Diameter Growth of Juvenile Trees after Gap Formation in a Bolivian Rain Forest: Responses are Strongly Species-specific and Size-dependent

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ABSTRACT

We evaluated growth responses to gap formation for juvenile individuals of three canopy rain forest species: *Peltogyne cf. heterophylla*, *Clarisia racemosa* and *Cedrelinga catenaeformis*. Gaps were formed during selective logging operations 7 yr before sampling in a Bolivian rain forest. We collected wood samples for tree-ring analyses at different distances to the stump (< 10, 10–40 and > 40 m) and from trees with different diameters (5–30 cm diameter at breast height [dbh]). Tree-rings width was measured in at least two radii and converted to average diameter growth. Changes in 7-yr median diameter growth before and after selective logging were analyzed. Diameter growth rates significantly increased by 0.7–0.8 mm/yr after gap formation for *P. heterophylla* and *C. catenaeformis*, but not for *C. racemosa*. We applied a multiple regression analysis to explain variation in growth responses of *P. heterophylla* and *C. catenaeformis* by distance to logging gap and tree size. For *P. heterophylla* we found that growth increase occurring close to logging gaps was strongest for large juvenile trees (20–25 cm dbh) and almost absent in small juveniles. For *C. catenaeformis*, variation in growth responses was not related to tree size or distance to gaps. Our results show that growth responses to gap formation strongly differ across species and tree sizes. This finding calls for caution in the interpretation of growth releases in tree-ring series, as gap formation does not necessarily invoke growth responses and if such growth responses occur, their strength is species- and size specific.

Foreign language abstract is available in the online version of this article.

Key words: *Cedrelinga catenaeformis*; *Clarisia racemosa*; increased light levels; juvenile growth response; *Peltogyne cf. heterophylla*; release; tree rings; tropics.

BIOTROPICA
THE JOURNAL OF TROPICAL BIOLOGY AND CONSERVATION

LIGHT CONDITIONS OF JUVENILE TREES GROWING IN THE UNDERSTORY OF TROPICAL FOREST VARY STRONGLY OVER TIME due to canopy dynamics (*e.g.*, Clark & Clark 1992). It is known from studies in permanent plots that diameter growth rates of those trees respond to such changes (*e.g.*, Clark & Clark 1992, Peña-Claros *et al.* 2008). Based on these studies, ecologists have pointed to light conditions as the main limiting factor for juvenile tree growth (*e.g.*, Hartshorn 1978, Martinez-Ramos *et al.* 1988, 1989, Clark & Clark 1992, Blundell & Peart 2001). Studies of tree-rings in tropical forests have recently gained interest as they allow reconstructing long-term patterns of diameter growth (*e.g.*, Worbes 1995, Worbes & Junk 1999, Brienen & Zuidema 2005, 2006a, b, Rozendaal *et al.* 2010a, b).

In tree-ring series of tropical and temperate species, distinct periods of fast and slow growth of juveniles are often recorded. These periods are identified by comparing radial tree-growth with mean radial growth of previous years on the same tree. Episodes of strongly increased radial growth in tree-ring series are called 'releases' if such elevated growth rates are sustained over several years. As light is thought to be the key limiting factor, such increases are considered to be caused by favorable changes in the light environment (*e.g.,* Wright *et al.* 2000, Baker & Bunyavejchewin 2006, Coomes & Allen 2007). If tree-ring widths reveal a much slower growth over a certain number of years, this is called 'suppression.' One of the difficulties in the analysis of releases and suppressions from tree-ring series is that no information is available on historical light conditions. Without such information the interpretation of release events remains difficult. So far, several methods and various criteria have been used that yielded very different results (Black & Abrams 2003, 2004, Rubino *et al.* 2004). Thus there is a strong need to improve the interpretation of temporal growth variation in tree-ring series using empirical information on responses of trees to real increases in light interception.

Forests where trees have been felled for timber production provide the opportunity to analyze changes in diameter growth resulting from gap formation that occurred at the same time. Since light conditions change in a gradient away from a logged tree (Asner *et al.* 2004), it is possible to assess whether growth responses of remaining trees are correlated with the distance to the disturbance.

In this study we used tree-ring analysis to evaluate the growth changes of juvenile understory trees over 7 yr before and after

Received 6 August 2010; revision accepted 8 May 2011.
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selective logging in a managed forest in northeast Bolivia. The effect of the distance from the logged trees was evaluated for three canopy species *Peltogyne cf. heterophylla*, *Clarisia racemosa* and *Cedrelinga catenaeformis* (two shade-tolerant and one long-lived pioneer species, respectively). We address the following questions: first, does gap formation increase diameter growth? Second, are growth responses related to the distance from the logged tree? Third, do growth responses differ among species? And finally, is the growth response related to tree diameter? We expect that the results on the responses of tree species to a known disturbance will provide insights on forest dynamics after gap formation.

METHODS

STUDY AREA AND SPECIES.—The study was carried out at the Forest Stewardship Council (FSC) certified logging concession 'Los Indios' (10°26′ S, 65°33′ W) located at 86 km northeast of the town of Riberalta, Bolivia. Mean annual precipitation is 1690 mm and mean annual temperature is 27°C (Riberalta, 11°00′ S 66°07′ W, averages for 1943–2007 and 1951–2004, respectively). Forests in the region are semi-deciduous with a dense canopy at 30–35 m and some emergent trees up to 45 m. The overstory is composed of trees of 15–25 m and a shrub level of variable density of 1–6 m height (Navarro & Maldonado 2006). Density of stems larger than 10 cm diameter at breast height (dbh) is 423 stems/ha (Toledo *et al.* 2008).

The parcel within the concession where the study took place was selectively logged during May to September 2001. It has an area of 4759 ha and corresponds to the Annual Logging Area 1999 (ALA 1999). Selective logging included 16 species (*Alnus acuminata*, *Dipteryx odorata*, *Cedrela odorata*, *Phyllostylon rhamnoides*, *Couratari macrosperma*, *Couratari* sp., *Heisteria spruceana*, *Pithecellobium corymbosum*, *C. catenaeformis*, *Peltogyne* sp., *Cordia* sp., *Tabebuia serratifolia*, *Enterolobium contortisiliquum*, *Enterolobium* sp2, *Amburana cearensis*, and *Cariniana estrellensis*) and the logging intensity was 1.4 trees/ha. Logging in the area was conducted following standards of Reduced Impact Logging (RIL; Pinard & Putz 1996), *i.e.*, lianas were removed (approximately 1 yr before logging), skidder trails and directional felling were planned according to the ALA 1999 map, and streams and seedlings of the trees were identified in this map. In August 2008, we selected this area for fieldwork knowing that since logging in 2001 no further disturbances had taken place. This allowed us to evaluate diameter growth during 7 yr after the disturbance and compare that to the 7 yr before logging.

We established 56 transects in order to locate logging gaps. We based decisions about length and direction of transects on the ALA map. The length of transects was 1000–1500 m and 120 m wide (60 m on both sides). Transects started from main and secondary extraction roads. The main road divides ALA 1999 in two halves and was kept open because it is used to access other ALAs. Secondary extraction roads were often difficult to access but allowed us to reach the limits of the area. Transects avoid the effect of the main and secondary roads by starting at more than 100 m and 50 m away from them, respectively. We avoided areas near streams or on slopes. Transects covered a total area of 834 ha.

We studied three canopy tree species of relevance for their timber value and of interest for their differences in shade tolerance: *P. cf. heterophylla*, *C. racemosa* and *Cedrelinga catanaeformis* (hereafter referred to by genus name). Characteristics of the study species are listed in Table 1. Tree-ring studies have been conducted before on each of these species (Brienen & Zuidema 2005, 2006a, b, Brienen *et al.* 2006, Rozendaal *et al.* 2010a, b) and the annual nature of juvenile rings has been established (Soliz-Gamboa *et al.* 2011). *Peltogyne* and *Cedrelinga* were listed for selective logging in ALA 1999. *Clarisia* was included in the selective logging list of the concession since the year 2000 (ALA 2000).

DATA COLLECTION AND TREE-RING MEASUREMENTS.—We selected juvenile individuals of the three study species on the basis of two criteria: distance to stumps or crowns of logged trees and tree diameter. As it is difficult to identify gap edges after 7 yr, we took the position of the stump or crown of a logged tree as the center of the logging gap. Per species, we aimed to select an equal number of trees from each of three distance categories: trees within 10 m distance from the stump or crown of a logged tree, or from a skidder trail (A); trees at 10–40 m from the stump or crown of a logged tree (B); and trees farther than 40 m from the stump or crown of a logged tree (C). For each of these distance categories we selected approximately 30 trees per species, evenly distributed over three diameter categories. These diameter categories slightly differed across species. For *Peltogyne* and *Clarisia* we employed categories of 5–10, 10–20, and 20–25 cm dbh while for *Cedrelinga* this was 10–15, 15–25, and 25–30 cm dbh. We explicitly avoided sampling badly damaged trees.

TABLE 1. *Characteristics of the study species and collected samples.*

			Leaf fall behavior		Collected samples		
Species	Family	Ecological group[a]	Juvenile	Adult	No.	dbh range[e]	Min. Age[f]
Clarisia racemosa Ruiz & Pavón	Moraceae	Shade- tolerant[b]	Evergreen[b]	Evergreen[c]	76	5–25	30
Peltogyne cf. *heterophylla* M.F.Silva	Fabaceae	Shade- tolerant[b]	Evergreen[b]	Brevi-deciduous[d]	94	5–25	59
Cedrelinga catenaeformis Ducke	Fabaceae	Ligth-demanding [c]	Evergreen[b]	Brevi-deciduous[d]	61	10–30	34

[a]Defined on the light dependence of regeneration, all study species are canopy species. [b]Personal observations. [c]Mostacedo *et al.* (2003). [d]Pinard *et al.* (1999). [e]dbh measured in centimeters at 1.30 m height. [f]Minimum age of the samples determined by tree-ring counting.

For each of the selected individuals, we calculated the Canopy Closure Index (CCI; Lieberman & Lieberman 1989, 1995). The index gives a relative measure of the shading at crown level of the focal tree. It does so by using the density and height of the trees neighboring the focal tree. The neighboring trees taken into account were those standing within ten meters from the focal tree (Lieberman *et al.* 1995). For each taller neighboring tree of a focal tree, we determined the horizontal distance to the focal tree (d) and the difference in height with the focal tree (ΔH), and used these to calculate the hypotenuse (h). We then calculated the sine of the angle θ that is formed by h and d, as $\sin\theta = \Delta H/h$. Finally the CCI for each focal tree was obtained by summing the $\sin\theta$ values of all taller trees around the focal tree. Low CCI values indicate a low degree of overshadowing by neighboring trees. Trees near stumps or crowns of logged trees were expected to have a lower CCI in comparison with trees farther away, which may still be surrounded by an undisturbed patch of forest. Tree height was estimated with a clinometer to the nearest centimeter.

From each of the selected trees we collected samples for tree-ring analysis. The number of samples varied among species (see Table 1); all samples were collected at 50 cm height. For all three species, tree discs (cross-sections) were collected from trees up to 20 cm dbh using a chainsaw. Trees larger than 20 cm dbh were collected in two ways for *Peltogyne* and *Clarisia*, (1) half of the trees of 20–25 cm dbh were sampled using a 22-mm increment borer mounted on a motor (Stihl BT42), and (2) the rest of the samples consisted of a piece of less than one-third of the tree diameter collected with a chainsaw. For *Cedrelinga* all samples from trees of 20–30 cm dbh were collected using the 22-mm increment borer. All cores were immediately mounted on a wooden support. All samples were air-dried and polished using grits up to 1000 µm. In order to improve the quality of the sanding, *Peltogyne* and *Clarisia* samples were polished in a constant flow of water.

Tree rings in the discs, cores and pieces were first identified in at least two radii, subsequently they were dated following the Schulman (1956) convention by which the last formed ring belongs to 2007, and finally they were visually cross-dated within each sample. Then, ring widths were measured to the nearest 0.01 mm using a LINTAB 5 measurement device and TSAP software (Rinntech). The radial tree-ring series were averaged per sample to correct for irregular growth, and then converted into diameter growth series. We corrected for shrinkage due to desiccation by rescaling the diameter growth series by the ratio of radii of fresh and dry discs.

DATA ANALYSIS.—To facilitate the data interpretation and to improve our knowledge of the study species we first checked all Pearson correlations between measurements done on the study trees (*i.e.*, dbh, height and age). Then we proceed to evaluate the type of relationships between dbh and height (D:H) and dbh and age (D:A) by fitting the data to several curve types. We only included trees of which the pith was comprised in the wood sample, so that the age could be estimated. Finally, in order evaluate differences in the D:H relationships among the species we performed an ANCOVA with height as the dependent variable and diameter and species as predictors. We performed *post-hoc* test to check for differences in the y-intercept among the species. For all the analysis mentioned above we used solely data from trees of distance category C, for which no effect of logging gaps on growth was expected.

To evaluate the effect of selective logging on light conditions after 7 yr, we tested for differences in Canopy Closure Index (CCI) among distance categories (A, B and C) within and among species. Within species we tested using a regression analysis with CCI as dependent variable and distance category, dbh and their interaction as independent variables. To test among species we used CCI as dependent variable and species, dbh and their interaction as independent variables. CCI was log-transformed before the analysis to account for its non-linear relation with dbh.

For the subsequent analysis we used the median diameter growth of 7 yr. We chose to use a 7-yr period because that was the time passed since logging took place and as it averages out year-to-year variation in diameter growth. Preliminary tests that used shorter periods and excluded several years after logging yielded a lower amount of positive differences between periods at lower confidence intervals. We tested for differences in the median diameter growth between 7 yr both the logging event (1994–2000) and 7 yr after the logging event (2001–2007). We first calculated the percentage of samples in which the 7-yr median growth after logging was larger than the 7-yr median before the logging. Second, as the distribution of median diameter growth data was non-normal, we used multiple Wilcoxon signed-rank tests to evaluate differences per distance category. It is important to notice that the period after logging includes the year 2001. This may seem confusing because it is the same year in which the logging took place, but logging occurred before the onset of ring formation, which usually starts in the rainy season (from October onwards).

Finally, due to the lack of a non-parametrical test equivalent to mixed repeated measures ANOVA, we used the resulting change in growth (Δgrowth) between the period before and after logging, in a multiple regression analysis. In this way we could evaluate the effect of tree diameter and distance category on Δgrowth. We created dummy variables for the distance categories with category C as control and also took interaction between distance category and tree diameter into account. Multiple regressions were performed using forward variable selection. All statistical analyses were performed using SPSS v.16

RESULTS

DIAMETER VS. HEIGHT AND DIAMETER VS. AGE RELATIONSHIPS.—A significant Pearson correlation ($P < 0.01$) between dbh and height was found for all the species. Significant correlations between dbh and age, as well as between height and age, were found for *Peltogyne* and *Clarisia* ($P < 0.01$) but not for *Cedrelinga* (Table 2). Furthermore, the evaluation of the best curve fit for the relationships D:H and D:A showed that both linear and logarithmic models can be used to characterize these relationships (Fig. S1).

The analysis of differences in height across the species (ANCOVA) showed that *Cedrelinga* is significantly taller than *Peltogyne* but not than *Clarisia* ($R^2 = 0.72$; $P < 0.05$; data not shown).

TABLE 2. *Pearson correlations of dbh, height and age of the study species. Only trees far away from logging gaps (i.e., category C) are included. Shown are correlation coefficients and sample sizes (between parentheses).* **P < 0.01; [a]*marginally significant (0.05 < P < 0.10) and* [ns]*non-significant.*

	Peltogyne	Clarisia	Cedrelinga
dbh vs. height	0.93 (33)**	0.90 (26)**	0.60 (20)**
dbh vs. age	0.62 (29)**	0.85 (20)**	0.40 (21)[a]
Height vs. age	0.68 (29)**	0.88 (20)**	0.29 (20)[ns]

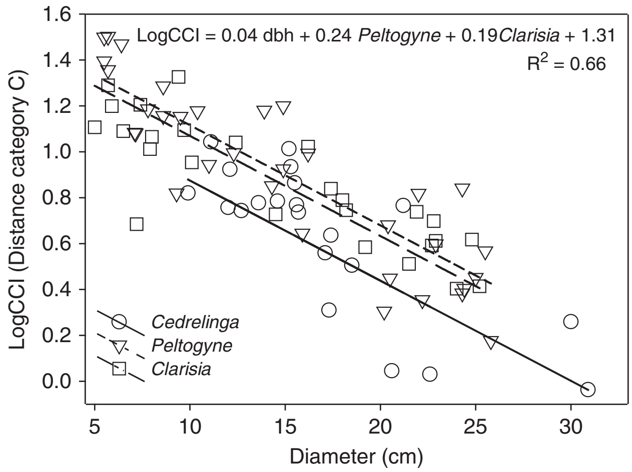

FIGURE 2. Canopy closure index (CCI) of trees growing in undisturbed conditions (> 40 m from logging stump) in relation to diameter and species. CCI values for *Cedrelinga* were clearly lower than those for *Peltogyne* and *Clarisia*.

LIGHT CONDITIONS.—Values of CCI varied strongly within the species, among individuals of similar diameter and across different diameter sizes. In spite of the high degree of variation, the overall pattern of CCI values in relation to tree size and distance was comparable among species (Fig. 1). Multiple regression models showed a significant negative relationship between CCI and diameter ($P < 0.001$) for all species (Fig. 1). Furthermore, in two out of three species, light conditions differed for trees close to logging stumps compared with those farther away (*i.e.*, slopes differed among lines in Fig. 1). Thus, 7 yr after logging took place the CCI for these species was lower close to the logging gaps (Fig. 1). More specifically, for *Peltogyne*, the CCI of trees in the distance categories A (within 10 m from the stump) and B (10–40 m from the stump) differed significantly from trees in C (> 40 m away from the stump) (Fig. 1), *i.e.*, trees in distance category C had a darker environment than those in distance categories A and B. For *Clarisia*, the CCI of trees in distance category A differed from those in B and C (Fig. 1). Trees in distance category A were in lighter conditions than those in distance category B and C. This difference, however, was not the same for all diameters as shown by the interaction between diameter and distance category A. Thus, the difference in CCI between the A and C categories was stronger for large trees than for small ones. This could be reflecting a rapid overgrown of smaller trees by faster growing neighbors. By contrast, no effect of distance on CCI was found for *Cedrelinga* (Fig. 1).

The multiple regression analysis performed per distance category using CCI as dependent variable and diameter and species as predictors, showed that there is no effect of species on the light conditions of the study trees in Distance category A and B. An effect of species, however, was detected for distance category C, whereas CCI was lower for *Cedrelinga* compared with the other two species (multiple regression; $R^2 = 0.66$; $P < 0.05$; Fig. 2). Thus, *Cedrelinga* trees occur in higher light conditions compared with *Peltogyne* or *Clarisia* trees of the same diameter size.

CHANGES IN DIAMETER GROWTH AFTER LOGGING.—The changes in tree growth after logging varied between individuals. We observed all three possible types of changes following logging: increased growth, no detectable change and reduced growth (Fig. 3). The distribution of growth changes (of 7-yr median growth) is shown in Fig. 4. These boxplots also show that diameter growth varied strongly between individuals in the period before and after logging and that this variation was similar in all the species (Fig. 4).

The percentage of samples in which the 7-yr median growth after logging was larger than the 7-yr median before the logging was greater than 50 percent for all species in all distance categories, only *Peltogyne* in distance category C reported a lower value (38.24%; ns; Table 3). We assessed the difference in diameter growth before and

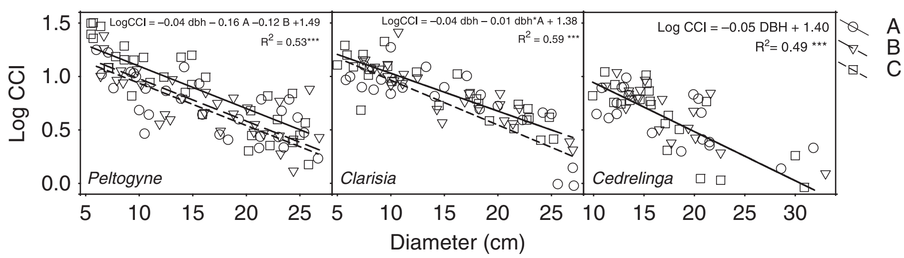

FIGURE 1. Multiple regression models showing a significant negative relationship between Canopy closure index (CCI) and diameter ($P < 0.001$) for all species. Scatter plots show all trees in three distance categories: A, < 10 m, circles; B, 10–40 m, triangles; C, > 40 m, squares. Regression lines are shown for each distance category from logged trees: A, dotted line; B, dashed line; C, solid line. The models for *Peltogyne* and *Clarisia* showed that light conditions differed for trees close to logging stumps compared with those farther away from these stumps. No effect of distance on CCI was detected in *Cedrelinga* (see text for more details).

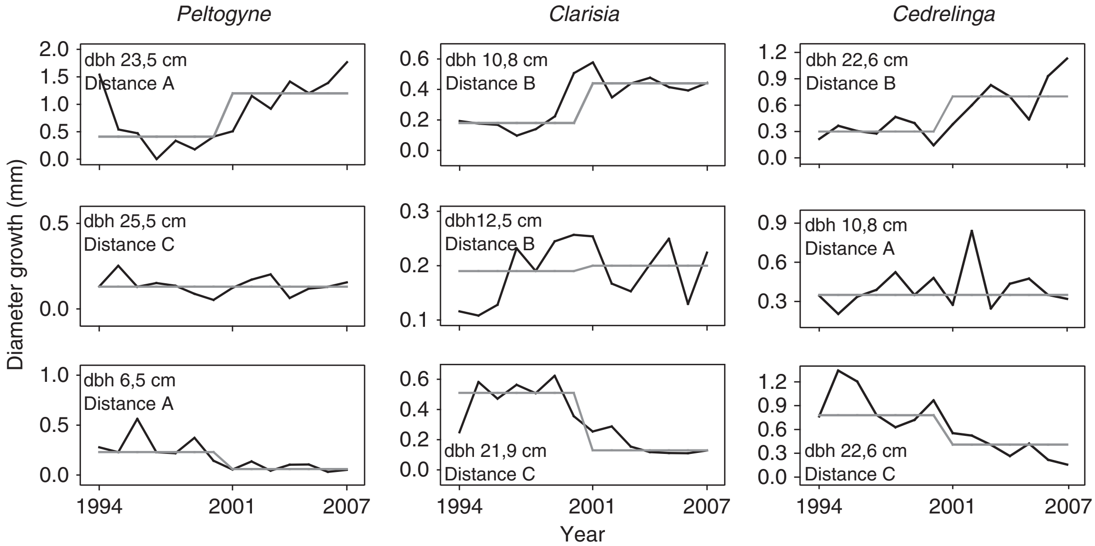

FIGURE 3. Examples of annual diameter growth rates of juvenile trees before and after a logging event in 2001. Some trees show apparent changes in growth while others maintain the same growth rate. The gray line shows the median growth prior and post logging. The diameter (dbh) and distance categories of the trees are indicated for each curve. In distance A, trees were less than 10 m from stump; distance B, trees are between 10 and 40 m from stump and in distance C, trees are > 40 m from stump.

after logging (Δgrowth) and the overall sign of this difference using a paired test, and checked which of the measured factors may explain the magnitude of these differences. The Wilcoxon test showed that diameter growth rates before and after logging were significantly different for *Peltogyne* and *Cedrelinga* while no differences were detected for *Clarisia* (Table 3). The sign of the *z*-score indicates that post-logging diameter growth was higher than pre-logging values (Table 3).

We evaluated the effect of tree diameter and distance category on Δgrowth for *Peltogyne* and C*edrelinga*. We restricted the tests to these two species as Δgrowth differed significantly from zero in these species (Table 3). For *Peltogyne* we found a significant effect of diameter and of the interaction of Δgrowth and distance categories, with distance category A having a steeper slope. (Fig. 5; Table S1), demonstrating that positive changes in diameter growth depended on the relationship between diameter and distance to the stump. Thus, large-size trees were likely to experience an increase in diameter growth when close to stump. It is important to notice that for trees farther away from the stump or crown of felled trees (B and C categories), diameter had no effect on Δgrowth. In contrast, no effect of any of the independent variables (diameter, distance and their interaction) on Δgrowth was detected for *Cedrelinga*.

DISCUSSION

TEMPORAL CHANGES IN LIGHT CONDITIONS.—Our results revealed strong variation in light conditions among individuals of our study species (Fig. 1). Partially, this variation can be explained by the size-dependence of light conditions that is typically found for tropical trees (Poorter *et al.* 2005, Brienen *et al.* 2009). Trees that have reached a larger diameter are taller and intercept more light. Strong variation in light conditions was, however, also observed among individuals of similar diameter. Part of this variation is explained by the distance to the logged tree, *i.e.*, closer to gaps the increase on light availability is more persistent over time, in both logging and naturally occurring gaps (Asner *et al.* 2004, Van der Meer 1996, Sterck 1999). Additionally, random distribution of similar diameter-size trees in the forest light gradient has been shown to be a common pattern (Lieberman *et al.* 1995) and may account for the remaining variation in light conditions among individuals.

An effect of selective logging on light conditions of trees close to the logging stump was found for *Peltogyne* and *Clarisia*, but no effect could be detected for *Cedrelinga* (Fig. 1). These differences may be due to spatial heterogeneity in light conditions (Lieberman & Lieberman 1989, 1995, Clark & Clark 1992) and species-specific regeneration niches (Denslow 1980, Clark & Clark 1992, Poorter *et al*. 2005). Our results on differences of CCI among species (Fig. 2) indicate that in undisturbed conditions (distance category C) *Cedrelinga* trees occur in lighter conditions than *Peltogyne* or *Clarisia* trees. This result suggests that *Cedrelinga* has a distinct regeneration niche and may explain why selective logging does not change light conditions for this species. Additionally, *Cedrelinga* trees showed to be significantly taller than *Peltogyne* but not than *Clarisia* ($R^2 = 0.72$; $P < 0.05$; data not shown). This result strengthens the idea of a different regeneration niche of *Cedrelinga*. It also indicates that diameter–height relationships are different across species, as suggested by Rozendaal (2010).

The absence of detectable differences among species in CCI for the distance between categories A and B may also be considered as an indicator of the logging effect on light conditions, *i.e.*, *Peltogyne* and *Clarisia* trees present light conditions after logging comparable with those of *Cedrelinga* before logging. On the other hand,

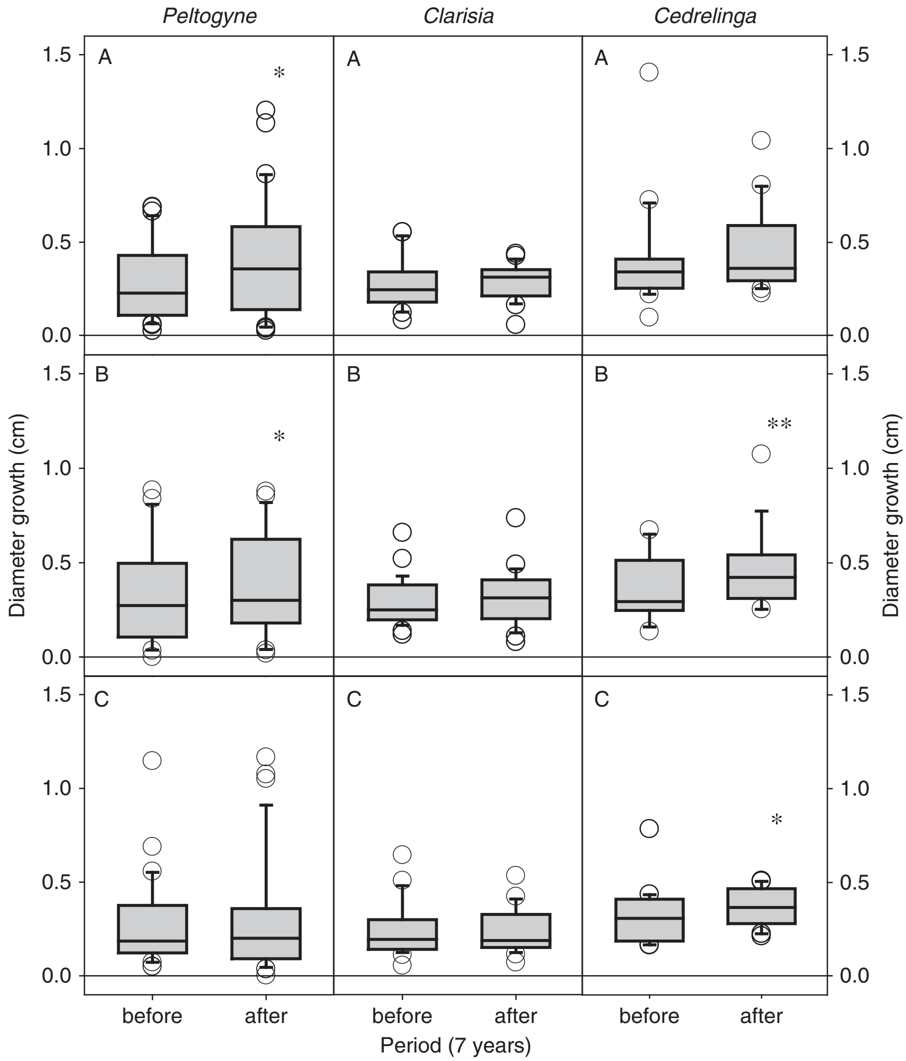

FIGURE 4. Box plots of 7-yr median diameter growth before and after selective logging for sampled trees of all sizes in three distance categories (< 10 m: A; 10–40: B and > 40 m: C). Marks above the boxplot indicate whether the diameter tree growth after the disturbance was higher than before ($^{*}P < 0.05$; $^{**}P < 0.01$).

this result may also indicate that important growth in height took place in the last 7 yr, allowing trees to increase light capture at crown level; however, we lack data to support this hypothesis.

VARIATION IN RESPONSE TO INCREASED LIGHT.—The change in diameter growth of individual trees due to disturbance caused by selective logging was highly variable within species (Figs. 3 and 4). This variation may be caused by differences in the degree of increase in light conditions of the 'gap' trees (Jones & Thomas 2004), differences in individual tree-growth histories (*e.g.*, Wright *et al.* 2000, Palomaki *et al.* 2006, Miya *et al.* 2009), differences in growth rates among trees of different size or age (*e.g.*, Wright *et al.* 2000), variation in the increase of heat load experienced by the gap trees and time for physiological acclimation (Bebber *et al.* 2004), and variation in crown area and damage caused by selective logging that was no longer visible at the moment of sampling (Jones & Thomas 2004). Without additional measurements on these variables, it is difficult to explain the variation in growth responses among gap trees. More detailed studies in which light conditions are measured before and after disturbances and responses are measured in terms of crown expansion, height growth and photosynthetic responses will help to better understand those individual tree responses.

Despite the high degree of variation in growth response to increased light, we found an overall positive response of diameter growth to gap formation (Table 3). This response was significant for two of the three species (Fig. 4; Table 3). Contrary to our expectations, C*larisia* did not show a response to gap formation (Table 3), in spite of the finding that light conditions of this species increased close to logging gaps. Shade-tolerant species may not be able to respond to high–light conditions due to photoinhibition or slow acclimation of leaves to high–light conditions (Bebber *et al.* 2004, Jones & Thomas 2004), but it is unclear whether these factors would also impede growth responses over a 7-yr period.

For *Peltogyne*, we found an overall positive response of diameter growth to gap formation, a pattern that was consistent with our expectation. However, the stronger response of large trees

TABLE 3. *Percentage of samples in which the median diameter growth after logging is larger than prior logging (%) and the Wilcoxon paired test of the median diameter growth of the study species before and after the logging event at different distances from stumps. Distance A: < 10 m from stump or crown of logged tree; Distance B: 10–40 m from stump or crown; Distance C: > 40 m from stump or crown. z, z-score; *P < 0.05, **P < 0.01 and ns, non-significant.*

	Distance A		Distance B		Distance C	
Species	%	*z*	%	*z*	%	*z*
Peltogyne	66.67	− 2.33*	65.52	− 2.26*	38.24	− 0.30 ns
Clarisia	60.87	− 0.52ns	62.96	− 1.43 ns	53.85	− 0.36 ns
Cedrelinga	57.14	− 1.37ns	73.68	− 2.85**	71.43	− 2.19*

(> 15 cm dbh) was unexpected, as previous findings suggested that small, suppressed trees would respond more strongly to increased light conditions (Lorimer *et al.* 1988, Black and Abrams 2004, Black *et al.* 2009, but see Miya *et al.* 2009). Our results showed a weak response of small *Peltogyne* individuals (5–15 cm dbh) to gap formation. Although these results contrast those of many earlier studies, they are consistent with those presented by Miya *et al.* (2009). These authors suggested that stronger response to increased light by larger trees may be more frequent than expected given that smaller individuals could be negatively affected by crowding, which may be the factor limiting their diameter growth.

The growth response to gap formation of *Cedrelinga* was rather complex. We did not find increased growth of trees occurring close to the logging gaps (<10 m), but growth increases were found for trees at longer distances. For the latter trees, however, no evidence for increased light conditions was found. Additionally, growth changes were not found to be size-dependent. There are a couple of possible explanations for this finding. First, we had a smaller number of samples for this species (61) compared with the other species (Table 1), which could prevent finding a treatment effect. Second, tree size could be a weak proxy of tree performance for this

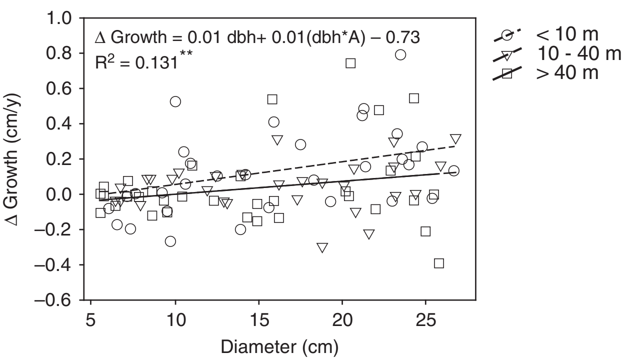

FIGURE 5. Effect of diameter and diameter × distance interaction on change in diameter after gap formation for *Peltogyne*. The change in diameter growth increased with diameter and this relation was different for distance category A compared with categories B and C.

species; individual life history could be a more reliable predictor (Grogan & Landis 2009). Third, being a light-demanding species, this species may respond to increased light levels with maximized resource allocation to height growth (Blundell & Peart 2001, Montgomery & Chazdon 2001, Coutand *et al.* 2010), at the cost of diameter growth (Montgomery & Chazdon 2001, Rozendaal 2010). Fourth, responses to gap formation may be concentrated in the first couple of years (Peña-Claros *et al.* 2008) and could therefore be undetectable over a period of 7 yr.

Studies including more samples and taking into account changes in height growth and crown development as well as more precise measurements of changes in light conditions (*i.e.*, gap size, PAR), competition, heat load, and water stress are needed for a better understanding of the tree growth response to increased light levels.

CONSEQUENCES FOR INTERPRETATION OF RELEASES.—A wide range of criteria for the detection of releases from tree-ring series have been developed and applied (Rubino *et al.* 2004, Black *et al.* 2009). These methods are based on the identification of periods of increased growth, 'releases.' In most cases, releases found in tree-ring series are interpreted as periods in which trees experienced high light levels. However, only few studies (Nowacki & Abrams 1997, Fraver & White 2005, Miya *et al.* 2009) have actually evaluated the real response of species to increased light levels, and used this information to interpret temporal growth variation in tree-ring series. It is remarkable that suppression-release studies in which thresholds were based on empirical knowledge of the species-specific effect of increased light level applied very different thresholds to detect releases compared with studies that did not have such information. For example, Nowacki & Abrams (1997) needed to adjust the threshold of percentage growth change (%GC) from 100 to 25% GC to be able to detect empirically known disturbances.

Our results show that the responses to gap formation are highly species specific and diameter dependent, with small trees being less responsive than large trees. This suggests that responses to gap formation are not simple and are hard to predict: many factors, both inherent and external, may affect tree growth (Cook 1987, Nowacki & Abrams 1997). Therefore, individual tree responses to given disturbances may vary to a great extent. This has important consequences for the interpretation of releases in tree-ring series. The strong species specificity of responses to gap formation suggests that application of the same threshold to detect releases for different species very likely results in erroneous differences between species. Furthermore, the detection of size-dependency in growth responses to gap formation indicates that size-dependent release thresholds probably provide a more realistic detection of release periods in tree-ring series. In all, our study clearly calls for a cautious interpretation of releases detected in tree-ring data.

ACKNOWLEDGMENTS

We thank Danaë Rozendaal, Edwin Rodriguez, Edmundo Pino, Rene Aramayo, Miguel Cuadiay, Albert Raven and many others for assistance during fieldwork, and staff of PROMAB-UAB for logistic support. Logging company 'MABET' granted permission to work in their concessions and provided logistic support. Marinus Werger provided constructive comments on earlier versions of the manuscript. PAZ was supported by ERC grant no. 242955.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article.

TABLE S1. *ANOVA table for forward multiple regression analyses of* Δ *growth of* Peltogyne *as dependent variable and independent variables.*

FIGURE S1. Curve fitting for the D:H relationship and curve fitting for the D:A relationship.

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LITERATURE CITED

ASNER, G. P., M. KELLER, R. PEREIRA, J. C. ZWEEDE, AND J. N. M. SILVA. 2004. Canopy damage and recovery after selective logging in amazonia: Field and satellite studies. Ecol. Appl. 14: S280–S298.

BAKER, P. J., AND S. BUNYAVEJCHEWIN. 2006. Suppression, release and canopy recruitment in five tree species from a seasonal tropical forest in western Thailand. J. Trop. Ecol. 22: 521–529.

BEBBER, D. P., S. C. THOMAS, W. G. COLE, AND D. BALSILLIE. 2004. Diameter increment in mature eastern white pine *Pinus strobus* L. following partial harvest of old-growth stands in Ontario, Canada. Trees-Struct. Funct. 18: 29–34.

BLACK, B. A., AND M. D. ABRAMS. 2003. Use of boundary-line growth patterns as a basis for dendroecological release criteria. Ecol. Appl. 13: 1733–1749.

BLACK, B. A., AND M. D. ABRAMS. 2004. Development and application of boundary-line release criteria. Dendrochronologia 22: 31–42.

BLACK, B. A., M. D. ABRAMS, J. S. RENTCH, AND P. J. GOULD. 2009. Properties of boundary-line release criteria in North American tree species. Ann. For. Sci. 66.

BLUNDELL, A. G., AND D. R. PEART. 2001. Growth strategies of a shade-tolerant tropical tree: The interactive effects of canopy gaps and simulated herbivory. J. Ecol. 89: 608–615.

BRIENEN, R. J. W., E. LEBRIJA-TREJOS, P. A. ZUIDEMA, AND M. MARTINEZ-RAMOS. 2009. Climate-growth analysis for a Mexican dry forest tree shows strong impact of sea surface temperatures and predicts future growth declines. Global Change Biol.

BRIENEN, R. J. W., AND P. ZUIDEMA. 2005. Relating tree growth to rainfall in Bolivian rain forests: A test for six species using tree ring analysis. Oecologia 146: 1–12.

BRIENEN, R. J. W., AND P. ZUIDEMA. 2006a. Lifetime growth patterns and ages of Bolivian rain forest trees obtained by tree ring analysis. J. Ecol. 94: 481–493.

BRIENEN, R. J. W., AND P. ZUIDEMA. 2006b. The use of tree rings in tropical forest management: Projecting timber yields of four Bolivian tree species. Forest Ecol. Manage. 226: 256–267.

BRIENEN, R. J. W., P. A. ZUIDEMA, AND H. J. DURING. 2006. Autocorrelated growth of tropical forest trees: Unraveling patterns and quantifying consequences. Forest Ecol. Manage. 237: 179–190.

CLARK, D. A., AND D. B. CLARK. 1992. Life history diversity of canopy and emergent trees in a neotropical rain forest. Ecol. Monogr. 62: 315–344.

CLARK, D. A., AND D. B. CLARK. 1994. Climate-induced annual variation in canopy tree growth in a Costa Rican tropical rain forest. J. Ecol. 82: 865–872.

COOK, E. R. 1987. The decomposition of tree-ring series for environmental studies. Tree-Ring Bull. 47: 37–59.

COOMES, D. A., AND R. B. ALLEN. 2007. Effects of size, competition and altitude on tree growth. J. Ecol. 95: 1084–1097.

COUTAND, C., M. CHEVOLOT, A. LACOINTE, N. ROWE, AND I. SCOTTI. 2010. Mechanosensing of stem bending and its interspecific variability in five neotropical rainforest species. Ann. Bot. 105: 341–347.

DENSLOW, J. S. 1980. Gap partitioning among tropical rainforest trees. Biotropica 12: 47–55.

FRAVER, S., AND A. S. WHITE. 2005. Identifying growth releases in dendrochronological studies of forest disturbance. Can. J. For. Res. 35: 1648–1656.

GROGAN, J., AND R. M. LANDIS. 2009. Growth history and crown vine coverage are principal factors influencing growth and mortality rates of big-leaf mahogany *Swietenia macrophylla* in Brazil. J. Appl. Ecol. 46: 1283–1291.

HARTSHORN, G. S. 1978. Tree falls and tropical forest dynamics. Tropical trees as living systems. Cambridge University Press, Cambridge, 617–638.

JONES, T. A., AND S. C. THOMAS. 2004. The time course of diameter increment responses to selection harvests in *Acer saccharum*. Can. J. For. Res. 34: 1525–1533.

LIEBERMAN, M., AND D. LIEBERMAN. 1989. Forests are not just Swiss cheese: Canopy stereogeometry of non-gaps in tropical forests. Ecology 70: 550–552.

LIEBERMAN, M., D. LIEBERMAN, R. PERALTA, AND G. S. HARTSHORN. 1995. Canopy closure and the distribution of tropical forest tree species at La Selva, Costa Rica. J. Trop. Ecol. 11: 161–177.

LORIMER, C. G., L. E. FRELICH, AND E. V. NORDHEIM. 1988. Estimating gap origin probabilities for canopy trees. Ecology 69: 778–785.

MARTINEZ-RAMOS, M., E. ALVAREZ-BUYLLA, AND J. SARUKHAN. 1989. Tree demography and gap dynamics in a tropical rain forest. Ecology 70: 555–558.

MARTINEZ-RAMOS, M., E. ALVAREZ-BUYLLA, J. SARUKHAN, AND D. PINERO. 1988. Treefall age determination and gap dynamics in a tropical forest. J. Ecol. 76: 700.

MIYA, H., T. YOSHIDA, AND M. NOGUCHI. 2009. Individual growing conditions that affect diameter increment of tree saplings after selection harvesting in a mixed forest in northern Japan. J. For. Res. 14: 302–310.

MONTGOMERY, R. A., AND R. L. CHAZDON. 2001. Forest structure, canopy architecture and light transmittance in tropical wet forests. Ecology 82: 2707–2718.

MOSTACEDO, B., J. JUSTINIANO, M. TOLEDO, AND T. FREDERICKSEN. 2003. Guía dendrológica de especies forestales de Bolivia (2nd edition). EL PAIS, Santa Cruz, Bolivia.

NAVARRO, G., AND M. MALDONADO. 2006. Geografia ecológica de Bolivia: Vegetacion y Ambientes Acuaticos (4th edition). Centro de Ecologia Simon I. Patiño, Departamento de Difusión, Cochabamaba, Bolvia.

NOWACKI, G. J., AND M. D. ABRAMS. 1997. Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. Ecol. Monogr. 67: 225–249.

PALOMAKI, M. B., R. L. CHAZDON, J. P. ARROYO, AND S. G. LETCHER. 2006. Juvenile tree growth in relation to light availability in second-growth tropical rain forests. J. Trop. Ecol. 22: 223–226.

PEÑA-CLAROS, M., T. S. FREDERICKSEN, A. ALARCÓN, G. M. BLATE, U. CHOQUE, C. LEAÑO, J. C. LICONA, B. MOSTACEDO, W. PARIONA, Z. VILLEGAS, AND F. E. PUTZ. 2008. Beyond reduced-impact logging: Silvicultural treatments to increase growth rates of tropical trees. For. Ecol. Manag. 256: 1458–1467.

PINARD, M. A., AND F. E. PUTZ. 1996. Retaining forest biomass by reducing logging damage. Biotropica 28: 278–295.

PINARD, M. A., F. E. PUTZ, D. RUMÍZ, R. GUZMÁN, AND A. JARDIM. 1999. Ecological characterization of tree species for guiding forest management decisions in seasonally dry forests in Lomerío, Bolivia. For. Ecol. Manag. 113: 201–213.

POORTER, L., F. BONGERS, FJ. STERCK, AND H. WÖLL. 2005. Beyond the regeneration phase: Differentiation of height-light trajectories among tropical tree species. J. Ecol. 93: 256–267.

ROZENDAAL, D. M. A. 2010. Looking backwards: Using tree rings to evaluate long-term growth patterns. PROMAB scientific series, Vol. 2. Utrecht University, Utrecht.

ROZENDAAL, D. M. A., R. J. W. BRIENEN, C. C. SOLIZ-GAMBOA, AND P. A. ZUIDEMA. 2010a. Tropical tree rings reveal preferential survival of fast-growing juveniles and increased juvenile growth rates over time. New Phytol. 185: 759–769.

ROZENDAAL, D. M. A., R. J. W. BRIENEN, C. C. SOLIZ-GAMBOA, AND P. A. ZUIDEMA. 2010b. Timber yield projections for tropical tree species: The influence of fast juvenile growth on timber volume recovery. For. Ecol. Manage. 259: 2292–2300.

RUBINO, D. L., C. BRIAN, AND B. C. MCCARTHY. 2004. Comparative analysis of dendroecological methods used to assess disturbance events. Dendrochronologia 21: 97–115.

SCHULMAN, E. 1956. Dendroclimatic change in semiarid America. University of Arizona Press, Tucson, Arizona.

SOLIZ-GAMBOA, C. C., D. M. A. ROZENDAAL, G. CECCANTINI, V. ANGYALOSSY, K. VAN DER BORG, AND P. A. ZUIDEMA. 2011. Evaluating the annual nature of juvenile rings in bolivian tropical rainforest trees. Trees Struc. Funct. 25: 17–27.

STERCK, F. J. 1999. Crown development in tropical rain forest trees in gaps and understory. Plant Ecol. 143: 89–98.

TOLEDO, M., L. POORTER, M. PENA-CLAROS, C. LEANO, AND F. BONGERS. 2008. Diferencias, en las características edáficas y la estructura del bosque, de cuatro ecoregiones forestales de Bolivia. Rev. Bol. Ecol. Conserv. Amb. 24: 11–26.

VAN DER MEER, P. J. 1996. Vegetation development in canopy gaps in a tropical rain forest in French Guiana. Selbyana 18: 38–50.

WORBES, M. 1995. How to measure growth dynamics in tropical trees – A review. IAWA J. 16: 337–351.

WORBES, M., AND W. J. JUNK. 1999. How old are tropical trees? The persistence of a myth. IAWA J. 20: 255–260.

WRIGHT, E. F., C. D. CANHAM, AND K. D. COATES. 2000. Effects of suppression and release on sapling growth for 11 tree species of northern, interior British Columbia. Can. J. For. Res. 30: 1571–1580.