, 2004; Hawthorne et al., 2012; Schulze et al., 2005; Sist and Ferreira, 2007; van Gardingen et al., 2006). A major concern is the yield of harvested timber species, which may recover to less than 50% between the first and second harvest (e.g., Putz et al., 2012; Rozendaal et al., 2010; Sist and Ferreira, 2007). Thus, subsequent harvests often comprise a different cohort of timber species and may include less valuable ones (e.g., Hawthorne et al., 2012; Macpherson et al., 2012; Reis et al., 2010; Yosi et al., 2011). This reduction in commercial value leaves tropical forests vulnerable to land-use conversion (Petrokofsky et al., 2015), which can threaten the conservation value of managed forests (Burivalova et al., 2014; Edwards et al., 2014).

The post-logging dynamics of a given species depends on its post-intervention regeneration and release of remaining trees (i.e., recruitment and growth; Brienen and Zuidema, 2006; Oliver and Larson, 1996; Sebbenn et al., 2008; Vinson et al., 2015). Recruitment is related to seed dispersal and predation (Janzen and Vázquez-Yanes, 1991), and the amount of solar radiation required by each species for seed germination and seedling establishment (Swaine and Whitmore, 1988). Changes in light incidence following logging will influence not only species recruitment but also growth of remaining trees (e.g., Bazzaz, 1991; Brokaw, 1985; de Graaf et al., 1999; Peña-Claros et al., 2008a; Silva et al., 1995; Souza et al., 2015; Villegas et al., 2009). Large gaps created by logging can trigger recruitment and growth of light demanding species (Carreño-Rocabado et al., 2012; Hawthorne et al., 2012; Villegas et al., 2009), whereas small gaps may favour shade-tolerant species (Peña-Claros et al., 2008a; Whitmore, 1991). Growth rates of remaining, undamaged trees generally increase with harvesting intensity due to increased light availability and decreased competition (Carvalho et al., 2004; Peña-Claros et al., 2008a, 2008b; Souza et al., 2015; van Gardingen et al., 2006), but this effect does not last for a long time at the stand level (de Graaf et al., 1999; Schwartz et al., 2012; Silva et al., 1995; Vatrax et al., 2016).

Damage to remaining crop trees, presence of lianas, and competition with neighbouring trees affect post-harvesting tree growth (Finegan, 2015). In this sense, reduced impact logging (RIL) can substantially lessen unintended damage to the ecosystem contributing to biodiversity conservation (Bicknell et al., 2015) and to the recovery of timber stocks and biomass (Macpherson et al., 2010; Vidal et al., 2016). Related to RIL, pre-harvest liana cutting aims to reduce damage to the stand and promote tree growth owing to reduced competition and increased light availability to existing crowns (Finegan, 2015; Gerwing and Vidal, 2002; Schnitzer et al., 2000; Villegas et al., 2009). However, canopy opening through RIL does commonly not increase growth rates and therefore post-harvesting tending interventions are required to facilitate recruitment and growth of valuable timber species (de Azevedo et al., 2008; Peña-Claros et al., 2008b; Putz and Ruslandi, 2015; Schwartz et al., 2013; Vatrax et al., 2016). The elimination of competing trees, in particular those of non-commercial species or of poor shape, can promote post-harvesting growth of target species (de Graaf, 1991). This is carried out by reducing stand density uniformly across the stand (i.e., refinement and in this study referred to as thinning) or around individual crop trees (i.e., liberation thinning) (Finegan, 2015; Montagnini and Jordan, 2005). Some studies have reported increased growth rates at the tree level following both types of thinning interventions (Jonkers, 2011; Peña-Claros et al., 2008a; Villegas et al., 2009).

Post-harvesting silvicultural practices can promote recovery of timber stocks of commercial species over time (Finegan, 2015; Putz and Ruslandi, 2015; Schwartz et al., 2012). However, when growing stocks of previously harvested species do not recover within a felling cycle or when species have harvesting restrictions due to their biological vulnerability or conservation status (e.g., *Bertholletia excelsa* in Brazil; Casa Civil Brasil, 2006), species that had not been previously harvested might be considered for a second harvest (e.g., de Graaf et al., 1999; Silva et al., 1995). Thus, the pool of commercial species may actually change from felling cycle to felling cycle by the harvest of lesser-known timber species associated with increased demand and enhanced marketability (Martini et al., 1994; Putz et al., 2012; Putz and Romero, 2015; van Gardingen et al., 2003). The complexity of factors affecting post-logging tree species regeneration poses a challenge for tropical silviculture, and little is known about the medium-term effects of harvesting intensity and post-logging silvicultural interventions on the recovery of harvestable growing stocks (Petrokofsky et al., 2015).

In this study, we analysed how the intensity and type (harvesting and thinning) of silvicultural interventions affect recruitment of small stems, growth of future crop trees and recovery of harvestable growing stocks to pre-logging levels. The intensity of interventions was measured as the total reduction in basal area relative to initial stocks. We considered 52 commercial timber species that were assigned to ecological groups (long-lived pioneer, partially shade-tolerant, and shade-tolerant) and to pools of commercial species (pool 1 - previously harvested; pool 2 - potentially commercial species for a second harvest). The dynamics were analysed at the stand level over 30 years and analyses included comparisons among treatments (including unlogged control forest) and to pre-logging stands to address the following hypotheses:

- (1) Recruitment of small stems ($5 \text{ cm} \leq \text{DBH} < 15 \text{ cm}$) and growth of future crop trees ($15 \text{ cm} \leq \text{DBH} < 50 \text{ cm}$) increase after harvesting and thinning interventions;
- (2) Long-lived pioneer species respond more strongly (higher recruitment and higher growth) to silvicultural intervention intensity than shade-tolerant species.
- (3) Previously harvested species (pool 1) respond more strongly (higher recruitment and higher growth) to silvicultural intervention intensity than species of pool 2, which have not been specifically promoted through thinning.
- (4) Harvestable growing stock of previously harvested species (pool 1) does not recover completely in any logged treatment within 30 years after initial logging. However, if potentially commercial species (pool 2) are included, the total harvestable growing stock (pool 1 + pool 2) reaches pre-logging levels after 30-years of recovery.

2. Materials and methods

2.1. Study area

The experiment (180 ha) is located in the Tapajós National Forest, Pará state, Brazil ($3^{\circ}19'S$, $54^{\circ}57'W$). The topography of the region is flat to slightly undulating and the altitude is around 175 m above sea level. The climate is tropical (Am in the Köppen classification) with average annual rainfall of 2000 mm, one dry season (August to November) and average annual temperature of 25°C . The predominant soil type is a Dystrophic Yellow Latosol or Oxisol, with heavy clay texture, deep profile and low fertility (de Oliveira Junior et al., 2015; de Oliveira Junior and Correa, 2001). The vegetation type is ombrophilous dense forest. At the experimental area, there is a high canopy forest with emergent

species, such as *Bertholletia excelsa*, *Manilkara elata*, *Vatairea sericea* and *Handrohanthus* spp. (Silva et al., 1985).

2.2. Experiment

The experiment was established in 1981 with a pre-harvest inventory (forest census) of trees ≥ 45 cm in DBH. In the same year, the first assessment of permanent sample plots and liana cutting (at the level of 100% across the stand) took place (Table 1). The treated area comprises 144 ha and is a randomized block design with four replicates. Each block (36 ha) is divided in four experimental units of 9 ha each, which contains 9 quadrats of 1 ha. Within each experimental unit, three quadrats were randomly selected to install the permanent sample plots of 0.25 ha each in their centre. In total, four silvicultural treatments were randomly applied among experimental units within each block. Each treatment has 12 permanent sample plots (0.25 ha each) distributed within the four blocks. A 36-ha block of unlogged forest was added in 1983 as a control (Fig. S1, Supplementary material).

Logging was carried out in 1982 (Table 1). Directional felling and bucking of trees were done with chainsaws and logs were extracted using skidders. By the time the experiment was set up, the Brazilian management regulations accepted that any commercial species over 45 cm in DBH could be harvested. A total of 38 commercial species were harvested in the experimental area of 144 ha, of which 22 occurred inside of the permanent sample plots. The selection of harvested species was based on the availability of large trees (> 45 cm in DBH) and on the local market demand. Only *Carapa guianensis*, *Manilkara elata* and *Lecythis lurida* were harvested in all treatments (Table S1). These three species comprised 54% of the total number of logged trees and 45% of the total harvested volume. Due to their rarity, most species were harvested in only one treatment. The most important principles of reduced impact logging, such as pre-harvest inventory, liana cutting, mapping of trees to be harvested, skid trail planning and directional felling were already applied in this experiment, a decade before this approach became more widely adopted.

Thinning through poison-girdling was carried out between 1993 and 1994 to eliminate non-commercial trees and favour

recruitment and growth of commercial species (de Oliveira et al., 2006). This technique devitalizes and leaves trees standing, reducing application costs and damage on the remaining trees (Bertault et al., 1992). The application did not aim at liberating individual crop trees but alleviation of competition and general promotion of commercial tree species by reducing stand density uniformly across the stand (i.e., refinement). Therefore, no diagnostic sampling was carried prior to thinning to identify trees to be devitalized or promoted. This was the first experiment with this objective established in the Brazilian Amazon.

Silvicultural intervention intensities comprised logging, damage to trees not harvested (i.e., trees unintentionally killed by logging) and thinning, together ranging from 19 to 53% of basal area reduction in relation to the original value in 1981 (Table 1). An accidental fire occurred in the experimental area in December 1997 after a long drought in an El Niño period, which affected 19 permanent sample plots (Table 1). Since fire was not treated as a silvicultural intervention, all data from these plots were excluded from this study.

2.3. Measurements and studied species

Permanent sample plots were inventoried in 1981, 1983, 1987, 1989, 1995, 2003, 2008 and 2012, except for plots in the control area which were not measured in 1981. All trees with DBH ≥ 5 cm were measured in 41 permanent sample plots and permanently labelled with aluminium tags. In this study, we included 52 species, which were assigned to two pools: “pool 1” comprising species recognized as commercial and harvested in the permanent sample plots in 1982 (Table S1), and “pool 2” comprising species not harvested in the permanent sample plots in 1982 but now potentially commercial to be harvested (Table S2). The 52 species belonging to these two pools were classified according to their ecological group in: long-lived pioneer (LLP; 5 species), partially shade-tolerant (PST; 21), and shade-tolerant (ST; 26) species (Tables S1 and S2). This classification was based on literature review (Condé and Tonini, 2013; do Amaral et al., 2009; Pinheiro et al., 2007) and on authors’ knowledge (G. S., A. R. R. and J. do C. L.) about species light requirement for seed germination and seed-

Table 1

Details on the silvicultural interventions (treatments) applied in a tropical rain forest in the Tapajós National Forest, Brazil. Mean and standard deviation are provided. C: control; L: logging only; LLTI: logging and light thinning intensity; LMTI: logging and medium thinning intensity; LHTI: logging and high thinning intensity.

	Treatments				
	C	L	LLTI	LMTI	LHTI
<i>Pre-logging (1981)</i>					
Pre-harvest inventory	No	Yes	Yes	Yes	Yes
Liana cutting	No	Yes	Yes	Yes	Yes
Initial basal area (m ² ha ⁻¹ ; DBH ≥ 5 cm)	30.5 \pm 2.6*	31.9 \pm 2.7	31.9 \pm 7.9	28.9 \pm 6.1	28.8 \pm 3.8
<i>Logging (1982)</i>					
Minimum-harvesting diameter (cm)	–	45**	55	55	55
Volume removed (m ³ ha ⁻¹)	–	61.6 \pm 39.2	72.3 \pm 92.2	43.5 \pm 30.4	66.8 \pm 53.8
Basal area removed (m ² ha ⁻¹)	–	4.6 \pm 2.9	5.2 \pm 6.4	3.2 \pm 2.2	4.9 \pm 3.9
Number (#) of logged (trees ha ⁻¹)	–	13 \pm 8	11 \pm 12	8 \pm 6	11 \pm 7
Basal area lost due to damage (m ² ha ⁻¹)	–	1.5 \pm 3.6	0.5 \pm 0.8	0.1 \pm 0.3	1.2 \pm 1.2
<i>Thinning (1993–1994)</i>					
Basal area reduced (m ² ha ⁻¹)	–	–	0.9 \pm 0.8	4.7 \pm 2.4	9.2 \pm 1.8
# of killed (trees ha ⁻¹)	–	–	4 \pm 2	100 \pm 39	202 \pm 37
# of thinned species	–	–	6	42	62
<i>General overview of the treatments</i>					
Mean total reduction in basal area (%)	–	19.1	20.8	27.6	53.2
# of plots included in this study	6	10	7	12	6
# of plots affected by fire (1997)	6	2	5	0	6

* First inventory and basal area measured in 1983 (first assessment of the permanent sample plots in the control area).

** Minimum-harvesting diameter applied by legislation in 1982.

ling establishment. LLP germinate and grow in direct sunlight, PST germinate in the understory and need sunlight to continue growth and ST species germinate in the understory and can grow beneath the main canopy.

Selection of species in pool 2 was done based on our list of 319 tree species recorded in the study area and by excluding species harvested in the permanent sample plots. We first consulted statistics on the total timber volume sold per species (2006–2014) from the Pará State Secretary of Environment to identify the traded ones (GF3, <http://monitoramento.sema.pa.gov.br/sisflora/index.php/relatorios>). Subsequently, we further refined this list to include only those species with a recognized potential market (based on authors' knowledge; G.S. and A.R.R.). At this stage, we reached 89 species, of which 87 were found in the experiment in the 2012 inventory. Twenty-two of these 87 species were harvested in 1982 and thus belonged to pool 1. For the remaining 65 species, we used the following selection criteria: (a) availability of at least one tree with $DBH \geq 50$ cm that could be harvested; and (b) the presence of at least one tree with $DBH < 50$ cm as potential crop tree for a future harvest. A total of 30 species met these criteria in 2012 in at least one treatment (Table S2). They represented 63% of the stems and 85% of the basal area above 5 cm in DBH among the 65 potentially commercial species in 2012. This indicates that our analysis captured most of the potentially commercial species. Out of 30 species in pool 2, five were already harvested in the experimental area of 144 ha in 1982 but not in the permanent sample plots. Thus, their dynamics could not be analysed as for the species in pool 1.

2.4. Data analyses

Annual recruitment between inventories was calculated as: $r = (\ln(Nt) - \ln(St))/t$, where Nt is the community size at the end of the interval, St is the number of survivors between the beginning and the end of the interval and t is the interval in years (Condit et al., 1999). Given that different lengths of inventory intervals affect the computation of demographic rates, the estimates were standardized using $r_{corr} = r * t^{0.08}$ (Lewis et al., 2004). Lewis et al. (2004) arrived at this correction factor by using the mean rate of decline, moving the estimate to a standardized interval of 1 year. The volume of each stem was calculated using two allometric equations developed for the study area: one for trees with $15 \text{ cm} \leq DBH < 45 \text{ cm}$ ($V = (-0.0994 + 9.1941 * 0.0001 * DBH^2)$; Silva and Araújo, 1984) and another for trees with $DBH \geq 45 \text{ cm}$ ($V = \exp(-7.62812 + 2.1809 * \ln(DBH))$; Silva et al., 1984). In cases where the point of diameter measurement was changed due to an irregular stem (e.g., growth of buttresses or swelling), a mean value between the previous and the new diameter was used to compute the volume in the year with change (see Talbot et al., 2014).

In each inventory interval, from 1983 to 2012, we computed the recruitment of small trees ($5 \text{ cm} \leq DBH < 15 \text{ cm}$) and growth of future crop trees ($15 \text{ cm} \leq DBH < 50 \text{ cm}$) for individuals of these diameter classes at the beginning of each interval. Annual volumetric growth ($\text{m}^3 \text{ ha}^{-1} \text{ year}^{-1}$) for each plot and scaled up to one hectare was computed in two ways: (a) as gross periodic annual increment $PAI_{gross} = ((V_f + I) - V_i)/t$, and (b) as net periodic annual increment $PAI_{net} = ((V_f + I) - (V_i + M))/t$, where V_i and V_f are standing volume of surviving trees at the beginning and at the end of the interval, respectively, I is the total volume of recruit trees at the end of the interval, M is the total volume of trees that died within the interval and t is the interval in years. We decided to use both measures of increment as response variables, as the use of PAI_{gross} alone may not reveal possible negative effects due to increased mortality.

The effect of silvicultural treatments on the recruitment of small stems ($5 \text{ cm} \leq DBH < 15 \text{ cm}$) and their trends over time (i.e., longitudinal effect given by the interaction between treatment and time after logging) was examined using linear mixed effect models (LMMs) (Pinheiro and Bates, 2000) to account for the unbalanced design and with block as random effect term. Recruitment was $\log(\ln + 1)$ transformed to fit a negative exponential curve and to make this response variable less skewed and residuals homoscedastic. The effect of silvicultural treatments on PAI_{net} and PAI_{gross} of future crop trees ($15 \text{ cm} \leq DBH < 50 \text{ cm}$) and their trends over time were examined using LMMs with block as random effect term and accounting for heterogeneity. Heterogeneity was modelled with variance covariates to achieve homogeneity of residuals using varIdent variance structure to permit for different variances per stratum for treatments (Zuur et al., 2009). The selection of this variance structure was based on model selection considering different structures and using as selection criteria the sample adjusted Akaike Information Criterion (AICc) and likelihood ratio test for nested models.

The effect of treatment on average recruitment ($5 \leq DBH < 15 \text{ cm}$) and growth ($15 \leq DBH < 50 \text{ cm}$) was evaluated separately for ecological groups and pools of commercial species. Values of recruitment and gross periodic annual increment were averaged over all census intervals to obtain average recruitment ($\% \text{ year}^{-1}$) and average PAI_{gross} ($\text{m}^3 \text{ ha}^{-1} \text{ year}^{-1}$) over time for each species group in each plot. The effect on relative recovery of harvestable growing stock (also referred to as merchantable growing stock), given by the ratio between the volume in 2012 and the volume in 1981, of commercial species in pool 1 and of species in both pools 1 and 2 (total harvestable growing stock) was compared among treatments. Harvestable growing stock was here defined as the sum of the volume of all living trees with $DBH \geq 50 \text{ cm}$, which is the minimum felling diameter allowed by the Brazilian legislation. To analyse treatment effects on both average recruitment/volume increment and relative recovery, we used LMMs with block as random effect term and heterogeneity modelled using varIdent. In case of significant treatment effects, a multiple comparison was done with Tukey HSD (honest significant difference) test using least-squares (adjusted) means.

Spatial autocorrelation of model residuals was tested using a spatial correlogram and not detected in any case. To perform the analyses, we employed R version 3.1.2 (R Development Core Team, 2014). Linear mixed effect models were fitted with the package nlme 3.1-118 (Pinheiro et al., 2015). Coefficients of determination were obtained using the package piecewiseSEM (Lefcheck, 2016). Multiple comparisons for unbalanced design using least-squares (adjusted) means were carried out using package lsmeans (Lenth, 2016). Correlograms were obtained using package ncf 1.1-7 (Bjornstad, 2016).

3. Results

Following logging, recruitment rates of small stems ($5 \text{ cm} \leq DBH < 15 \text{ cm}$) of commercial species (pool 1 and 2) were significantly higher in treated stands than in the unlogged control forest (C). However, recruitment rates had a significant negative temporal trend in all logged treatments (Table 2), indicating high recruitment after logging, which decreased as the forest canopy closed again. After 15 years, recruitment rates decreased to the levels of the unlogged forest and thinning did not significantly raise these rates (Figs. S2 and S5). Gross periodic annual increment (PAI_{gross}) of future crop trees ($15 \text{ cm} \leq DBH < 50 \text{ cm}$; pool 1 and 2) in all logged treatments was higher than in the control area, except for LHTI (Table 2). PAI_{gross} of future crop trees increased significantly but moderately over time in LHTI (Figs. S3a and b). For net

Table 2

Estimated regression parameters of effects of silvicultural treatments and their trends over time (predictors) on the response variables: recruitment of small stems ($5 \text{ cm} \leq \text{DBH} < 15 \text{ cm}$), gross and net volume periodic annual increment ($\text{PAI}_{\text{gross}}$ and PAI_{net}) of future crop trees ($15 \leq \text{DBH} < 50 \text{ cm}$) of 52 commercial species in the Tapajós National Forest, Brazil. Response variables were evaluated separately. Model estimates for the unlogged control (C) and the differences of the other treatments relative to the control are provided.

Predictors	Response variables		
	Recruitment (% year ⁻¹) Estimate (SE) ^a	$\text{PAI}_{\text{gross}}$ (m ³ ha ⁻¹ year ⁻¹) Estimate (SE) ^a	PAI_{net} (m ³ ha ⁻¹ year ⁻¹) Estimate (SE)
C**	0.419 (0.279)	0.634 (0.234)	0.514 (0.293)
L	1.904 (0.352)	0.447 (0.293)	0.426 (0.370)
LLTI	1.623 (0.379)	1.065 (0.338)	0.303 (0.469)
LMTI	1.964 (0.341)	0.524 (0.313)	0.206 (0.377)
LHTI	2.281 (0.393)	0.409 (0.366)	0.143 (0.434)
C × TAL	0.020 (0.014)	0.005 (0.004)	0.002 (0.011)
L × TAL	-0.054 (0.018)	-0.008 (0.008)	-0.011 (0.015)
LLTI × TAL	-0.059 (0.019)	-0.015 (0.012)	0.014 (0.021)
LMTI × TAL	-0.064 (0.017)	0.015 (0.010)	0.021 (0.016)
LHTI × TAL	-0.072 (0.020)	0.035 (0.014)	0.032 (0.019)
R ² ***	0.29	0.27	0.14

^a Estimates in bold are significant ($P < 0.05$).

** C: control, L: logging only, LLTI: logging and light thinning intensity, LMTI: logging and medium thinning intensity, LHTI: logging and high thinning intensity. TAL: time after logging.

*** R²: Conditional coefficient of determination.

periodic annual increment (PAI_{net}), no significant differences in relation to the control were found for both growth of future crop trees and trends over time in all treatments (Table 2). Nonetheless, similar trends as observed for $\text{PAI}_{\text{gross}}$ occurred for PAI_{net} in all treatments (Figs. S3c and d). Additionally, mortality of shade-tolerant species was high after high thinning intensities so that net increment was not promoted in LHTI (Fig. S4f).

Treatment effects on average recruitment of small stems ($5 \text{ cm} \leq \text{DBH} < 15 \text{ cm}$) varied among ecological groups ($F = 7.25$, $P < 0.001$, $n = 41$; Fig. 1a) and between pools of commercial tree species ($F = 5.53$, $P < 0.001$, $n = 41$; Fig. 1b). Regarding ecological groups, long-lived pioneer (LLP) species had higher recruitment than partially and shade-tolerant species (PST and ST, respectively). Recruitment rates of ST species were higher in treatment LHTI than in the control area (Fig. 1a). Regarding species pools, those in pool 1 had higher recruitment rates than those in pool 2 in treatments with logging only (L) and LHTI (Fig. 1b). Species in pool 1 responded significantly positive to all silvicultural treatments in terms of recruitment, while those in pool 2 had higher recruitment rates than in the unlogged forest only following logging and medium to high follow-up thinning intensities (LMTI and LHTI). Recruitment rates over time for each ecological group and species pool is shown in Fig. S5.

Treatment effects on average volume increments of future crop trees ($15 \text{ cm} \leq \text{DBH} < 50 \text{ cm}$) varied among ecological groups ($F = 2.63$, $P < 0.05$, $n = 41$; Fig. 2a) and between pools of commercial tree species ($F = 2.55$, $P = 0.05$, $n = 41$; Fig. 2b). The average $\text{PAI}_{\text{gross}}$ of LLP species increased with silvicultural treatment intensity, whereas PST and ST species did not respond to silvicultural interventions (Fig. 2a). $\text{PAI}_{\text{gross}}$ in species pool 1 increased with silvicultural treatment intensity, whereas species in pool 2 were not affected by silvicultural treatments (Fig. 2b). $\text{PAI}_{\text{gross}}$ was highest in LHTI for long-lived pioneer and harvested species (Fig. 2a and b). Species in pool 1 presented higher volume increments than species in pool 2 in LMTI and LHTI. This response was mainly driven by long-lived pioneer species from pool 1, in particular *Jacaranda copaia* (Fig. S7). Volume increments over time for each ecological group and species pool are shown in Fig. S6.

In absolute terms, volume of the harvestable growing stock of commercial species in pool 1 remained low in all silvicultural treatments when compared to the control area and pre-logging stocks (Fig. 3a). Relative recovery (harvestable growing stock in 2012 relative to 1981) was significantly lower in all logged treatments than in the control area ($F = 7.86$, $P < 0.01$, $n = 41$). Increased recovery was found when stands were logged with subsequent light (LLTI, 48% on average among plots) or medium thinning intensity (LMTI, 57%). Lower recovery was found when stands were only logged (L, 28%) or logged and followed by high thinning intensity (LHTI, 19%). Volume of total harvestable growing stock (species in pools 1 and 2) showed a positive recovery trend in all logged treatments, except for the highest intervention intensity (Fig. 3b). When considering relative recovery, significant differences among treatments ($F = 18.06$, $P < 0.0001$, $n = 41$) indicated that LHTI had the lowest relative recovery (27%). In the other treatments, relative recovery achieved 83% in L, 143% in LLTI and 101% in LMTI in relation to pre-logging stocks. In treatments L, LLTI and LMTI, enough volume of 52 commercial species has recovered for a second harvest according to current management regulations (maximum harvest of $30 \text{ m}^3 \text{ ha}^{-1}$). Furthermore, the composition of growing stock in logged treatments is changing towards a high proportion of LLP at the expense of ST species, mainly in size classes below 50 cm DBH (Fig. S8). In unlogged control forest, harvestable growing stock in 2012 was 119% of that in 1981 (Fig. 3).

4. Discussion

We investigated how intensity and type of silvicultural intervention affect recruitment, growth and recovery of timber stocks of 52 timber species in the Brazilian Amazon over 30 years after initial logging. Silvicultural interventions promoted recruitment and growth of commercial timber species during a short time span. Positive responses were mainly driven by long-lived pioneer species. Increased recovery in harvestable growing stock was observed when light to medium thinning intensities were applied following harvesting, whereas high thinning intensity had a negative impact on recovery. Additionally, the composition of the growing stock changed towards increased dominance of long-lived pioneer species and subsequent harvests will have to deal with a different composition of commercial species.

4.1. Silvicultural interventions promote recruitment and growth of timber species

Improved recruitment and growth rates following silvicultural interventions found in this study are in agreement with observations from other harvested and thinned tropical forests (e.g., Delcamp et al., 2008; Peña-Claros et al., 2008a, 2008b; Souza et al., 2015). The short-lived nature of increased recruitment and growth rates can be attributed to a fast closure of canopy gaps that reduces light availability and increases competition for limited resources. Some studies have reported that enhanced recruitment and growth do not last longer than a decade after silvicultural interventions (de Graaf and van Eldik, 2011; Schwartz et al., 2012; Silva et al., 1995; Vatrás et al., 2016). This points to the importance of subsequent tending treatments within felling cycles to improve and maintain recruitment and increment rates over time (Lamprecht, 1989; Lopes et al., 2008; Schwartz and Lopes, 2015).

Light availability in logging gaps is substantially higher than under the canopy of natural forests (Bazzaz, 1991; Lamprecht, 1989; Whitmore, 1998). In our study, thinning did not have the same effects as logging on recruitment rates, although basal area reduction in the medium and high thinning intensity was higher

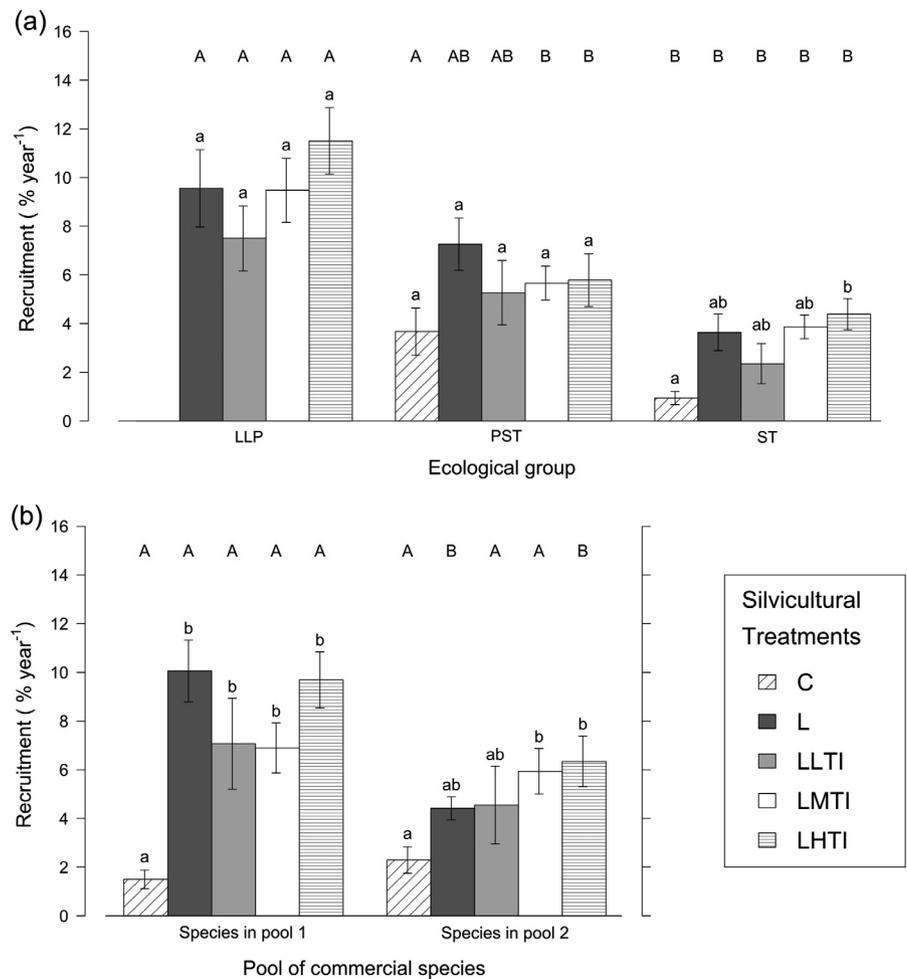


Fig. 1. Average recruitment rates (mean \pm SE, $n = 41$) of small stems ($5 \leq \text{DBH} < 15$ cm) of 52 commercial species over 30 years after logging in the Tapajós National Forest, Brazil: (a) ecological groups by treatment and (b) pools of commercial species by treatment. Small letters indicate significant differences among treatments within the same group and capital letters indicate significant differences among species groups within each treatment using a Tukey HSD test ($P < 0.05$). There were no LLP species in the control area. Silvicultural treatments: (C) control, (L) logging only, (LLTI) logging and light thinning intensity, (LMTI) logging and medium thinning intensity, and (LHTI) logging and high thinning intensity. Ecological groups: (LLP) long-lived pioneer, (PST) partially shade-tolerant and (ST) shade-tolerant species. Pools of commercial species: (pool 1) previously harvested and (pool 2) potentially commercial species for a second harvest.

than basal area removed through logging (Table 1). This could have several reasons such as: (a) canopy gaps opened by thinning were smaller and of shorter duration than gaps created by selection logging combined with liana cutting; (b) less leaf area per unit of basal area was removed through thinning when compared to logging, and therefore change in light availability was less pronounced; (c) poison girdling, which was employed in the thinning, possibly led to a protracted death of trees with a gradual and moderate increase in light availability; and (d) the regeneration layer was already occupied by recruited trees following the preceding logging and further recruitment was limited by available growing space. Unfortunately, there are only few data from this study to assess the plausibility of these assumptions and the relative importance of these different mechanisms. The third assumption is supported by observations of effects of poison girdling in other forests in the region (de Carvalho, 1981; Lamprecht, 1989; Pariona et al., 2003; Sandel and de Carvalho, 2000). The last assumption is supported by the fact that thinning was applied 11–12 years after initial logging and by that time the regeneration layer was already occupied due to high recruitment soon after logging (Fig. S2b).

Thinning interventions were rather effective to increase growth of future crop trees, as also observed in other tropical forests (e.g., de Graaf et al., 1999; Peña-Claros et al., 2008b; Villegas et al.,

2009). Nonetheless, in our study, these stems were not able to grow into harvestable dimensions ($\text{DBH} \geq 50$ cm) over 30 years. Similarly, thinning interventions in a tropical forest of Central Africa mostly promoted the growth of medium sized trees (Gourlet-Fleury et al., 2013). Furthermore, increased gross periodic annual increment of future crop trees following high thinning intensity (LHTI) was driven by long-lived pioneer (LLP) species (Fig. S6d) and partially offset by high volume loss of shade-tolerant (ST) species (Fig. S4f). This explains the absence of significant trends for net periodic annual increment in LHTI. The observed mortality of ST species may be related to their sensitivity to changes in environmental conditions (Bazzaz, 1991). Similarly, among species lost from permanent sample plots ($\text{DBH} \geq 5$ cm) between logged treatments, about half belonged to ST species, while no species were lost in the control area. It has been observed that ST species also benefit from better light conditions, but competition from pioneer species and lianas seems to be the main factor that prevent shade-tolerant species to thrive (authors' personal observation, G. S. and J. O. P. C.; Clark and Clark, 1990; de Graaf, 1991; Frederickson and Mostacedo, 2000; Schnitzer et al., 2000; Schwartz and Lopes, 2015). However, factors driving growth and mortality of ST species require further investigation to guide appropriate silvicultural interventions. Similar to our results, an

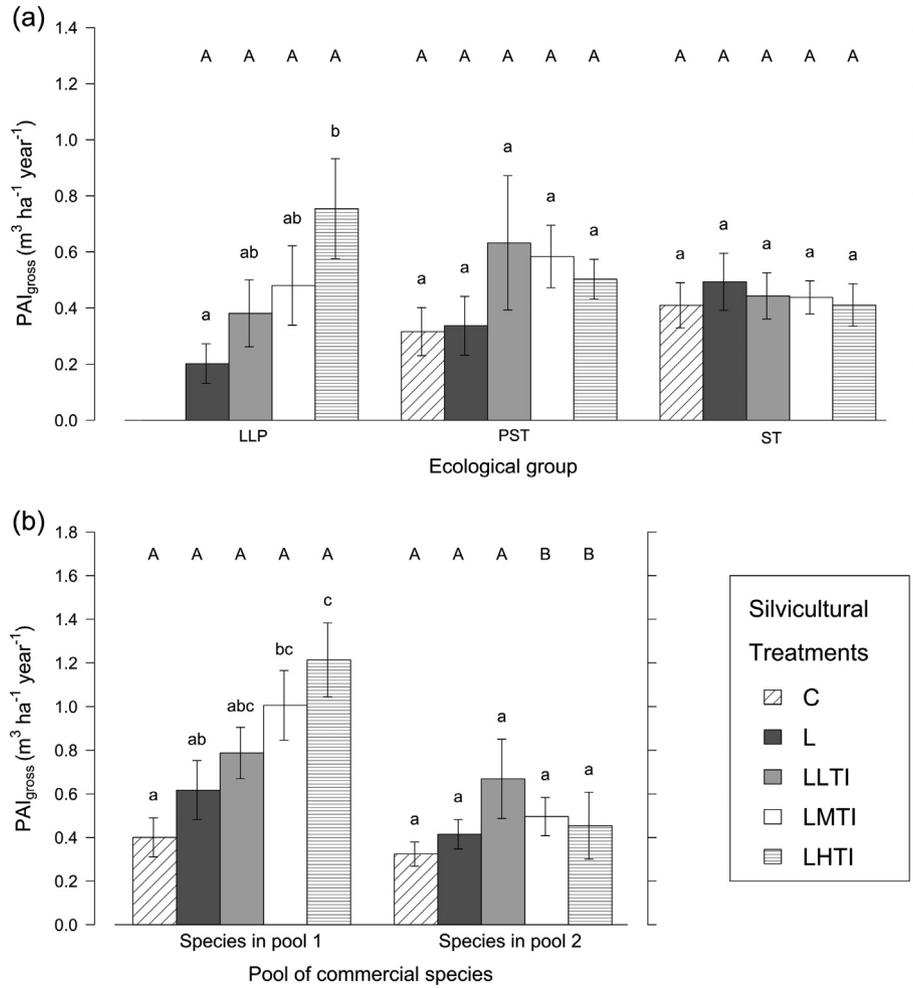


Fig. 2. Average volume increments (PAI_{gross}; mean ± SE, n = 41) of future crop trees (15 ≤ DBH < 50 cm) of 52 commercial species over 30 years after logging in the Tapajós National Forest, Brazil: (a) ecological groups by treatment and (b) pools of commercial species by treatment. Small letters indicate significant differences among treatments within the same group and capital letters indicate significant differences among species groups within each treatment using a Tukey HSD test (P < 0.05). There were no LLP species in the control area. Silvicultural treatments: (C) control, (L) logging only, (LLTI) logging and light thinning intensity, (LMTI) logging and medium thinning intensity, and (LHTI) logging and high thinning intensity. Ecological groups: (LLP) long-lived pioneer, (PST) partially shade-tolerant and (ST) shade-tolerant species. Pools of commercial species: (pool 1) previously harvested and (pool 2) potentially commercial species for a second harvest.

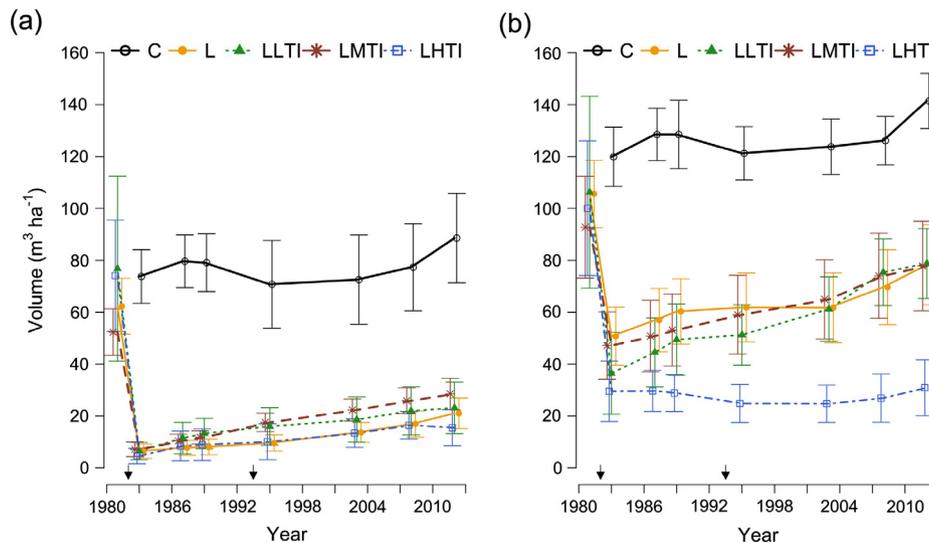


Fig. 3. Volume (mean ± SE, n = 41) of harvestable growing stock (DBH ≥ 50 cm) over time in each treatment in the Tapajós National Forest, Brazil: (a) only previously harvested species (pool 1), and (b) total growing stock with harvested and potentially commercial species for a second harvest (pool 1 + pool 2). Silvicultural treatments: (C) Control, (L) Logging only, (LLTI) Logging and light thinning intensity, (LMTI) Logging and medium thinning intensity, and (LHTI) Logging and high thinning intensity. Interventions of logging (1982) and thinning (1993–1994) are shown by downwards arrows above the time axis.

increased mortality of ST species following harvesting and thinning interventions was also observed in French-Guiana (Delcamp et al., 2008) and slow-growing species were more sensitive to drought in a managed forest in the Brazilian Amazon (Vidal et al., 2016).

Our expectation that LLP as well as harvested species would be more responsive to silvicultural intervention intensity was supported by our results. Similarly, LLP species responded better to intensive silviculture in managed forests in Bolivia in terms of recruitment (Peña-Claros et al., 2008b) and growth of future crop trees (Peña-Claros et al., 2008a; Villegas et al., 2009). Higher recruitment and growth of commercial species in pool 1 when compared to those in pool 2 is likely attributable to the fact that interventions were applied to favour species in pool 1. Moreover, this can be influenced by LLP species, as four out of five LLP species of this study belong to pool 1 (Table S1). Therefore, the better response of species in pool 1 was possibly driven by LLP species. Indeed, when removing all LLP species or only *Jacaranda copaia* from the analysis, the recruitment of small stems soon after logging and the growth of future crop trees after thinning substantially declined (Fig. S7). The number of *J. copaia* trees (DBH \geq 5 cm) increased on average among logged treatments from less than 2 trees ha⁻¹ before logging to less than 25 trees ha⁻¹ in 2012. Increased abundance of *J. copaia* following silvicultural interventions can be attributed to seed persistence in the soil seed bank (Quanz et al., 2012), high seed production (high quantity and early sexual maturity) (Vinson et al., 2015), anemochoric seed dispersal and fast growth (Carvalho, 2008). In addition, simulations indicated that management of this species for timber production could be sustained over time under current logging prescription in the Brazilian Amazon, as its population density and genetic diversity seems to be only marginally affected by subsequent logging interventions (Vinson et al., 2015).

4.2. Recovery of harvestable growing stock is impaired by strong thinning intensity

The results support our hypothesis that, in all logged treatments, harvestable growing stock of previously-harvested timber species (pool 1) would not recover to original pre-logging levels. The insufficient recovery of harvestable volume of initially harvested species for a second harvest within 30-year felling cycles has been also observed in other logged tropical forests (Dauber et al., 2005; Gourlet-Fleury et al., 2013; Putz et al., 2012; Rozendaal et al., 2010; Sebbenn et al., 2008; van Gardingen et al., 2006). The highest recovery of harvestable growing stock observed in treatments with light and medium thinning intensities (LLTI and LMTI) corroborates the potential of such interventions to increase recovery of timber stocks of target species (de Graaf et al., 1999; Lamprecht, 1989; Ohlson-Kiehn et al., 2006; Villegas et al., 2009).

The lowest relative recoveries, which were found in treatments with logging only (L) or logging followed by high thinning intensity (LHTI), may be attributed to the high logging damage in both treatments and strong thinning in LHTI. The degree of damage affects the potential response to release of future crop trees, either due to direct damage as a result of loss of branches or to increased stress caused by substantial changes in environmental conditions (Miller et al., 2007; Montagnini and Jordan, 2005; Sist and Ferreira, 2007). Here, the number of stems killed by logging damage among the 52 commercial species was between 4 and 7 trees ha⁻¹ in L and LHTI respectively, in contrast to less than 1 tree ha⁻¹ in LLTI and zero in LMTI (DBH \geq 5 cm). This points to the potential of reduced impact logging to reduce direct damage and physiological stress to existing growing stock (Miller et al., 2011).

In the Brazilian Amazon, it was observed that alterations in environment of forest edges increased the abundance of lianas

and affected the vitality of large trees (DBH \geq 60 cm) through increased eco-physiological stress (Laurance et al., 2000, 2001). Changes in forest structure driven by intensive damage and thinning interventions might have similar effects (e.g., Fredericksen and Mostacedo, 2000; Miller et al., 2007; Park et al., 2005). Even by carrying out pre-logging liana cutting, as done in our plots, high post-logging recruitment of liana is common in forests of the Eastern Amazon (authors' personal observation, G. S., A. R. R. and J. N. M. S.). Here, mortality of future crop trees (15 \leq DBH < 50 cm) increased after high thinning intensity and volume losses of large trees (DBH \geq 50 cm) were high and constant over time in LHTI. Large trees seem to be sensitive to changes in environmental conditions, as it was observed for trees with DBH > 40 cm in response to drought in the Brazilian Amazon (Rowland et al., 2015).

The inclusion of an additional pool of commercial tree species (pool 2) increased recovery of harvestable growing stock in 2012 in relation to 1981. In all treatments but for the highest intervention intensity (LHTI), enough volume had recovered for a second harvest under the current Brazilian forest management regulations. This indicates that high intensities of selection harvesting and follow-up thinning impeded recovery of the merchantable growing stock. Moreover, the culling of unwanted species typically places emphasis on current timber value. For instance, around 8% of thinned basal area in LHTI belonged to species in pool 2. The inclusion of lesser-known timber species, which had not been previously harvested in the first cycle, contributes to the recovery of timber stocks (e.g., de Graaf et al., 1999; Putz et al., 2012; Silva et al., 1995). Nonetheless, a new harvest will partially or mostly consist of new species. Under a polycyclic silvicultural system, it is important to consider different species cohorts in each felling cycle to provide time for recovery of timber stocks of previously-harvested species. Eventually, the growing stock is a product of many decades of recruitment and growth of long-lived tree species, and therefore recovery will not be attained within current (short) felling cycles (Bawa and Seidler, 1998; Dauber et al., 2005; Putz and Romero, 2015; Zarin et al., 2007).

4.3. Silvicultural implications

A polycyclic silvicultural system based on a felling cycle of 25–35 years with a maximum harvesting volume of 30 m³ ha⁻¹ is in the model for the Brazilian Amazon (Ministério do Meio Ambiente, 2006). The current maximum harvest allowed by law is half of the average volume harvested in this experiment in 1982 (61 m³ ha⁻¹). Similar to our results, predicted future yields in forests of the Eastern Amazon indicated that such high logging intensities are unsustainable under 30-year felling cycles. Furthermore, the same study indicated that even under current management regulations, the composition of harvestable species will vary from cycle to cycle (Alder and Silva, 2001). Post-logging silvicultural treatments may enhance recovery of growing stocks because logging gaps will not necessarily be occupied by valuable timber species. Thus, silvicultural treatments such as elimination of competitors and enrichment planting may be required to increase the density and growth of valuable timber species (Fredericksen and Mostacedo, 2000; Gómez-Pompa and Burley, 1991; Lamprecht, 1989; Lopes et al., 2008; Park et al., 2005; Schwartz and Lopes, 2015).

High thinning interventions may impair recovery of timber stocks in the region, as commercial growing stocks in forests of the Eastern Amazon are typically dominated by shade-tolerant and slow growing species (e.g., de Carvalho, 2000; Martini et al., 1994). They normally do not benefit much from strong interventions like LLP species do (Carvalho et al., 2004; Gourlet-Fleury et al., 2013; Schwartz and Lopes, 2015; Villegas et al., 2009; Whitmore, 1991; Yosi et al., 2011). Much lower intensities of liber-

ation thinning than applied in our study were reported to improve growth rates of ST species in Bolivian forests (Peña-Claros et al., 2008a), but did not improve growth rates of individual ST species in the Brazilian Amazon (Taffarel et al., 2014, 2015). Thus, further studies are needed on effects of thinning interventions. In our study area, harvesting of generalist pioneer and commercial LLP species may improve conditions for regeneration of ST species through reduction in competition. Nevertheless, silvicultural interventions should be oriented towards liberation of future crop trees (i.e., liberation thinning) and avoid substantial changes in forest structure, which may lead to high recruitment of pioneer species in the forest stand as already observed in the study area (de Avila et al., 2015).

Ultimately, growth and persistence of a given species depend on the presence of seedlings in the understory at the time of gap opening (Grogan et al., 2016; Jennings et al., 2001; Whitmore, 1998). Thus, attention should be paid to the recruitment of commercial species in management plans. While increment is important for the short-term recovery of growing stocks within a felling cycle, recruitment in smaller diameter classes is important to enable the long-term sustainability of timber yields (Jennings et al., 2001; Lopes et al., 2008; Schwartz and Lopes, 2015; Uhl et al., 1997). We observed that recruitment rates of more valuable ST species were insufficient to maintain their continuing harvest. In such situations, enrichment planting and tending of planted seedlings or naturally-established regeneration may help improve recruitment, survival and growth rates of target commercial species (Dauber et al., 2005; Schwartz et al., 2013; Schwartz and Lopes, 2015). Finally, adequate knowledge about the autecology of target species is important to guide silvicultural interventions (Gómez-Pompa and Burley, 1991; Park et al., 2005; Vinson et al., 2015).

5. Conclusions

Recruitment and growth temporarily increased, while recovery of harvestable growing stock decreased with intensity of silvicultural interventions. High harvesting and thinning intensities mainly promoted recruitment and growth of long-lived pioneer species. Future harvests will therefore have to rely on a different pool of timber species than the one previously harvested. When considering additional, lesser-known timber species, all treatments were able to recover a sufficient timber volume for a second harvest under current management regulations, except for the highest intervention intensity with strong follow-up thinning. Low to medium levels of thinning may promote timber recovery. Nonetheless, high intensities of selection harvesting and follow-up thinning impede recovery of the merchantable growing stock. The available regeneration of target species at the time of harvesting is very important to facilitate recovery of timber stocks of valuable tree species. Given that sustainable timber yield of commercial timber species remains a paramount challenge for tropical silviculture, it is fundamental to understand and consider potential effects of active silviculture oriented on future crop trees and based on the autecology of important tree species and species groups.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2016.11.039>.

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