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Tree Height Reduction After Selective Logging in a Tropical Forest

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ABSTRACT

By harvesting scattered large trees, selective logging increases light availability and thereby stimulates growth and crown expansion at early-life stage among remnant trees. We assessed the effects of logging on total and merchantable bole (*i.e.*, lowest branch at crown base) heights on 952 tropical canopy trees in French Guiana. We observed reductions in both total (mean, −2.3 m) and bole (mean, −2.0 m) heights more than a decade after selective logging. Depending on local logging intensity, height reductions resulted in 2–13 percent decreases in aboveground tree biomass and 3–17 percent decreases in bole volume. These results highlight the adverse effects of logging at both tree and stand levels. This decrease in height is a further threat to future provision of key environmental services, such as timber production and carbon sequestration.

Abstract in French is available with online material.

Key words: carbon sequestration; forest management; logging; tropical forests; wood production.

RECENT PAN-TROPICAL STUDIES OF TREE HEIGHTS HAVE REVEALED CONSIDERABLE REGIONAL (Nogueira *et al.* 2008, Hunter *et al.* 2013) AND CONTINENTAL VARIATIONS (Banin *et al.* 2012). At large scales, climatic variables such as rainfall and temperature seem to drive tree heights (Feldpausch *et al.* 2011). At smaller scale, differences in adult stature (Bohlman & O'Brien 2006, Poorter *et al.* 2006) and capacity to cope with light competition (Poorter *et al.* 2005, Laurans *et al.* 2014) explain most variations in tree height. For instance, tropical trees surrounded by tall individuals reportedly grow faster and become more slender for a given height to access light, approaching their critical buckling height (King *et al.* 2009). Evidence of greater heights and narrower crowns among trees growing in competitive neighborhood was reported in both temperate (Lines *et al.* 2012) and tropical (Sterck & Bongers 1998) forests.

By creating large gaps, selective timber harvesting affects both forest structures (*e.g*, Pereira *et al.* 2002, Sist & Nguyen-Té 2002) and light conditions (Yamada *et al.* 2014). Selective logging of tall trees is likely to alleviate competition in the residual stand, primarily for light (Romell *et al.* 2009) and in a lesser extent for soil resources (Shenkin *et al.* 2015). Benefiting from enhanced light conditions in logged forests (Nicotra *et al.* 1999), developing trees are more likely to fork and expand their crown at the expense of height growth (Sterck & Bongers 2001). For instance, in Indonesia, trees growing in fully open versus shaded condi-

tions were on average 31 percent shorter for the same diameter (Harja *et al.* 2012). Similar pattern was observed in fragmented forests, where trees benefiting from enhanced light environment near edges and reduced densities of large trees were found 30–40 percent shorter than in closed forests (Oliveira *et al.* 2008, Osuri *et al.* 2014). A dwarfing effect of trees post-logging would hence substantially reduce biomass stocks and carbon sequestration. Similarly, a reduction of the merchantable log volumes would also seriously challenge future wood production in these forests.

We investigated whether logging affected H:D relationship at Paracou experimental site (5°18′ N, 52°23′ W), a network of 16 permanent forest plots (PSP) logged in 1987–1988 with intensities ranging from 32.5 to 53.4 m³/ha depending on use of timber stand improvement. We estimated logging intensity in 125 m × 125 m (1.56 ha) plots, in summing the biomass of harvested trees and those that were damaged and died up to 4 yr after logging operation, as described in Rutishauser *et al.* (2015). For the sake of comparison, natural biomass losses (*i.e.*, tree death) were summed over 4 yr since 1988 in control plots. We assumed a proportional relationship between the percentage of biomass lost and enhancement of light conditions for surrounding trees (Table 1) (Hérault *et al.* 2010).

In 1999, 11 yr after logging and silvicultural treatments, total (H_T) and bole (H_B) heights were measured with a laser hypsometer on a randomly selected sample of 471 trees in control plots and 207 trees in logged plots (Table 1). Bole height refers to the distance between the ground and the lowest branch at crown

TABLE 1. *Year of census, forest type, pre-logging biomass stocks, biomass lost and relative biomass lost due to logging operations or natural mortality over 4 yr and number of trees sampled by plot.*

Census	Plot	Subplot	Forest type	AGB stock (Mg/ha)	AGB lost (Mg/ha)	AGB lost (%)	# tree sampled
1999	10	2	Logged	407.0	216.8	53	207
1999	11	1	Unlogged	409.6	14.7	4	471
2014	4	1	Logged	404.7	197.3	49	31
2014	4	2	Logged	419.9	205.8	49	26
2014	4	3	Logged	422.8	245.6	58	12
2014	4	4	Logged	375.5	216.3	58	24
2014	5	1	Logged	406.2	152.3	38	19
2014	5	2	Logged	435.2	174.2	40	10
2014	5	3	Logged	375.0	123.8	33	18
2014	5	4	Logged	348.9	141.5	41	29
2014	6	1	Unlogged	480.2	5.2	1	9
2014	6	2	Unlogged	418.4	7.2	2	7
2014	6	3	Unlogged	387.6	6.0	2	17
2014	6	4	Unlogged	381.7	17.8	5	17
2014	14	1	Unlogged	429.7	18.2	4	6
2014	14	2	Unlogged	410.1	58.1	14	6
2014	14	3	Unlogged	415.6	19.1	5	18
2014	14	4	Unlogged	352.0	16.9	5	25

base (Husch *et al.* 2002). While small unreiterated or epicormics branches may still be found below crown base (Nicolini *et al.* 2003, Barthélémy & Caraglio 2007), these branches do not affect timber quality and were hence disregarded. Henceforth, bole height is a widely used measure in forestry to estimate the commercial volume of tree stems (*e.g.*, Vibrans *et al.* 2015).

A similar survey was carried in 2014 on 105 and 169 trees (different from those measured in 1999) in control and logged plots, respectively, accounting for H_T, H_B, and a crown illumination index (CI, as proposed by Dawkins 1958). Only trees exposed to direct vertical light were monitored and classified as follows: (CI 3) Lower canopy trees, partly exposed and partly shaded vertically by others crowns; (CI 4) upper canopy trees, exposed in entire vertical plan but with other crowns laterally; (CI 5) crown entirely exposed, free from competition for light.

Seeking to exclude trees with fully formed crowns before logging in 1987–1988, only trees 10–40 cm DBH were included. With progressive post-harvest canopy closure, a reduction of tree responses to the initial disturbance might be expected over time. To formally test this hypothesis, we explicitly accounted for the year of recruitment into the 10 cm DBH class since logging. Trees recruited up to 11 yr after logging (mean = 5.3 yr) were included ($N = 136$), as they might also have benefited from reduced light competition. Once an adult tree has formed its crown, the length to crown base (*i.e.*, bole height) is not expected to markedly evolve, while branches and therefore total height are likely to increase over time (King 1996, Rutishauser *et al.* 2011).

The date of survey was, therefore, included to detect a potential compensatory effect of enhanced vertical crown expansion over time, assessed through crown width/bole height ratios (hereafter C/B).

To circumvent any differences in tree species composition in logged and unlogged forests, we selected only species with > 5 individuals in both treatments. *Dicorynia guianensis, Eperua falcata, Eschweilera sagotiana, Licania alba,* and *Pradosia cochlearia* were monitored at both censuses, while *Lecythis persistens, Pogonophora schomburgkiana, Simaba cedron, Carapa procera, Couratari multiflora, Oxandra asbeckii, Licania heteromorpha, Bocoa prouacensis, Tovomita sp.,* and *Symphonia sp.* were monitored in 1999 only.

We combined the data from 1999 and 2014 censuses ($N = 953$) to test for a general effect of logging on H_T and H_B. We used mixed linear models, accounting for effects of logging intensity (LOG), the year of recruitment into the 10 cm DBH class after logging (RSL), and date of survey (DATE) on height–diameter relationships. Species and plots were treated as random effects, allowing a specific response to disturbance. Both heights and DBH were normalized using log-transformation to avoid large residual heteroscedasticity, ending up with a model of the form:

$$log(H_{isp}) = \theta_1 \times log(DBH_{isp}) + (\theta_2 + \theta_s + \theta_p) \times log(DBH_{isp})$$
$$\times LOG + \theta_3 \times log(DBH_{isp}) \times RSL + \theta_4$$
$$\times log(DBH_{isp}) \times DATE + \varepsilon$$

where H_{isp} is the height of tree *i* of species *s* in plot *p*, DBH the diameter at breast height at year of census, DATE the year of survey as a factor, θ the model parameters, θ_s the species and θ_p the plot effects approximated with two normal laws $N(0; \sigma^2)$, LOG the logging intensity and RSL the years of recruitment after logging (set to 0 for trees present before logging), and ε the model residual error approximated with a normal law $N(0; \sigma^2)$.

Effect of direct crown illumination (CI) was tested separately on data gathered in 2014, 25 yr after logging ($N = 274$) and the model used is as follows:

$$log(H_{isp}) = \theta_1 \times log(DBH_{isp}) + (\theta_2 + \theta_s + \theta_p)$$
$$\times log(DBH_{isp}) \times LOG + \theta_3 \times log(DBH_{isp})$$
$$\times RSL + \theta_{CI} \times log(DBH_{isp}) \times CI + \varepsilon$$

where CI is the crown illumination index treated as a categorical factor. A similar procedure was carried out with crown/bole ratios.

To quantify the goodness-of-fit of our models and the role of fixed effects in explaining the variance, we used R^2 coefficients proposed by Nakagawa and Schielzeth (2013): marginal R^2 (R^2_m) represents the variance explained by fixed effects only and conditional R^2 (R^2_c) interpreted as the variance explained by both fixed and random effects (i.e. the global model). Predicted total heights were used to compute aboveground tree biomass using a generic allometric model (Chave *et al.* 2014) and a Global Wood Density Database (Zanne *et al.* 2009). Bole volumes were approximated by a classical Smalian method: $V = \frac{\pi}{4} \times FF \times H_B \times DBH^2$, where V is in m^3, FF is the form factor equal to 0.7, H_B and

TABLE 2. *Response variable, data set used, coefficient estimates (inter = intercept, θ_1 = DBH, θ_2 = logging intensity [LOG], θ_3 = date of recruitment since logging [RSL], θ_4 = date of census [DATE], θ_{CI} = crown illumination index [CI]), marginal (R^2m) and conditional (R^2c) goodness-of-fits, log likelihood (logLik), Bayesian Information Criterion (BIC), degree of freedom (df) ,and variance of random effects ($\sigma^2_{rd.ef}$) on total height (H_T), bole height (H_B) and crown/bole ratio (C/B) among all trees (N = 952) and trees censused in 2014 (N = 274).*

Response var.	Data	Inter.	θ_1	θ_2	θ_3	θ_4	θ_{CI4}	θ_{CI5}	R^2_m	R^2_c	LogLik	BIC	df	$\sigma^2_{rd.ef}$
H_T	All trees	1.585	0.504	−0.062	−0.002	0.002			0.50	0.66	339.95	−556.46	934	0.01
H_B	All trees	1.364	0.428	−0.096	−0.001	0.005			0.37	0.56	214.47	−305.50	934	0.02
C/B	All trees	0.856	−0.072	−0.017	0.001	0.046			0.19	0.38	760.09	−1396.75	934	0.09
H_T	2014	2.159	0.330	−0.055	0.001		0.011	0.034	0.38	0.56	239.25	−388.74	258	0.00
H_B	2014	1.293	0.447	−0.088	−0.003		0.017	0.013	0.24	0.44	96.48	−86.38	255	0.47
C/B	2014	0.766	0.001	−0.010	−0.001		0.000	0.014	0.04	0.08	248.51	−390.44	255	0.01

BDH are expressed in m. Above-ground tree biomass (AGB) and volume were computed using estimated heights at different logging intensities (10–50% AGB loss) and compared with those of trees not affected by logging.

Overall, DBH and logging intensity were the main predictors of total and bole heights (Table 2). While heights were positively correlated with diameter (θ_1, Table 2), logging intensity affected tree heights negatively (θ_2, Table 2). Post-logging recruitment and time since logging had only very limited effects on heights. Increasing crown illumination indices (CI) favored both total and bole heights (θ_{CI4} & θ_{CI5} > 0, Table 2). Overall, our models explained 44–66 percent of the variance observed in heights
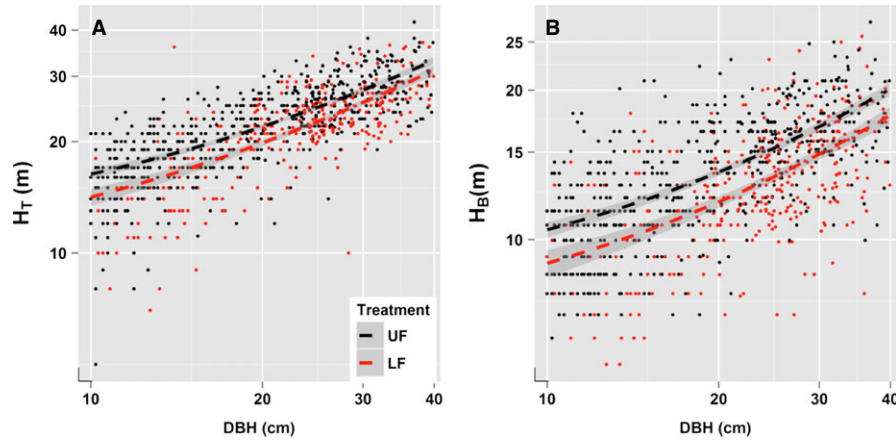

FIGURE 1. Total (H_T) and bole (H_B) heights (A and B respectively) in unlogged (UF) and logged forests (LF) that were selectively logged 11 (N = 678) and 25 (N = 274) years before measurement. OLS regressions (stripped lines) and error prediction envelopes are shown.
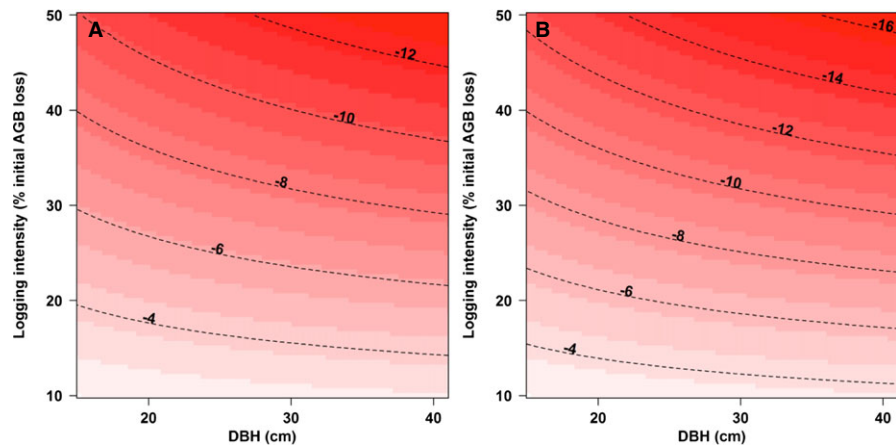

FIGURE 2. Predicted difference in tree AGB (A) or bole volume (B) 11 yr after logging in relation to increasing diameter and logging intensity.

(R_c^2, Table 2) of which 24–50 percent was from the fixed effects of species and plot (R_m^2, Table 2). Greater variation was found among bole heights in 2014 than among total heights, due to larger inter-species variability ($\sigma_{rd.ef.}^2$, Table 2). Crown/bole ratios were much more difficult to predict, with large residual variance. As for tree heights, crown/bole ratios were reduced by logging, but poorly explained by any predictor tested (R_m^2 range: 4–7%). At the stand level, average tree heights were 0.22–3.8 m shorter along a gradient of logging intensity of 10–50 percent AGB loss, compared with those from unlogged forest stands (Fig. 1). This reduction in heights resulted in a 2–13 percent reduction of aboveground tree biomass (Fig. 2A) and a 3–17 percent reduction in bole volume (Fig. 2B).

If the harvest of a few tall trees lower mean canopy heights (Okuda *et al.* 2004), we provide a strong evidence of a concomitant dwarfing effect among remnant trees. Our explanation of decreased heights lies into reduced light competition, due to the creation of canopy gaps. While many studies have explored the role of gaps in tree recruitment and diversity maintenance (*e.g.*, Chazdon & Fetcher 1984, Hubbell *et al.* 1999), our results suggest crown development at lower stature due to enhanced light conditions. While it might be argued that in the observed reduction in tree heights is temporary due to rapid gap closure, we observed little variation of H-DBH relationship over time (11 and 25 yr post-logging), with similar height reductions among recruited trees (*i.e.*, entering the 10 cm DBH class) up to a decade post-logging.

Bole heights were indeed more variable within and among species (Fig. 1) and harder to predict (Table 2). This likely reflects the variability of development phases at which trees have reacted to canopy openness. Observed bole reductions will in turn negatively affect future commercial stand volumes. If volume yields are to be sustained in managed forests, more trees will need to be harvested in the future. Such logging intensification would counter the current recommendation to reduce logging intensities in order to lower logging impacts in the tropics.

While the generality of our findings await tests across a wide range of logged forests, this study is a further evidence of the importance of accounting for tree height in forest carbon stock estimates (Hunter *et al.* 2013, Rutishauser *et al.* 2013). Overall, our study supports the idea of a net decrease in potential carbon sequestration and wood production in logged forests. It further highlights the importance of minimizing logging impacts in tropical forests.

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