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Projection of tree growth and timber volume following strip clear-cutting in the Peruvian Amazon

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ABSTRACT

As part of an assessment of sustainability for the strip clear-cutting system (or Palcazú Forest Management System), we determined whether commercial tree species regenerating in two strips (30 m × 150 m) clear-cut in the Peruvian Amazon in 1989 would reach commercial size (≥30 cm diameter at breast height (dbh)) 40 years after the initial cutting, the expected harvesting cycle. We projected the growth of six common commercial species (*Eschweilera bracteosa*, *Guarea cinnamomea*, *Micropholis guyanensis*, *Pouteria guianensis*, *Qualea paraensis*, and *Cedrelinga catenaeformis*) and two pioneer species (*Alchornea triplinervia* and *Miconia phaeophylla*) using bootstrapping techniques (the Lieberman model), based on 2-year diameter increments (2004–2006) and mortality rates obtained from 1630 trees growing in secondary forest sites including the regenerating strips. These demographic data were further used to project the growth of all trees ≥6.5 cm dbh of commercial (sawnwood value) species from each strip, and from a deferment-cut treatment applied to half of one of the strips. Three models were used for growth projections: (1) using all diameter increments to simulate average growing conditions, (2) using diameter increments of trees exposed to high light to simulate growing conditions under intensive forest management with low mortality rates and (3) using diameter increments of the fastest growing individuals. Roundwood volume was calculated using allometric equations for emergent, canopy, and subcanopy species.

Projections of all three growth models indicate that only two of the six focal commercial species, *Cedrelinga* and *Qualea*, would reach commercial size in 40 years. In the clear-cut strips, growth models 1 and 2 predict that 1–3% of the commercial trees (≥6.5 cm dbh) modeled would reach commercial size at the time of a second harvest, producing 3–8 m^3/ha of roundwood, as opposed to 12–14% (54–65 m^3/ha) of the commercial trees in the deferment-cut portion of strip 2. Growth model 3 predicted the highest number of trees reaching commercial size and thus the highest roundwood production for both the clear-cut strips (>30 m^3/ha) and deferment-cut (>130 m^3/ha). However, growth model 3 is the least realistic model out of the three; not all commercial trees in the strips are likely to grow continuously with such high growth rates in the next years. Thus, realistic growth projections (models 1 and 2) suggest that the strip clear-cutting system will not be financially profitable in a potential second harvest.

1. Introduction

Strip clear-cutting (or Palcazú Forest Management System) is a natural forest management system proposed as a sustainable alternative for timber extraction in the tropics (Tosi, 1982; Hartshorn, 1989, 1995). In this system, heterogeneous tropical forests are managed for native gap-dependent timber species by simulating gap dynamics through clear-cutting long, narrow strips (30–40 m wide) (Hartshorn, 1989, 1995). Cutting cycles are every 30–40 years (Hartshorn, 1989, 1995). Initially, the strip clear-cutting system was thought to be a sustainable alternative for timber extraction as compared to uncontrolled clearing and selective logging. The rationale for the assumed sustainability in this system was that most valuable tropical timber species are gap-dependent canopy tree species (Swaine and Whitmore, 1988). Gap-dependent tree species have rapid height growth and diameter increments (Lieberman et al., 1985). Tosi (1982) and Hartshorn (1989) also predicted that non-commercial pioneer species would not regenerate well in this system because the strips were too narrow to allow sufficient sunlight.

Recent studies, however, have questioned the sustainability of the strip clear-cutting system. Although clear-cut strips have high

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tree species richness at the early stages of regeneration (Hartshorn, 1989), composition is dominated by pioneer species (Gorchov et al., 1993). Stems of commercial species regenerating in this system had low diameter growth rates, averaging <0.3 cm/year 10 years after clear-cutting, even after silvicultural thinning (Dolanc et al., 2003). After 15 years of regeneration, commercial species comprised only 8–15% of the strips' basal area (Rondon et al., 2008). In order to determine if the strip clear-cutting system is economically sustainable, it is necessary to determine whether the commercial species regenerating in this system will reach commercial size and produce viable timber volumes in time for a second cutting.

Information on tree growth rates is essential for forest management decisions, but tree growth in the tropics is difficult to assess. Formation of annual tree growth rings is limited to areas with a strong dry season (Worbes, 1999; Fichtler et al., 2003; Brienen and Zuidema, 2005) or annual flood (Worbes and Junk, 1989; Schöngart et al., 2002, 2005; Dezzeo et al., 2003). Many tropical trees do not form annual growth rings and stem increments can only be obtained through repeated trunk measurements (Martinez-Ramos and Alvarez-Buylla, 1998; Clark and Clark, 1999), as has been done for tree species of Amazonian upland forests (Korning and Balslev, 1994; Laurance et al., 2004a). Also, tree growth can vary greatly due to several factors. Tree growth can vary over the lifetime of a tree (Clark and Clark, 1999) and due to climatic factors among years (Clark and Clark, 1992, 1994; Pereira da Silva et al., 2002), including El Niño events (Schöngart et al., 2004). The same species can show different growth rates across successional stands (Primack et al., 1985; Silva et al., 1995; Vandermeer et al., 1997); and among sites with contrasting soil fertility (Cavelier et al., 2000; Schöngart et al., 2005).

As part of an assessment of the economic sustainability of the strip clear-cutting system, we projected the growth of six common commercial species regenerating in two strips (30 m × 150 m) clear-cut in the Peruvian Amazon in 1989. The goal was to determine if these species would reach commercial size 40 years after the initial felling (the expected harvest cycle for this system). Using the demographic data of these focal species, we also projected the growth of all commercial species ≥6.5 cm diameter at breast height (dbh) regenerating in the clear-cut strips at the time of a second harvesting. We used three different approaches representing different growing conditions that these species may encounter in the strips over the next years. Growth projections were performed based on a stochastic growth simulation model (Lieberman and Lieberman, 1985), using three approaches: (1) using all diameter increments of trees exposed to both high and low light levels to simulate the range of growing conditions that trees encounter in the strips; (2) using diameter increments of only trees exposed to high light levels to simulate growing conditions in the strips under intensive forest management techniques; (3) using diameter increments of only the fastest growing individuals to simulate these individuals continuing to grow fast due to genotype or micro-environment.

We predicted that most commercial species in the strips would not reach commercial size in time for a second cutting due to slow growth rates reported for commercial stems in this system (Dolanc et al., 2003). For comparison purposes, we also projected the growth of two abundant non-commercial pioneer species regenerating in the strips.

2. Materials and methods

2.1. Study site

This study took place at the Centro de Investigaciones Jenaro Herrera (CIJH S 4°53.952′ W 73°39.041′), 200 km south of Iquitos, Loreto, Peru. Mean annual temperature is 26.5 °C and mean annual precipitation is 2521 mm (Spichiger et al., 1989). A relatively dry period occurs from June to August, but rainfall is highly variable each month of the year (Ascorra et al., 1993) (Fig. 1). Soils are sandy-loam and the vegetation is considered lowland tropical rainforest on high terrace (Spichiger et al., 1989). The families with highest tree densities on high terrace at CIJH are Sapotaceae, Leguminosae, Lecythidaceae, Chrysobalanaceae, Lauraceae, and Myristicaceae (Spichiger et al., 1996).

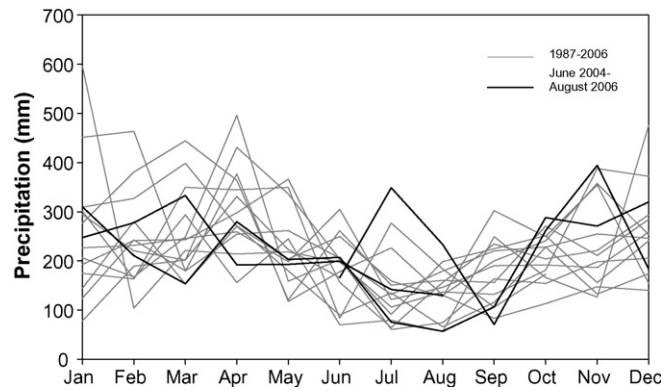

Fig. 1. Monthly precipitation for CIJH in 1987–2006 and June 2004–August 2006 (when this study took place) (data from IIAP and Oliver Phillips, pers. comm.).

2.2. Clear-cut strips in CIJH

Two 30 m × 150 m strips, 150 m apart, were clear-cut in 1989 in primary high terrace tropical rain forest at CIJH (Cornejo and Gorchov, 1993). Strip 1 was cleared in April–May 1989 and strip 2 in October–November 1989. Most trees >5 cm in diameter at breast height were felled in each strip using directional felling to ensure that the cut trees landed in the strips (Gorchov et al., 1993). An experimental deferment cut was applied to the south half of strip 2; subcanopy trees of commercial species (n = 56, 5–28 cm dbh) were left uncut (Cornejo and Gorchov, 1993). All timber was either used locally or carried off site. All stump sprouts and survivors (saplings <5 cm dbh that survived the clearing in 1989) were identified and tagged throughout each strip, with each strip divided into 20 15 m × 15 m plots. In June 1989 an enrichment planting of 20 *Cedrelinga catenaeformis* seedlings (<0.4 m height) was done along the central axis of the south half of strip 1, with one seedling planted every 7.5 m. Stump sprouts, survivors and planted *Cedrelinga* throughout each strip were censused once per year during 1990–1994, and in 1996, 2000, as were recruits (seedlings >2 m tall) on 8 of the 20 plots in each strip. An experimental silvicultural thinning treatment took place in March 1996 (Dolanc et al., 2003); pioneer trees (all *Cecropia* trees and trees <10 m tall of the genus *Alchornea* and the family Melastomataceae) were girdled by machete in 12 plots of each strip. The last census in strip 1 took place in 2004 and in strip 2 in 2005 (Rondon et al., 2008).

2.3. Species selection and trees marked in secondary sites

Six commercial and two non-commercial pioneer species were selected for growth projections and are hereafter referred to by genus only (Table 1 gives full details). The six commercial species were among the most common of those deemed 'commercial' based on sawnwood value at local markets in 1989 (Rondon, 2008; Rondon et al., 2008). The pioneer species selected were the most abundant species in 2004 and previous censuses (Rondon et al., 2008). Because the two strips did not have sufficient number of

Table 1
Tree species studied, functional group, number of individual trees (for timber species: >3 cm dbh in two strips, for pioneer species: >5 cm dbh in strip 1), and number of trees modeled in growth projections with minimum and maximum dbh size in 2004 in two strips cleared in 1989 at CIJH. Functional group was determined from Spichiger et al. (1990), Vásquez Martínez et al. (1997), and Laurance et al. (2004a,b).

Timber species	Functional group	Total no. trees >3 cm dbh in both strips	No. trees modeled from both strips	Dbh (cm) of trees modeled	
				Min.	Max.
Cedrelinga catenaeformis (Ducke) Ducke	Emergent	15	9	8.5	19.5
Eschweilera bracteosa (Poepp. ex O. Berg) Miers	Canopy	55	26	4.5	9.1
Guarea cinnamomea Harms	Subcanopy	17	11	4.2	6.4
Micropholis guyanensis (A. DC.) Pierre	Canopy	13	8	4.4	8.3
Pouteria gianensis Aubl.	Canopy	12	7	4.0	8.8
Qualea paraensis Ducke	Emergent	11	6	6.5	13.9
Pioneer species		**Total no. trees >5 cm dbh in strip 1**	**No. trees modeled from strip 1**	**Dbh (cm) of trees modeled**	
				Min.	Max.
Alchornea triplinervia (Sprengel) Mull. Arg.		194	92	17.1	36.6
Miconia phaeophylla Triana		67	44	7.4	24.7

trees in the larger size classes to perform the growth projections of the selected species (Table 1), we permanently marked and measured 1427 trees in several secondary growth sites during June–August 2004 and June–August 2006 (Table 2) to supplement the 203 trees marked in the strips (Table 1). Two-year (2004–2006) diameter increments from 1557 trees were used to perform growth projections of the selected species in the strips (Table 2). Seven negative diameter increments, ranging from −0.1 to −0.3 cm/2-year interval, were removed from growth projections. During this period, 46 trees died and 27 trees were lost. These trees were used to calculate mortality rates.

We assured that the selected trees in the strips and the trees marked in secondary sites had similar light conditions using a modified version of Dawkins and Field's (1978) 5-point crown illumination (CI) index: 1-crown not exposed to direct light (vertically or laterally); 2-crown only exposed to lateral light; 3-crown exposed to some overhead light (10–90% vertical light); 4-crown fully exposed to overhead light (≥90% vertical light); 5-emergent crown (fully exposed to vertical light and lateral light).

Diameter tapes were used to take dbh measurements to the nearest millimeter. Measurements were taken at 130 cm above the ground ('at breast height') and paint was used to mark and ensure that remeasurement was done at the same point.

2.4. Tree growth modeling

Growth curves have traditionally been constructed using periodic increments and passage time (Lieberman and Lieberman, 1985; Lieberman et al., 1985; Martinez-Ramos and Alvarez-Buylla, 1998). However, both techniques disregard inter-tree variation. Lieberman and Lieberman (1985) developed a stochastic growth simulation model for estimating size–age relationships from diameter increments taken at a single time interval that represents typical environmental conditions. This model incorporates individual growth variation in periodic increments using stratified random bootstraping. It is important to include growth variation in tree growth models in order to make more realistic growth projections and timber yield predictions (Brienen and Zuidema, 2006a, 2007)

In the Lieberman model, a growth curve for a particular species is simulated by random selection of actual increments from a group of trees (of the same species) with similar sizes to the growing tree for each period of its simulated life. The process is repeated 1000 times to obtain 1000 growth trajectories for each species, sufficient to obtain reliable growth curves (Lieberman and Lieberman, 1985). Simulated growth curves are rather conservative because they reflect the entire frequency distributions of

Table 2
Diameter ranges of trees marked in secondary growth sites, including the logged strips at CIJH, coefficients for partial correlation of 2004–2006 diameter increments with crown illumination (CI ranged from 1 to 5) and with initial tree diameter (2004), mean annual growth rates of these species observed in secondary sites and projected using models 1–3 (described in text), and annual mortality rates used in models 1 and 2. Note that model 3 used the same mortality rates as model 2.

	No. trees alive 2004–2006	Diam. range (cm)	Partial correlation[a] diameter increments		Mean annual growth in sec. sites (cm/year)	Model 1		Model 2		Model 3
			With CI index	With tree size		Mean growth rate (cm/year)	Mort. rate (%/year)	Mean growth rate (cm/year)	Mort. rate (year/%)	Growth rate (cm/year)
Timber species										
Cedrelinga catenaeformis	155	8–36	0.28**	0.30***	0.27	0.24	5.17	0.32	4.85	0.75
Eschweilera bracteosa	285	4–31	0.09	0.22**	0.23	0.21	0.26		0.17	0.43
Guarea cinnamomea	169	4–40	0.27**	0.28**	0.21	0.17	1.15	0.23	0.28	0.35
Micropholis guyanensis	159	5–38	0.46***	0.33***	0.23	0.15	1.23	0.22	0.61	0.29
Pouteria guianensis	195	4–37	0.23**	0.26**	0.18	0.12	1.13	0.22	0.50	0.3
Qualea paraensis	156	6–37	0.32***	0.07	0.54	0.52	1.09	0.59	0.31	0.97
Pioneer species										
Alchornea triplinervia	246	17–48	0.34***	0.02	0.5	0.50	0.90	0.53	0.80	1.02
Miconia phaeophylla	190	7–35	0.28***	0.16**	0.45	0.50	5.08	0.54	4.69	1.85

[a] *Notes*: For each species two coefficients are given: (a) for the partial correlation of diameter increment with CI, controlling for size; and (b) for the partial correlation of diameter increment with size, controlling for CI.
** $P < 0.05$; one-tailed probabilities for positive correlations.
*** $P < 0.001$; one-tailed probabilities for positive correlations.

increments (Lieberman et al., 1985). Several studies have used the Lieberman model to study size–age relationships of tropical trees (Korning and Balslev, 1994; Van Groenendael et al., 1996; Brienen et al., 2006). We used a modified version of the Lieberman model for all growth projections. This model was extended to include a mortality probability following Korning and Balslev (1994).

2.5. Growth models used for growth projections of eight focal species

The proposed time for a second cutting in the strips was 40 years (Hartshorn, 1989). The last census of the eight focal species in the strips was done in 2006, 17 years after the initial cutting. We projected the size of the selected tree species found in the strips 41 years after the cutting (year 2030). The goal was to determine if these focal commercial species would reach 30 cm dbh, minimum commercial size for this system (Cornejo and Gorchov, 1993), in time for a second cutting.

The selected commercial species had several small trees in the strips. We projected the growth of only the larger individuals of the selected species, which were most likely to reach commercial size over the next 24 years. For *Eschweilera* we projected the growth of the largest ~50% of individuals (Table 1). For each of the remaining five commercial species, we projected the growth of the largest ~65% of individuals (Table 1). A total of 67 trees of the selected commercial species from both strips were projected. *Miconia* and *Alchornea*, both pioneer species, had much larger sizes and higher densities in the strips than commercial species (Table 1). We projected the growth of the largest ~50% of *Alchornea* individuals and the largest ~65% of *Miconia* individuals found in strip 1. A total of 136 pioneer trees from strip 1 were modeled.

To perform the growth projections, individual trees of each of the eight species in the strips were grouped into size classes of 1 cm dbh. The growth of each size class was projected over the next 24 years (to year 2030) by randomly sampling an individual tree from a particular size class at the beginning of each iteration. The growth of this tree was simulated by randomly sampling diameter increments from trees with diameter sizes within ±2.5 cm (i.e. "window length (l)" was 5 cm). The window length (l) was delimited by diameter values as recommended by Brienen et al. (2006), instead of number of trees as was originally done in Lieberman and Lieberman (1985). This model was extended to include a mortality probability (%) in the 2-year time interval. Visual basic applications (VBA) 6.3 in Microsoft Excel was used for the growth projections.

We built three growth models based on the Lieberman and Lieberman (1985) model. All three growth models used a matrix where the rows were individual trees and the columns were initial (2004) dbh, 2-year (2004–2006) diameter increment, and mortality probabilities. The l for all three models was 5 cm. In *growth model 1*, tree growth was projected using high mortality rates (described below) and diameter increments of trees exposed to both high and low crown illumination levels (Table 2, and Fig. 2a and b). High mortality rates were calculated using the number of trees that died, and half of the number of trees that were not relocated within the 2-year period (Table 2); i.e. assuming 50% of the not relocated trees were dead. To calculate annual mortality, we used $m = 100(\log_e n_0 - \log_e n_t)/t$, where n_0 is the initial number of trees; n_t is the number of surviving trees, t years later (Swaine and Lieberman, 1987). In this case $t = 2$.

For each focal species, all trees regardless of size class were assumed to have the same mortality probability. For each 2-year time step for the projection of an individual tree, a random number from 0 to 100 was compared to the mortality probability for that species: if it fell below, the simulated tree "died" and growth simulation stopped. If the random number was greater than the mortality probability for that species, the simulated tree would continue living and a random diameter increment was sampled within a diameter range of ±2.5 cm. Thus, a tree's growth was modeled for 24 years or until it was registered dead. A thousand growth curves were simulated for each size class per focal species.

Growth model 2 was the same as model 1, except growth for a focal species was projected using low mortality rates and diameter increments of trees only exposed to high CI levels (CI ≥ 2) (Table 2 and Fig. 2b). We used lower mortality rates in growth models 2 and 3 to reflect the tendency for trees with faster growth to have lower mortality rates (Lieberman et al., 1985; Terborgh et al., 1997). Low mortality rates were calculated using only the number of trees known to have survived or died during the 2-year period.

In *growth model 3*, we simulated the possibility that commercial species in the strips would grow continuously with high growth rates and low mortality rates over the next years. This was done by randomly sampling from trees with the largest diameter increments (highest 25%) within l (Fig. 2b). Specifically, model 3 first identified all trees within ±2.5 cm of the simulated tree, then selected the 25% of these with the highest diameter increments, and then randomly sampled from this smaller pool. All

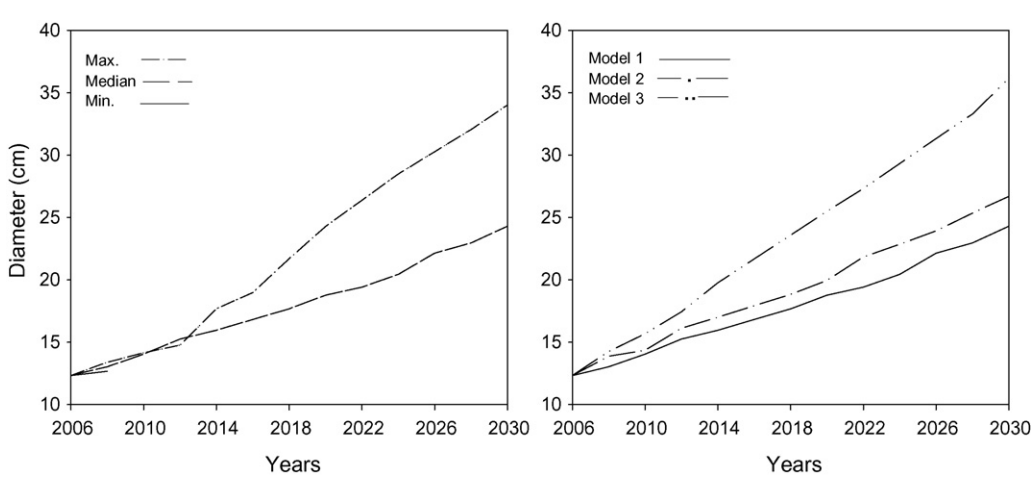

Fig. 2. Minimum, maximum, and median growth curve for a *Qualea paraensis* tree, size class 12 cm dbh, using a modified Lieberman model with all diameter increments and 1.05% annual mortality rate (model 1) (a). Median growth projections of model 1 (same as A), model 2 (diameter increments of individuals under high light and 0.31% annual mortality rate) and model 3 (individuals with fast diameter increments and 0.31% annual mortality rate) for 12 cm dbh (b).

trees had the same probability of mortality, which was the same as for growth model 2 (Table 2). In general, tree growth rates in tropical forests are highly variable, but there are some trees that are better performers than others and consistently grow at higher than average rates. This tendency has been referred as growth autocorrelation (Pfister and Stevens, 2003), temporal autocorrelation (Terborgh et al., 1997; Fox et al., 2001; Bullock et al., 2004; Koyama et al., 2005) or total autocorrelation (Brienen et al., 2006). This type of growth may be related to differences among trees in resource capture and allocation, genotype, microsite features, periods of pest pressure, and periods of growth suppression and release (Bullock et al., 2004).

2.5.1. Effect of crown illumination on growth

The effect of crown illumination on diameter increment was determined for each species in order to determine whether growth model 2 was appropriate. For each species partial correlations were used to separate the effect of CI (average CI 2004–2006) and tree size (initial diameter in 2004) on annual diameter increment (2004–2006). We did partial correlations of CI with annual diameter increment, controlling for tree size (initial diameter in 2004); and partial correlations of size with annual diameter increment, controlling for CI. Due to nonlinearity of residuals, diameter increments of all selected species were square root-transformed except for *Cedrelinga*, which was log-transformed.

2.5.2. Size distributions

Only growth curves that contained no dead trees at the end of 24 years (2030) were analyzed. For each growth model we projected the final (2030) number of trees expected in each size class for each of the eight species. We did this by multiplying the initial size distribution (the number of trees found in each size class in 2006 (Figs. 4 and 5)) by the growth projections (2006–2030) of the size classes. That is, for each initial size class we projected the proportion of individuals that would belong to each size class in 2030, and multiplied this frequency distribution by the number of stems in that initial size class (2006), and then summed these final size distributions. We also calculated for each growth model the total number of commercial trees per ha that would reach commercial size in a potential second cutting (Rondon, 2008).

2.6. Methods for projecting the growth of commercial taxa from the strips

2.6.1. Commercial taxa in the strips and assignment of functional groups

Commercial species projected from the strips were those in genera valued for sawnwood at international and local markets based on data from the International Tropical Timber Organization (ITTO) from 1997 to 2005 (ITTO, 1997–2005) and studies in the Peruvian Amazon (Peters et al., 1989; Pinedo-Vasquez et al., 1990). The list (Appendix 1A) did not include species valued for roundwood or non-timber forest products. We assigned each species to a successional group based on Laurance et al. (2004a,b) and Vásquez Martínez et al. (1997). Old growth species were further classified into subcanopy, canopy, and emergent functional groups using Laurance et al. (2004a,b), Spichiger et al. (1989, 1990), Vásquez Martínez et al. (1997), and height data from the site before clearing (Appendix 1B).

2.6.2. Growth projections based on functional group

The growth of trees ≥6.5 cm dbh of all commercial taxa in the strip 1, the clear-cut, and the deferment-cut half was projected in time for a second harvest. Both strips were about 15 years old when the last censuses took place (2004–2005). The growth of these trees was projected for the next 26 years. In strip 1, tree growth was projected to year 2030 and in strip 2 to year 2031, about 41 years after the initial cutting. Diameter increments and mortality rates of the six focal commercial species were used in the growth projections of appropriate subsets of functional/successional groups of commercial taxa (Appendix 1C). All three growth models were used to model the growth of each commercial taxon in the strips.

2.6.3. Size distribution, tree density, basal area, and volume of commercial taxa

Size distributions in 2030/2031 were calculated for each strip using growth models 1–3 following the same approach as for the focal species. Tree density, basal area, and roundwood volume of commercial species that would reach ≥30 cm dbh at the time of second harvest were also calculated for each of the strips, under the three growth models. Roundwood volume calculations were done using allometric equations, developed for these species as well as for functional/successional groups using the pre-clearing data of the strips (Appendix 2).

2.7. Model assumptions

In this study, we assumed that a 2-year interval was long enough to obtain valid and representative measures for growth rates of the selected focal species. A second assumption was that environmental conditions during June 2004–August 2006 were typical for this area. While Amazonia underwent a very severe drought in 2005, this mainly affected southwestern Amazonia (Aragao et al., 2007). Monthly precipitation during this period at CIJH was within the range of previous 10 years (Fig. 1), meeting the assumption of typical environmental conditions.

3. Results

3.1. Effect of crown illumination on growth

Diameter increment was strongly associated with size for all species except for one commercial (*Qualea*) and pioneer

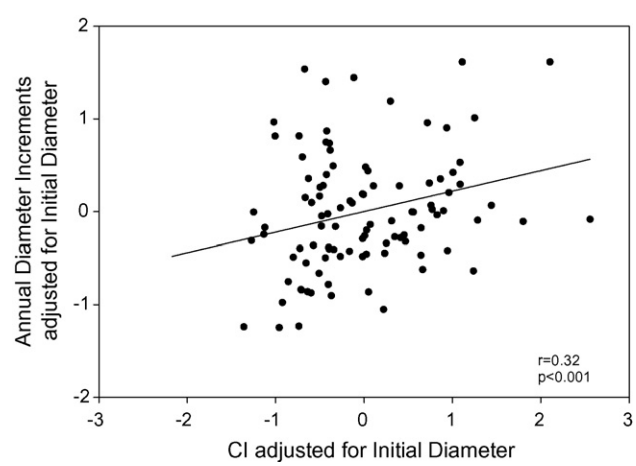

Fig. 3. Partial correlation of diameter increment with crown illumination (CI) index, controlling for initial tree diameter, for individual trees of *Qualea paraensis*. Annual diameter increment adjusted for diameter is the residuals of regressing diameter increments on initial tree diameter. CI adjusted for initial diameter is the residuals of regressing CI on initial tree diameter. The probability shown ($P < 0.001$) is for a one-tailed test for positive correlation. All other species also had positive partial correlations, except for *Eschweilera* (Table 2).

(*Alchornea*) species (Table 2) when controlling for CI. When controlling for size, diameter increment was strongly associated with CI for both pioneer species (*Alchornea* and *Miconia*) as well as five of the six commercial species (*Cedrelinga*, *Guarea*, *Micropholis*, *Pouteria*, and *Qualea*) (Fig. 3), but not for *Eschweilera* (Table 2). Since diameter increment was not strongly associated with CI for *Eschweilera*, model 2 was not used to model growth for this species. For both pioneer species and the other five commercial species, growth projections were done using all three growth models.

3.2. Growth projections of focal species

Projections using the three growth models showed that the selected larger individuals of *Guarea*, *Micropholis*, and *Pouteria* in 2006 would not reach commercial size in 2030 (Fig. 4). Growth projections using models 1 and 3 also showed that larger individuals of *Eschweilera* would not reach commercial size in this time period. For these four species, growth model 3 projected the largest sizes in 2030 (Fig. 4). Based on growth model 3, the largest size class that these four taxa were projected to reach in 2030 was about 17–21 cm dbh, and very few individuals were projected to even grow to this size (Fig. 4).

In contrast, the three growth models projected that some of the larger individuals of selected *Cedrelinga* and *Qualea* trees in 2006 would reach commercial size (≥30 cm dbh) in 2030 (Figs. 2 and 5). Growth model 3 also projected the largest sizes for these species (Fig. 5). Based on growth model 3, the largest size class that *Cedrelinga* and *Qualea* trees would reach in 2030 was about 40–43 cm dbh, but very few individuals would grow to this size, 4.38 trees/ha for *Qualea* and 1.28 trees/ha for *Cedrelinga*. Growth models 1 and 2 projected few individuals (<1 tree/ha) of *Qualea* and *Cedrelinga* trees would reach commercial size in 2030.

The three growth models for the two pioneer species, *Miconia* and *Alchornea*, projected many trees would have diameters >30 cm dbh in 2030 (Fig. 5). Model 3 projected larger sizes for both species than models 1 and 2, which projected similar sizes.

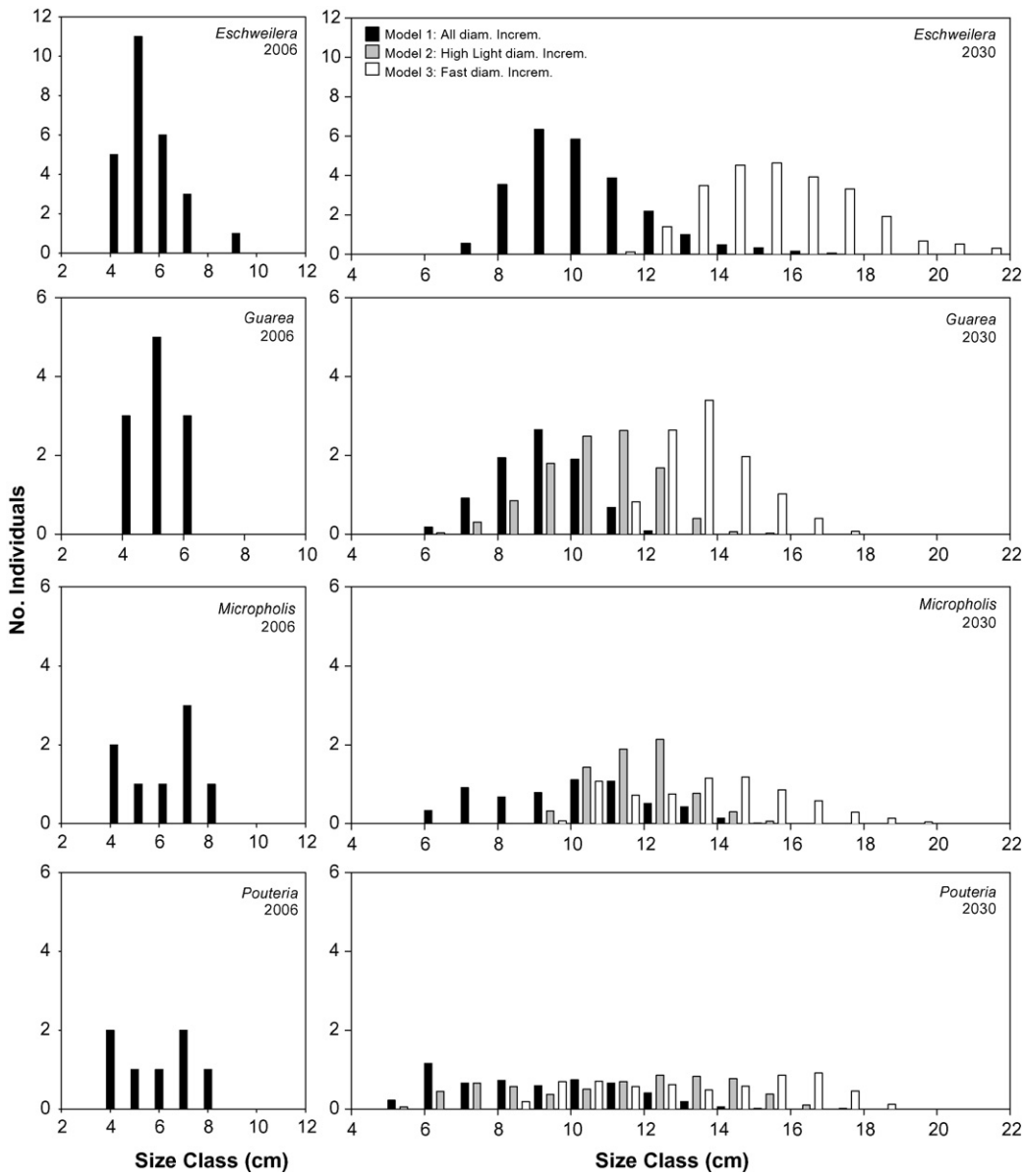

Fig. 4. Size distributions of four abundant commercial species found in two clear-cut strips in 2006, and their projected size class distribution in 2030, based on three different growth models (see Table 1 for binomials). The threshold for commercial size is 30 cm.

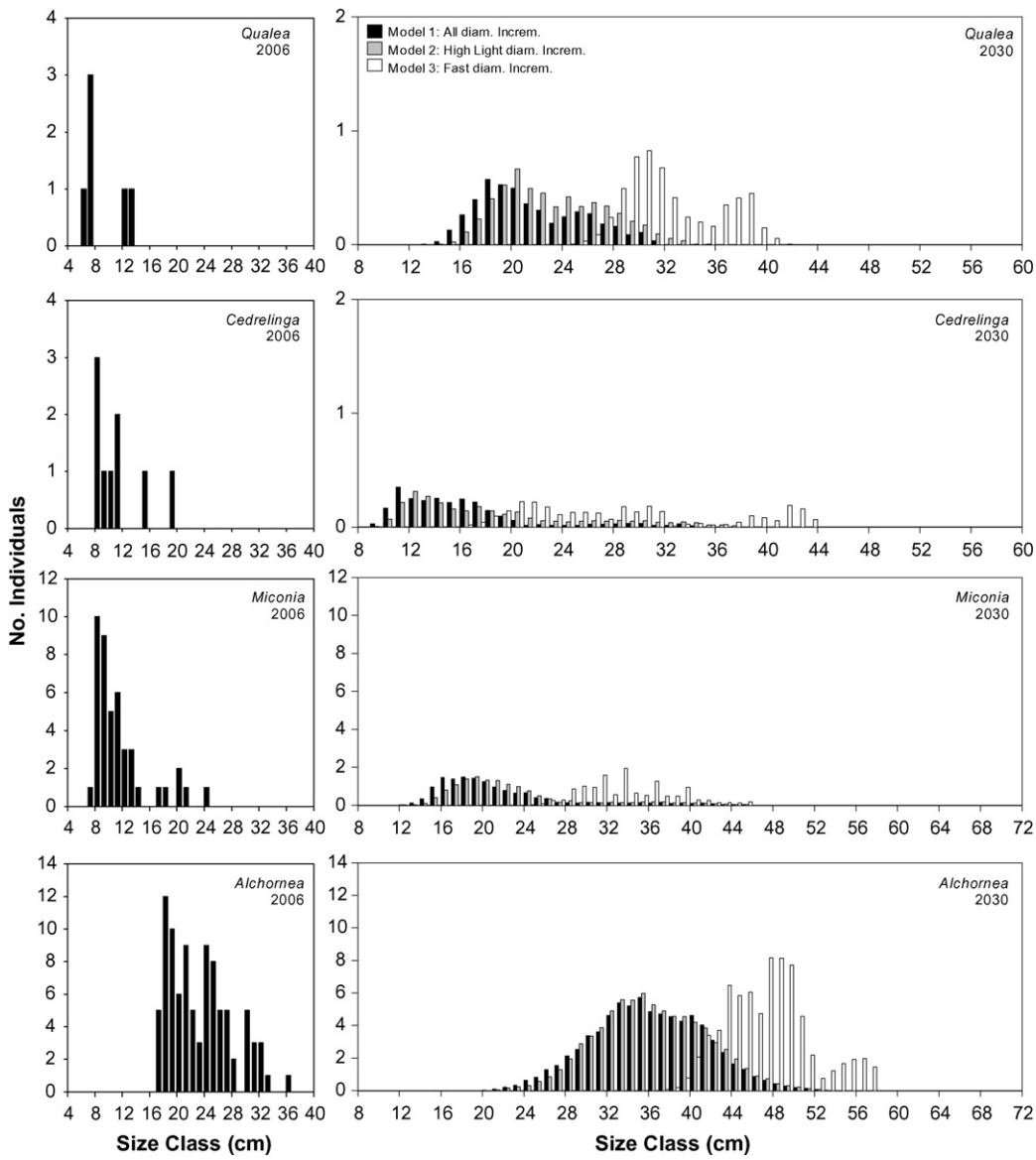

Fig. 5. Size distributions of two abundant commercial species (*Qualea* and *Cedrelinga*) and two pioneer species (*Miconia* and *Alchornea*) found in two clear-cut strips in 2006, and their projected size class distribution in 2030, based on three different growth models. Binomials are provided in Table 1. The threshold for commercial size is 30 cm.

3.3. Growth projections of commercial taxa regenerating on the strips

While model 1 projected the smallest sizes for all commercial species, model 3 projected the largest sizes (Fig. 6). In the clear-cut strips, growth models 1 and 2 projected only a few trees would reach commercial size (30 cm dbh) after 40 years as opposed to growth model 3. Growth model 1 predicted that 2 trees/ha in strip 1 and 4 trees/ha in the clear-cut portion of strip 2 would reach commercial size in a potential second harvest (Fig. 6 and Table 3), producing a roundwood volume of 3–6 m^3/ha. Growth model 2 predicted that 3 trees/ha (strip 1) to 6 trees/ha (clear-cut portion of strip 2) would reach commercial size, yielding a timber volume of 4–8 m^3/ha. In contrast, growth model 3 predicted 23–26 trees/ha would reach commercial size producing 32–38 m^3/ha of timber.

Growth models 1 and 2 also projected fewer trees reaching commercial size in the deferment-cut half than growth model 3.

Table 3
Number of trees projected to reach commercial size (≥30 cm dbh), their basal area and timber volume, per ha in 2030/2031 in each of the three models for strip 1, the clear-cut, and deferment-cut portions of strip 2.

Timber Species ≥30 cm dbh in 2030/2031	Strip 1				Clear-cut in strip 2				Deferment-cut in strip 2			
	Model 1	Model 2	Model 3	25% model 3	Model 1	Model 2	Model 3	25% model 3	Model 1	Model 2	Model 3	25% model 3
No. trees/ha	2.08	3.03	22.82	5.71	3.78	5.56	26.07	6.52	32.77	38.56	65.55	16.39
Basal area (m^2/ha)	0.26	0.33	2.38	0.60	0.48	0.62	2.86	0.72	4.40	5.27	10.32	2.58
Volume (m^3/ha)	3.13	3.96	31.95	7.99	6.43	8.22	37.92	9.48	53.97	64.90	130.82	32.71

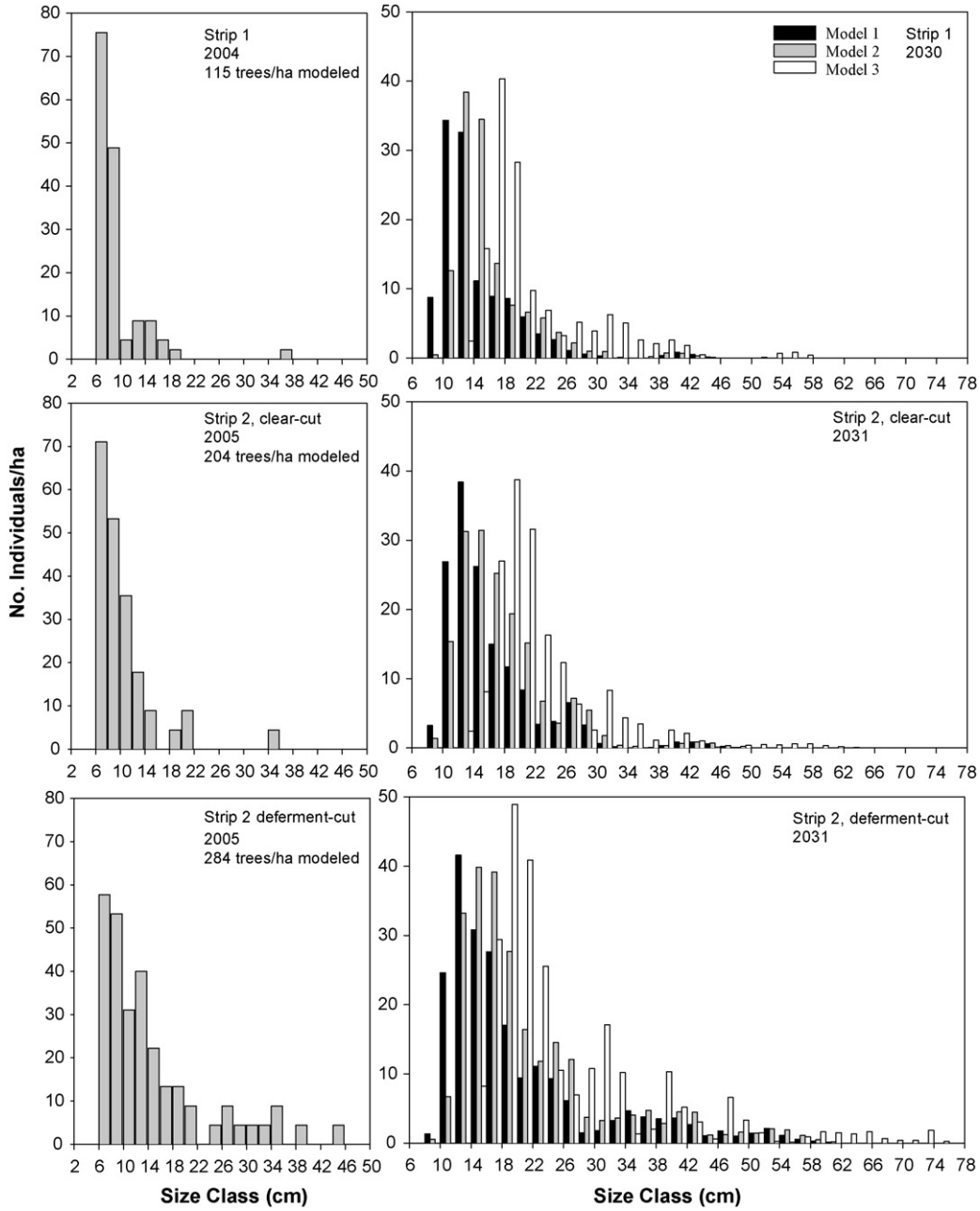

Fig. 6. Size class distributions of commercial species ≥6.5 cm dbh found in strip 1, the clear-cut, and deferment-cut half of strip 2 in 2004/2005 and their projected size class distributions in 2030/2031, at the time of a second cutting, using three growth models. Commercial size is 30 cm dbh.

Growth models 1 and 2 predicted 33 and 39 trees/ha would reach commercial size producing 54–65 m^3/ha of roundwood volume in a potential second harvest, whereas growth model 3 predicted 66 trees/ha would reach commercial size, producing 131 m^3/ha (Fig. 6 and Table 3). The deferment-cut was projected to have a greater number of commercial taxa reaching commercial size as well as greater roundwood volume production after 40 years than in the clear-cut under each of the three models (Fig. 6 and Table 3).

4. Discussion

4.1. Growth projections of focal species

The three growth models projected that, for the six focal commercial species, only a few larger individuals of *Cedrelinga* and *Qualea* would reach commercial size 40 years after the initial harvest. These emergent species would reach 30 cm dbh due to their higher growth rates (Table 2). Emergent trees are among the fastest growing trees in the forest; their growth rates are much greater than those of subcanopy trees (Lieberman and Lieberman, 1987; Korning and Balslev, 1994; Laurance et al., 2004a; Nascimento et al., 2005; Vieira et al., 2005) and in some cases larger (although not significantly) than those of canopy trees (Nascimento et al., 2005; Laurance et al., 2004a). These trees also have low annual mortality rates, <1%/year (Nascimento et al., 2005; Laurance et al., 2004b). In this study, emergent species had higher growth rates than canopy species, but their growth rates were within the range of growth rates (0.1–0.64 cm/year) for emergent tree species commercially harvested near Manus, Brazil (Chambers et al., 1998). During this study, more than half of the

Cedrelinga trees that died ($n = 16$) were of 8–≤15 cm dbh, increasing the overall annual mortality rate for this species; as a result, *Cedrelinga* had an annual mortality rate >1%/year (Rondon, 2008). Age-diameter relations for *Cedrelinga* (based on tree ring data) also showed that a few fast-growing individuals can reach 30 cm dbh in 40 years (Brienen and Zuidema, 2006a). *Cedrelinga* can have a median growth rate >1 cm/year (Brienen and Zuidema, 2006a) and a growth potential (the mean of the 5 highest growth rates) of 3.7 cm/year in the Bolivian Amazon (Brienen and Zuidema, 2006b). *Qualea* had a median growth rate of 0.1 cm/year in an undisturbed forest of central Amazonia, but some trees grew >0.2 cm/year (upper quartile) and >0.5 cm/year (upper decile) (Laurance et al., 2004a). The annual mortality rate for the emergent tree genus *Qualea* was 0.39%/year (Laurance et al., 2004b), which is within the mortality range for this study (Table 2).

The canopy species in this study would fail to reach commercial size in 40 years. In general, canopy trees have moderate, but variable growth rates (Nascimento et al., 2005). Annual mortality rates for canopy species in old growth Central Amazonia also ranged from <1%/year (Nascimento et al., 2005) to 1.6%/year (Laurance et al., 2004b). The median growth rate for *Micropholis guyanensis* in an undisturbed forest in central Amazonia was <0.2 cm/year, but growth rates >0.2 and >0.3 cm/year have also been recorded for this species (Laurance et al., 2004a). The annual mortality rate for the tree canopy genus *Micropholis* was 1.14%/year (Laurance et al., 2004b), within the range for this study (Table 2). *Pouteria guianensis* had lower growth rates and annual mortality rates than *M. guyanensis* in this study and also in an undisturbed forest of central Amazonia (Laurance et al., 2004a). The median growth rate for *P. guianensis* in central Amazonia was <0.1 cm/year, but the upper quartile and upper decile growth rates for this species was >0.1 and >0.2 cm/year (Laurance et al., 2004a). The annual mortality rate for this canopy tree genus was 0.79%/year (Laurance et al., 2004b), also within the range for this study. The median growth rate in Central Amazonia for the canopy tree genus *Eschweilera* was 0.1 cm/year, but it could also reach growth rates as high as 0.26 cm/year (Laurance et al., 2004b); the annual mortality rate for this canopy genus was 0.61%/year (Laurance et al., 2004b), a little higher than in this study (Table 2).

Guarea would also fail to reach commercial size in 40 years. This subcanopy tree had one of the lowest growth rates in this study (Table 2). Subcanopy trees grow much more slowly than pioneer, emergent, and canopy trees in undisturbed forests (Lieberman and Lieberman, 1987; Korning and Balslev, 1994; Condit et al., 1996; Laurance et al., 2004a,b; Nascimento et al., 2005), and have high mortality rates, up to 1.78%/year (Laurance et al., 2004b). The annual mortality rate for this subcanopy tree genus was 1.35%/year (Laurance et al., 2004b), close to the mortality rates in this study (Table 2).

Pioneer species in this study, on the other hand, would reach sizes >30 cm dbh in 40 years. Pioneer trees are the fastest growing trees. Their growth rates (>0.5 cm/year) are far higher than emergent, canopy, and subcanopy trees in an undisturbed forest as their annual mortality rates (>3%/year) (Laurance et al., 2004b; Nascimento et al., 2005). In central Amazonia, the annual mortality rate of the *Miconia* genus was 6% (Laurance et al., 2004b), very close to the mortality rate here (Table 2). In this study, *Alchornea* had a much lower annual mortality rate than *Miconia* (Table 2).

4.2. Growth projections of commercial taxa from the strips

In the clear-cut strips, growth models 1–3 projected that only 1–15% of the commercial taxa modeled would reach commercial size (≥30 cm dbh), producing lower timber yields than the deferment-cut half (Table 3). The greater number of commercial trees and timber volume projected for the clear-cut portion of strip 2 (vs. strip 1) (Table 3) was due largely to the greater abundance of commercial trees in strip 2 in 2004/2005 (Rondon et al., 2008). This may have been due to differences in seed input or seed predation. Similarly, the larger number of trees reaching commercial size, and greater timber volume, in the deferment-cut (vs. clear-cuts) in all growth models, was due to greater stocking of large (>15 cm dbh) commercial trees in the deferment-cut half in 2004/2005 (Rondon et al., 2008).

The small number of trees reaching commercial size after 40 years is due to low tree growth rates for this area. Radiocarbon and dendrometer annual growth rates for Amazonia showed that growth rates were ≤0.5 and ≤0.6 cm/year, respectively (Vieira et al., 2005). Growth rates from this study are comparable to the growth rates of commercial trees in the Bolivian Amazon, which had an average annual increment of 0.32 cm/year and a range of 0.21 and 0.49 cm/year (Dauber et al., 2005). Tree growth rates after logging are reported to be in the range of 0.25–0.6 cm/year (Finegan and Camacho, 1999; Silva et al., 1995). Several studies have found that even after the application of silvicultural thinning treatments, tree growth rates are still low (Silva et al., 1995; Graaf et al., 1999; Finegan and Camacho, 1999; Dolanc et al., 2003; Dauber et al., 2005).

Low growth rates in this site are likely related to its very acidic and nutrient poor soil (Marmillod, 1982 as cited in Spichiger et al., 1996); these rates are comparable to growth rates in upland central Amazonia (Laurance et al., 2004a,b). In more fertile soils such as the ones of the floodplain of Manu River in southeastern Peru, fast-growing successional species could attain diameter increments of ≥4.8 cm/year (Terborgh et al., 1997), much higher than the pioneer species in this study (Table 2). However, most species of the mature forest in the Manu river floodplain had lower growth rates, with girth increments of 0.1–1 cm/year (Gentry and Terborgh, 1990).

4.3. Growth models

We projected the growth of focal species and commercial taxa from the strips using three realistic growth models. To simulate growth in the clear-cut strips, for each model we used diameter increments and mortality rates from secondary sites, which tend to be higher than old growth or mature forest (Primack et al., 1985; Silva et al., 1995; Graaf et al., 1999; Guariguata, 1999; Feldpausch et al., 2007). However, most of the annual mortality rates (Table 2) were within the range of 1–2%, characteristic of tropical forests (Lieberman et al., 1985; Lieberman and Lieberman, 1987; Swaine et al., 1987). Only one commercial species had a mortality rate >2% (Table 2), but mortality rates exceeding 2% have been found for trees in the Peruvian Amazon (Phillips et al., 1994) and Ecuadorian Amazon (Korning and Balslev, 1994).

Growth model 1 aimed to simulate the entire range of growing conditions that trees in the strips would encounter over the next 26 years. The two strips, 15 years after clear-cutting, had closed canopies and already recovered 2/3 of their basal area (Rondon et al., 2008). Because trees are likely to encounter a wide range of light conditions, we used diameter increments of trees exposed to all levels of crown illumination.

In growth model 2, we used growth increments only of trees with high CI in order to simulate growing conditions that commercial species may encounter in strips under intensive forest management techniques such as silvicultural thinning and liberation treatments, which are commonly used in forest management in order to increase the growth of selected tree species. These treatments have been shown to increase growth rates of trees, including those of commercial value (Guariguata,

1999; Graaf et al., 1999; Finegan and Camacho, 1999; Parriona et al., 2003; Dolanc et al., 2003) by reducing competition and increasing CI. Many studies report strong correlations between tree growth and CI (Clark and Clark, 1992; Silva et al., 1995; Finegan and Camacho, 1999; this study) or crown class (Baker, 2003). However, some trees may not respond strongly to crown illumination (e.g. *Eschweilera* had no significant response in this study and Baker (2003) concluded that crown class did not predict the growth of shade-tolerant temperate trees). As expected, growth projections in model 2 showed a shift toward larger sizes for the focal commercial taxa compared to projections using all diameter increments (model 1). For both pioneer species, however, projections using models 1 and 2 resulted in similar sizes (Fig. 5) because nearly all trees we found of these pioneer species were growing under high CI.

In growth model 3, we simulated growth of individuals with higher than average growth rates by utilizing only increments in the top 25% of each size class. Thus, model 3 projected the largest sizes and greatest mean growth rates (Figs. 4–6 and Table 2). In this model, however, inter-tree growth variation was reduced since diameter increments were sampled from a smaller pool (25% largest).

Our use of high growth rates in model 3 was intended to qualitatively incorporate growth autocorrelation. We did not explicitly simulate growth autocorrelation as done by Bullock et al. (2004) and Brienen et al. (2006), because for most of the trees we only had data of diameter increments from a 2-year interval. Other studies in the past have used above-average growth rates to account for growth autocorrelation. Condit et al. (1993) and O'Brien et al. (1995) developed size–age relations that were one standard deviation above the mean growth trajectory. To estimate the age of successional stands, Terborgh et al. (1997) developed a mean growth trajectory by weighting slow growing trees with higher mortality. They also used the mean girth of the fastest individuals (the largest 50% and 25%) to estimate the "true" age of the stands and avoid underestimation due to suppressed growth and late recruiting individuals.

Growth model 3 can also be considered as the modeling of tree growth potential, defined as the maximum growth for a tree under conditions for a particular site (Clark and Clark, 1999). Our approach in model 3 is very similar to Clark and Clark (1999)'s calculation of growth potential, which was the mean of the five largest annual diameter increments in each size class.

4.4. Which model is most appropriate?

Based on the projections from the three models, model 1 produced the most conservative growth projections and model 2 produced more optimistic growth projections. Model 1, incorporating the full range of growing conditions in secondary sites, projected that only 1–2% of all the commercial trees in the clear-cut strips would reach commercial size at the time of a second cutting. Growth model 2, representing growing conditions under intensive forest management techniques in the strips, projected that 2–3% of all commercial trees would reach commercial size, a more optimistic prediction. Despite the differences between growth models 1 and 2, both models concur in predicting that only two of the six focal commercial species, *Qualea* and *Cedrelinga*, would reach commercial size in 40 years (Fig. 5).

Growth projections using model 3 had the largest sizes; thus the most optimistic prediction; however, it is very unlikely that all individuals of the selected species in the strips would continuously grow at such high growth rates over the next years. Using growth model 3, 13–15% (23–26 trees/ha) of the total projected taxa in the clear-cut strips would reach commercial size (Table 3). More realistically, if 25% of commercial trees grew with these growth rates (derived from the fastest growing 25% of measured trees), a total of 6–7 trees/ha would reach commercial size in the clear-cut strips. This is a low timber yield for a second cutting cycle and it is similar to our projections for the clear-cut strips using growth model 2 (3–6 trees/ha). For the deferment-cut, 25% of model 3 results in lower projections of timber volume than model 2 (Table 3).

Because we did not include negative diameter increments in our growth models of *Eshweilera*, *Guarea*, *Micropholis*, *Pouteria* and *Qualea*, we slightly overestimated the size projections of these species and commercial taxa with canopy and emergent functional groups. Even with the removal of negative diameter increments, four of the five species were still far from reaching commercial size (Fig. 3).

4.5. Sustainability of the strip clear-cutting system

Growth projections predict that very few commercial species would reach commercial size in a 40 years, the cutting cycle proposed by Tosi (1982) and Hartshorn (1989) for this system; this proposed cutting cycle is too short for the regeneration of commercial species in the strips. After the first 15 years of regeneration in the two clear-cut strips, most of the commercial species were too small to reach commercial size in only 26 more years. Although we did not project the growth of smaller recruits (trees <6.5 cm dbh) in the clear-cut strips, it is very unlikely that these trees, much smaller than the ones projected, would reach commercial size in a second cutting. Even when the six focal commercial species were modeled without mortality rates, only 0.67–8.25 trees/ha out of 74 trees/ha modeled would reach commercial size after 40 years (Rondon, 2008).

One of the assumptions in this system was that most commercial species are gap-dependent or shade intolerant, and thus they would establish in gaps and have high growth rates (Hartshorn, 1989). However, not all commercial species are gap-dependent. Commercial species exhibit a broad range of shade tolerances (Pinard et al., 1999) and growth rates (Martini et al., 1994), and belong to different functional groups (Table 1). This further complicates forest management and the implementation of appropriate cutting cycles. The strip clear-cutting system in a 40 year-cutting cycle may only benefit the regeneration of fast-growing species such as *Miconia* and *Alchornea* and a few valuable commercial species such as *Qualea* and *Cedrelinga*.

Growth projections in this study suggest that the strip clear-cutting system will produce low timber volumes in a potential second harvest. We projected only 3–8 m^3/ha timber volume of commercial species from the clear-cut strips using growth models 1 and 2, and 8–9 m^3/ha, if 25% of the commercial trees would grow continuously at high growth rates. This timber production would be much lower than the first harvest (1989), when 102–109 trees/ha >30 cm dbh (or 46–49 trees/strip) were felled in strips 1 and 2, producing 166–184 m^3/ha (or 75–83 m^3/strip) of roundwood (Cornejo and Gorchov, 1993). Timber production in a second harvest would also be lower than the timber production from an old growth forest in Iquitos, 94 m^3/ha (Peters et al., 1989) and that of an old growth communal forest near Iquitos, 67 m^3/ha (Pinedo-Vasquez et al., 1990). It is common for first harvests to yield higher timber volumes than second harvests because they usually take place in forests that have not suffered much human disturbance; the second harvests yield much lower volumes due to low growth rates (Dauber et al., 2005; Keller et al., 2007). However, our analyses indicate that the strip clear-cut system would produce much lower timber yields in a second harvest than would deferment-cutting (Table 3) or selective logging. In Amazonia,

selective logging systems harvest as little as 16 m^3/ha (Uhl et al., 1991) to 21 m^3/ha (Sist and Ferreira, 2007), or as much as 30–40 m^3/ha (van Gardingen et al., 2006) to 75 m^3/ha (Silva, 1989 as cited in Valle et al., 2007).

Timber production in the clear-cut strips after 40 years suggest that this system may not be as profitable as previously thought. The growth projections reported here are part of a broader assessment of economic sustainability. In order to more fully assess the economic sustainability of the strip clear-cutting system in a 40-year cutting cycle, we have also conducted a cost-benefit analysis, which includes the calculations of net present values (NPVs) in a potential second harvest (Rondon, 2008).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2008.09.051.

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