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Effects of selective logging on tropical forest tree growth

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[1] We combined measurements of tree growth and carbon dioxide exchange to investigate the effects of selective logging on the Aboveground Live Biomass (AGLB) of a tropical rain forest in the Amazon. Most of the measurements began at least 10 months before logging and continued at least 36 months after logging. The logging removed ~15% of the trees with Diameter at Breast Height (DBH) greater than 35 cm, which resulted in an instantaneous 10% reduction in AGLB. Both wood production and mortality increased following logging, while Gross Primary Production (GPP) was unchanged. The ratio of wood production to GPP (the wood Carbon Use Efficiency or wood CUE) more than doubled following logging. Small trees (10 cm < DBH < 35 cm) accounted for most of the enhanced wood production. Medium trees (35 cm < DBH < 55 cm) that were within 30 m of canopy gaps created by the logging also showed increased growth. The patterns of enhanced growth are most consistent with logging-induced increases in light availability. The AGLB continued to decline over the study, as mortality outpaced wood production. Wood CUE and mortality remained elevated throughout the 3 years of postlogging measurements. The future trajectory of AGLB and the forest's carbon balance are uncertain, and will depend on how long it takes for heterotrophic respiration, mortality, and CUE to return to prelogging levels.

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1. Introduction

[2] Selective logging of marketable trees is a major land use in the Amazon Basin, affecting 10,000 to 20,000 km² a⁻¹ between 1996 and 2002 [Asner *et al.*, 2005; Nepstad *et al.*, 1999]. The harvested trees often comprise only a small fraction of the total stems, but logging results in collateral damage to the remaining vegetation and a reduction in live carbon stocks. An accurate accounting of the effects of logging on regional carbon balance requires improved information on both the extent and intensity of logging and the rates that previously logged forest recovers biomass. Asner *et al.* [2005] showed that fine scale (~30 m) canopy disturbance due to selective logging can be detected using remote sensing. Progress has been made toward understanding the effects of logging on tropical forest structure and disturbance [Feldpausch *et al.*, 2005; Johns *et*

al., 1996; Keller *et al.*, 2001], nutrient cycles [Olander *et al.*, 2005], soil-atmosphere trace gas fluxes [Keller *et al.*, 2005], and canopy disturbance and recovery [Asner *et al.*, 2004a, 2004b]. Biomass recovery after logging has been reported at a relatively coarse temporal resolution (~6 years) [Carvalho *et al.*, 2004; Silva *et al.*, 1995], but there remains a need for a more mechanistic understanding of the response of tropical forest to logging.

[3] Selective logging affects forest carbon stocks and carbon cycling in several ways [Bazzaz and Pickett, 1980]. Wood biomass is directly exported [Nepstad *et al.*, 1999]; damaged tree crowns are deposited on the forest floor [Feldpausch *et al.*, 2005; Keller *et al.*, 2001]; skid trails and logging patios destroy vegetation and disturb the soil. The rate of carbon dioxide exchange between a logged forest and the atmosphere is affected by the decomposition of slash and the effect of canopy removal on photosynthesis and autotrophic respiration. Logging creates a heterogeneous canopy. Newly created gaps increase the light intensity in the lower canopy and understory [Denslow *et al.*, 1998], and possibly shift plant production downward [Uhl *et al.*, 1988]. The effect of logging on forest productivity may last several years, as the canopy regenerates and gaps fill. Asner *et al.* [2004b] found an 80 to 90% reduction in the area of canopy gaps over 3.5 years. Compared to changes in productivity, other components of the carbon cycle are expected to take longer to recover. The decomposition of coarse woody debris (CWD) requires ~10 years [Chambers *et al.*, 2004b], and full

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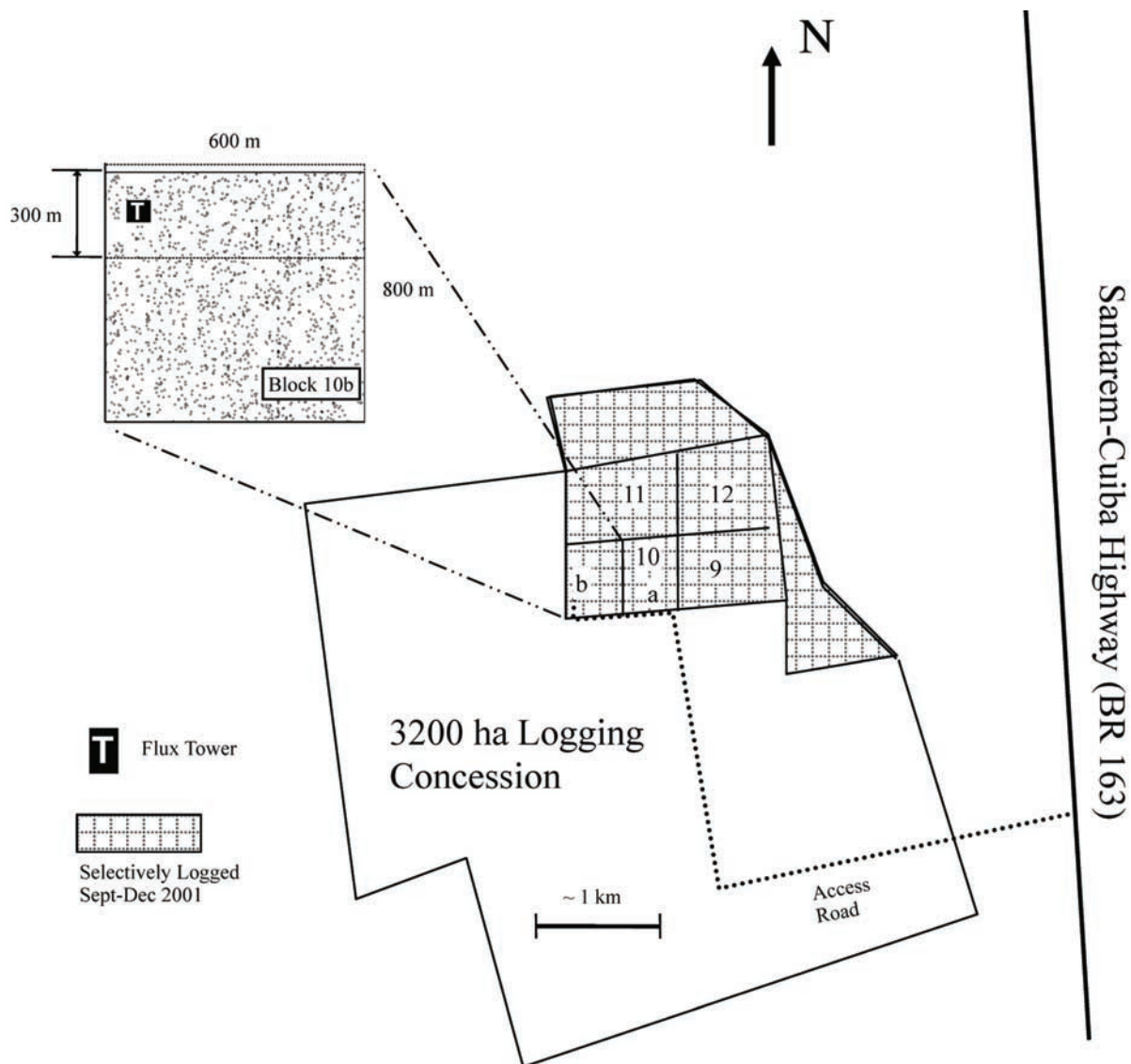


Figure 1. Site layout, Tapajós National Forest (TNF), Pará, Brazil. The hatched area denotes the approximately 700 ha portion of the 3200-ha logging concession that was scheduled for logging between September and December 2001. The location of the eddy-flux tower is denoted by the ‘T’ in Block 10b (see inset). The 300 m X 600 m intensively studied grid was located in the northern portion of Block 10b. Dots denote locations of trees with DBH > 55 cm from the 48-ha 2000 survey.

recovery of prelogging biomass requires decades [Chambers *et al.*, 2004a; Silva *et al.*, 1995].

[4] One of the goals of the Large Scale Biosphere-Atmosphere Experiment in Amazonia (LBA-ECO [Keller *et al.*, 2004]) was to quantify the effects of selective logging on tropical forest carbon cycling. We combined tree inventories, logging damage surveys, high-temporal-resolution measurements of tree growth, and micrometeorological measurements of CO₂ exchange to investigate the effects of logging on the rain forest at the LBA-ECO km-83 site. We used these data to determine tree growth rates before and after selective logging. Most of the measurements began at least 10 months before logging and continued at least 36 months after logging. A subsequent paper will

compare data at the km-83 site with an area of forest that was not logged (km-67).

2. Methods

2.1. Site

[5] The LBA-ECO km-83 site (S 3°01'3.0," W 54°58'14.99") was located in the Tapajós National Forest (TNF), about 50 km south of the city of Santarém, Pará, Brazil [da Rocha *et al.*, 2004; Goulden *et al.*, 2004; Miller *et al.*, 2004]. Access to the site was via a dirt road at the km-83 marker along the Santarém-Cuíbá highway (BR-163, Figure 1). The vegetation was closed tropical forest with canopy emergents (canopy height approximately 35–40m)

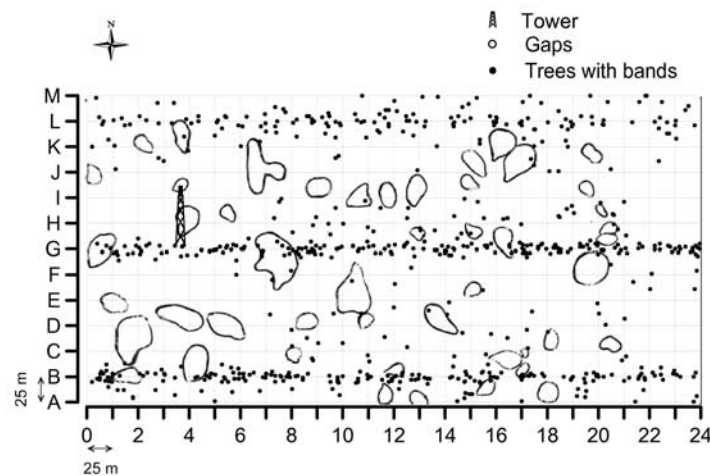


Figure 2. The 18 ha intensive study plot at km-83 site in TNF. Trees equipped with dendrometer bands before logging in November 2000 are shown as solid points. Gaps created by selective logging in September 2001 are shown as irregular shapes. The plot has 25 N-S transects (numbered 0 to 24) and 13 E-W transects (lettered A to M). The 65 m flux tower is indicated in block G4.

on flat upland terrain [Hernandez Filho *et al.*, 1993]. The average annual precipitation was ~ 1900 mm, with a distinct wet season from January through June and a dry season from July through December [da Rocha *et al.*, 2004]. The maximum daily temperature was 24° to 32°C and the minimum was 20° to 25°C , with the dry season 1° to 3°C warmer on average than the wet season.

[6] Installations at the site included an eddy covariance tower that operated beginning June 2000 and an 18-ha intensive study plot for ground-based measurements that was established in March 2000 (Figures 1 and 2). The 18-ha plot was 600-m in the west-east direction and 300-m in the south–north direction. The plot was gridded and marked in the field with stakes at 25-m intervals labeled 0 to 24 west-to-east and A to M south-to-north. The prevailing surface winds were generally from the east at 2 to 4 ms^{-1} , and occasionally shifted to westerly during calm afternoons as a result of a river circulation caused by the Tapajós River [Miller *et al.*, 2004]. The 18-ha plot was immediately upwind of the tower, and in the footprint during most daytime periods.

2.2. Logging

[7] Our measurements took place in a 700-ha area that was scheduled for logging in 2001 as part of a larger, 3200-ha reduced-impact-logging demonstration project over a 5-year period beginning in 1999 (Figure 1). The logging was managed by the Brazilian Institute for the Environment and Renewable Resources (IBAMA) and carried out by a commercial company (Fazenda Treviso/MAFLOPS). The logging employed techniques to reduce damage, including vine cutting before logging, directional felling, and preplanned skid trails and logging decks [Pinard *et al.*, 1995]. Other investigations in the TNF project considered the impacts of logging on forest structure and recovery [Silva *et al.*, 1995], soil trace-gas exchange [Keller *et al.*, 2005], and nutrient cycles [Olander *et al.*, 2005].

[8] The forest around the site was logged in three phases from August to December 2001. The first phase, which

occurred August 18, felled just a few trees in immediate proximity to the micrometeorological tower. This phase was needed to avoid infrastructure damage during the subsequent commercial logging, and likely had little or no effect on the measurements. The second phase, which occurred throughout September, involved logging a block that extended 1-km east, 0.1-km west, 0.1-km north and 0.7-km south of the eddy flux tower (Figure 1). This phase encompassed nearly all of the 18-ha intensive study area. The third phase, which occurred in November and December, involved logging blocks that extended 1-to-3 km east and north of the eddy flux tower (Figure 1). This phase encompassed all of the remainder of the 18-ha study area.

2.3. Aboveground Live Biomass (AGLB)

[9] We made an initial tree survey in March 2000 to quantify the amount and distribution of wood biomass. Trees were identified, numbered, tagged, and mapped, and the Diameter at Breast Height (DBH) was measured with diameter tape. We divided trees into three size classes: small trees, with a DBH from 10 cm to 35 cm, medium trees, with a DBH from 35 cm to 55 cm, and large trees, with a DBH greater than 55 cm. The area surveyed differed by size class. All of the medium and large trees (DBH greater than 35 cm) were measured in a 48-ha area that included the 18-ha intensive study area (Block 10b, Figure 1). All of the small trees (DBH greater than 10 cm) were measured along three 10-m wide west to east transects within the 18-ha study area (1.8-ha total area, Rows B, G and L in Figure 2). The March 2000 survey found 1815 trees. The total stem density was 491 trees ha^{-1} , with $434\text{ small trees ha}^{-1}$, $32\text{ medium trees ha}^{-1}$, and $25\text{ large trees ha}^{-1}$. The relationship between DBH and stem density was similar to that found in a nearby forest during 2000 (Figure 3) [Rice *et al.*, 2004].

[10] Tree biomass was calculated from DBH by averaging the results from four separate allometric equations that were developed for moist tropical forests [Araujo *et al.*, 1999; Chambers *et al.*, 2001; Keller *et al.*, 2001]. Biomass is expressed in $\text{Mg biomass ha}^{-1}$, which is roughly twice the carbon content (Mg C ha^{-1}).

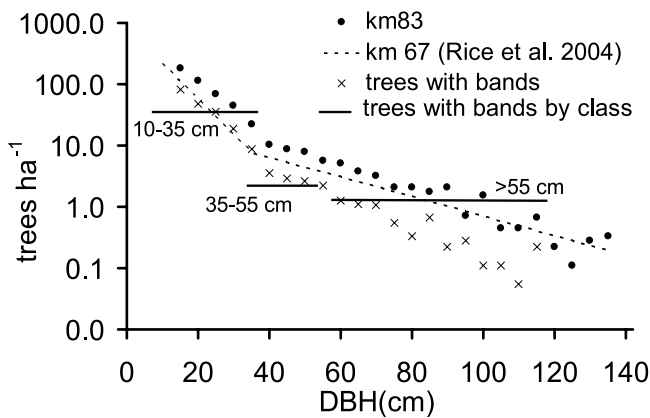


Figure 3. Stem density versus diameter at breast height (DBH) at the LBA-ECO km-83 and km-67 field sites in the Tapajos National Forest, Para, Brazil. For km-83, trees were grouped into 5-cm wide DBH bins based on a prelogging survey in March 2000 (solid points). A piecewise linear regression for stem density from the km-67 survey is shown as the dashed curve [Rice *et al.*, 2004]. Trees equipped with dendrometer bands at km-83 in November 2000 (before logging) are shown as crosses. The dendrometer density (trees ha^{-1}) for each DBH size class included in the analysis is shown as the horizontal lines.

2.4. Tree Growth Rates

[11] We used dendrometer bands [Liming, 1957] to measure the changes in tree diameter and to calculate the changes in aboveground biomass. The bands consisted of stainless steel strips held to the trees at breast height with springs. The distance between notches on the bands changed with tree diameter, providing a precise, repeatable measure of stem diameter change. We equipped 390 trees with dendrometers in November 2000, distributed primarily along three east-west transects in the 18-ha study area (Rows B, G and L in Figure 2). Trees were randomly selected for dendrometer installation from the March 2000 survey. Dendrometers were installed on 108 large trees

(24% of total large trees in 18-ha plot), 204 medium trees (35% of total medium trees in 18-ha plot), and 79 small trees (10% of total small trees in 1.8-ha sub-plot) (Figure 3). An additional 270 dendrometers were installed on small trees located within or near newly created logging gaps in Feb 2002. We refer to this sample as the “gap trees.”

[12] The initial DBH of each dendrometer tree was measured with diameter tape in March 2000 or February 2002. The change in tree circumference was measured at 6-week intervals from November 2000 to November 2004 using digital calipers, and converted to DBH increment. The DBH of each tree with a dendrometer band was updated every 6 weeks based on the previous DBH and measured increment. The biomass of each tree was calculated by averaging the results from four separate allometric equations [Keller *et al.*, 2001]. For each size class, the area-based biomass increment was calculated by scaling the average biomass increment of trees with dendrometers by the observed tree density (Figure 3). Growth rates are reported both in units of DBH increment (cm a^{-1}) and in units of biomass increment per unit forest area ($\text{Mg biomass ha}^{-1} \text{a}^{-1}$). Uncertainties in DBH growth rates reflect the variability in growth rates among a (specified) group of trees, calculated as 95% confidence intervals or standard error as noted in the text and figure captions. We do not present uncertainties in the growth rates expressed in units of biomass increment, due to the difficulties in assessing the uncertainty of the allometric equations used to convert DBH to biomass. Generally, we rounded growth rates in units of biomass to the nearest $0.5 \text{ Mg biomass ha}^{-1} \text{a}^{-1}$.

[13] We filtered the dendrometer data to select the highest quality, most continuous records. We removed the records for trees that died during the study or were removed by the logging or for cases where the dendrometer was damaged. The resulting data set includes a 3- or 4-year record of diameter increment for 234 trees (Table 1).

[14] We used the coordinates of the trees and gaps within the 18-ha study area to calculate the distance from each tree with a dendrometer band to the nearest gap ($D_{i,j}$). The distance $d_{i,j}$ (m) of tree i to the center of each canopy gap j was calculated based on the tree (x_i, y_i) and

Table 1. Aboveground Live Biomass Before and After Logging at Tapajos National Forest, Para, Brazil

	All Trees	10 cm < DBH < 35 cm (1.8 ha)	35 cm < DBH < 55 cm (18 ha)	DBH > 55 cm (18 ha)	Gap Trees 10 cm < DBH < 35 cm (18 ha)
Number of trees	1815	781	586	448	n/a
Mar 2000 survey					
Initial biomass (Feb 2001)	335	116	64	155	n/a
(Mg biomass ha^{-1})					
Dendrometer sample size	234	111	51	23	49
DBH growth rate (prelogging)	0.19 ± 0.05	0.09 ± 0.02	0.23 ± 0.04	0.24 ± 0.07	n/a
(cm a^{-1})					
DBH growth rate (postlogging)	0.27 ± 0.05	0.26 ± 0.01	0.31 ± 0.03	0.26 ± 0.05	0.44 ± 0.03
(cm a^{-1})					
Wood production (prelogging)	2.5	1.5	0.5	0.5	n/a
(Mg biomass $\text{ha}^{-1} \text{a}^{-1}$)					
Wood production (postlogging)	6	3.5	1	1	n/a
(Mg biomass $\text{ha}^{-1} \text{a}^{-1}$)					

gap (x_j, y_j) coordinates, $d_{ij} = ((x_i - x_j)^2 + (y_i - y_j)^2)^{1/2}$, where x is the south-north location in the study plot, and y is the west-east location. The distance to the nearest gap was then selected as the minimum value of d_{ij} , $D_i = \min(d_{ij})$.

2.5. Mortality

[15] We estimated the loss of live biomass due to tree mortality for each size class at 6-week intervals after logging. We recorded the death of any trees with bands during the dendrometer sampling. We then calculated the total number of trees that died within the six-week interval for each size class by scaling the densities of trees with dendrometers by the overall densities (Figure 3). The biomass lost per hectare for each six-week interval was then estimated by multiplying the number of dead trees by the average tree biomass for each DBH class.

2.6. Logging Damage

[16] We resurveyed the 18-ha study area following logging (November 2001) to quantify the loss of aboveground biomass. The location and dimensions of canopy gaps were recorded by GPS and survey tape, and the gap's shape and size were drawn by hand. The field notes were used to construct a map of the 18-ha study area following logging (Figure 2).

[17] The slash left on the forest floor by the logging consisted mainly of the logged tree canopies and portions of logged tree boles that were not removed. The removal or damage of all tagged trees was recorded. The total bole and total crown mass of logged trees were calculated from published allometric equations [Chambers *et al.*, 2001]. The bole wood was removed prior to the postlogging survey, and we estimated the length of bole extracted by measuring the distance between the stump and the remaining crown. This measurement was combined with a bole volume model [Ribeiro, 1996] to estimate the fraction of bole remaining on the forest floor. This fraction was multiplied by the total bole mass to calculate the bole mass remaining on the forest floor.

2.7. Micrometeorological Measurement of GPP

[18] The meteorological measurements were made from a 65-m-tall, 46-cm-triangular-cross-section tower (Rohn 55G, Peoria, IL) located within the logged area (Figures 1 and 2). Details of the measurements, data acquisition, and flux processing are given by Goulden *et al.* [2004] and Miller *et al.* [2004]. Briefly, the tower was instrumented at 64-m height to measure carbon dioxide flux (F_c) between the forest and the atmosphere using the eddy covariance technique [Wofsy *et al.*, 1993]. The CO_2 profile between the surface and the height of the eddy covariance instrumentation was also measured and used to calculate the amount of CO_2 stored within the air column (F_s). Net Ecosystem Exchange (NEE) was calculated for each half hour as the sum of the vertical turbulent CO_2 flux at the top of the tower and the change of CO_2 storage ($NEE = F_c + F_s$). Winds were predominantly from the east at the site. The tower footprint was estimated using measured temperature, momentum flux, and heat flux using an analytical model [Hsieh *et al.*, 2000]. The distance to the peak daytime source contribution was roughly 100 m, with 80% of the flux within ~ 1 km upwind of the tower, such that most of the eddy covariance tower's daytime footprint

was within the area selectively logged (which extended 2–3 km to the east of the tower, Figure 1).

[19] Ecosystem respiration (R) was calculated from nighttime measurements of NEE during periods with sufficient vertical mixing; i.e., friction velocity $u_* > 0.2 \text{ ms}^{-1}$ [Miller *et al.*, 2004]. The necessary u_* -threshold at this site was determined by comparing flux tower estimates of R with scaled-up estimates of respiration components [Chambers *et al.*, 2004b], and radon-based estimates of nocturnal mixing [Martens *et al.*, 2004]. Uncertainties in the calculation of respiration and NEE at the Tapajos sites are discussed in detail in Saleska *et al.* [2003] and Miller *et al.* [2004].

[20] The mean estimated nighttime flux footprint was much larger than the daytime footprint. The calculated average distance to the peak source area during windy nighttime periods was roughly 700 m, with 50% of the flux originating within 2 km, though we caution that the use of footprint models during stable nighttime conditions is uncertain. The effect of a potential contribution of forest that was not selectively logged (beyond 2 km upwind) to estimates of respiration based on nighttime NEE is discussed in the Discussion section.

[21] Gross Primary Production (GPP) was calculated by subtracting NEE from ecosystem respiration from ($GPP = R - NEE$). Continuous 30-min GPP was averaged to construct daily and monthly estimates of GPP. Uncertainty in monthly GPP was calculated as the 95% confidence interval based on averaging daily GPP.

2.8. Photosynthetic Photon Flux Densities

[22] We measured photosynthetic photon flux densities (PPFD) in the subcanopy using sensors mounted on plastic stakes 0.3 m above ground level (Apogee Instruments, Model QSO 100). We installed 15 sensors in intact forest areas before the logging (August 2001). Eight of the 15 sensors were moved to a 30 m by 30 m logging gap, which was ~ 75 m east of the meteorological tower, in November 2001. The sensors were spaced at 5 m intervals along east to west and north to south transects. We accounted for the effects of sun angle and cloudiness by restricting our analysis to sun zenith angles between 27° and 37° , and to incoming solar radiation above 330 W m^{-2} . Incoming solar radiation was measured throughout the study at the tower top with a thermopile pyranometer (Kipp & Zonen CM6B, Delft, The Netherlands).

3. Results

3.1. Stem Production Before Logging

[23] The aboveground biomass was $335 \text{ Mg biomass ha}^{-1}$ in February 2001, with 35% ($116 \text{ Mg biomass ha}^{-1}$) in small trees, 19% ($64 \text{ Mg biomass ha}^{-1}$) in medium trees, and 46% ($155 \text{ Mg biomass ha}^{-1}$) in large trees (Table 1). The total biomass and number of small trees at km-83 were similar to, or slightly greater than, those reported for the nearby LBA-ECO km-67 forest site (Figure 3) [Rice *et al.*, 2004]. The mean annual diameter increment before logging was $0.19 \pm 0.05 \text{ cm a}^{-1}$, which is similar to the rates of 0.16 to 0.2 cm a^{-1} reported for Amazonian forests [da Silva *et al.*, 2002]. The rates of stem increment (Table 1) and wood production (Figure 4) at km-83 for November 2000 to

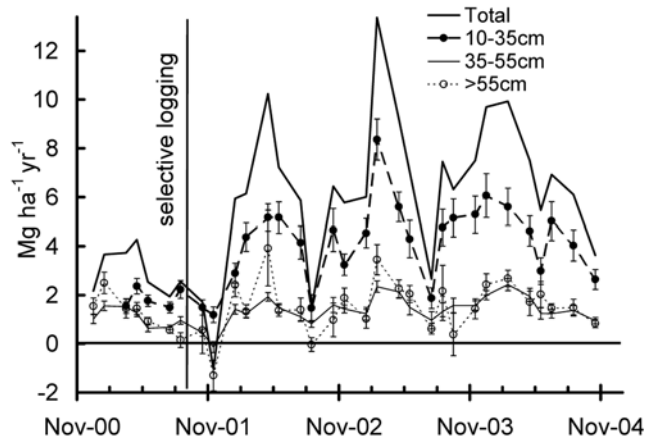


Figure 4. Biomass accumulation ($\text{Mg biomass ha}^{-1} \text{ a}^{-1}$) for the period November 2000 to November 2004 ($35 \text{ cm} < \text{DBH} < 55 \text{ cm}$ and $\text{DBH} > 55 \text{ cm}$ size classes), and February 2001 to November 2004 ($10 \text{ cm} < \text{DBH} < 35 \text{ cm}$ size class). The solid line represents total rate of biomass accumulation, and vertical bars represent standard error.

September 2001 were 30 to 40% less than those observed at km-67 for 1999 to 2001 [Rice *et al.*, 2004].

[24] The average DBH increment differed between the tree size classes during the period before logging. The small trees grew $0.09 \pm 0.02 \text{ cm a}^{-1}$, while the medium trees grew $0.23 \pm 0.04 \text{ cm a}^{-1}$ and the large trees grew $0.24 \pm 0.07 \text{ cm a}^{-1}$ (Table 1). The stem increment was highly variable within each size class; all classes included rapidly growing trees and trees that did not increase in DBH. The diameters of the fastest growing trees in the medium size classes increased by at least 0.9 cm a^{-1} before logging. The fastest growing trees in the large class grew more slowly, increasing by less than 0.5 cm a^{-1} .

[25] The rate of biomass increment at km-83 increased during the wet season (February through May) and decreased during the early part of the dry season (June through December) (Figure 4). The seasonal cycle continued after the logging, with minima observed during July to December and maxima during December to April. The seasonal increase in increment preceded the onset of wet-season rains in some years, a pattern that is similar to that reported by Rice *et al.* [2004] and consistent with the increased rates of photosynthesis late in the dry season that were observed at km-83 [Goulden *et al.*, 2004]. While increased bole swelling with improved hydration during the wet season may have contributed to some of the observed seasonal cycle, a change in stem water content cannot explain the increases in diameter observed before the onset of rains.

3.2. Biomass Lost During Logging

[26] The logging harvested $3.5 \text{ trees ha}^{-1}$, which was 14% of the trees with a DBH above 35 cm, and less than 1% of the trees with a DBH above 10 cm. The intensity was within the previously published range of 1 to 9 trees ha^{-1} for tropical logging [Keller *et al.*, 2005]. The logging created a patchwork of gaps surrounded by intact forest, and increased the area of forest in gaps from 4% to 12% (Figure 2) [Miller *et al.*, 2007]. The number of canopy gaps (2.5 gaps ha^{-1}) was less

than the number of trees logged, as some gaps included multiple tree falls. Canopy gap size varied due to the number of tree crowns felled into the same area, the size of logged trees, and the amount of canopy interconnected by vines.

[27] The loggers felled trees containing $30 \text{ Mg biomass ha}^{-1}$, which was 10% of the original aboveground biomass. We estimated from the damage survey and the bole volume model of Ribeiro [1996] that $9 \text{ Mg biomass ha}^{-1}$ of the harvested tree bole wood was removed from the site, and $5.5 \text{ Mg biomass ha}^{-1}$ of tree bole wood remained on the forest floor. The rate of wood extraction was somewhat greater than the 4.2 to $7.4 \text{ Mg biomass ha}^{-1}$ that has been reported for selective logging in the southern Amazon [Feldpausch *et al.*, 2005]. We estimated from the allometric equations of Chambers *et al.* [2004a] that $9.5 \text{ Mg biomass ha}^{-1}$ of the logged tree aboveground biomass was contained in the tree crowns left on the forest floor. We note that our estimate of logged tree biomass ($30 \text{ Mg biomass ha}^{-1}$) based on the average of four allometric equations (section 2.3) is larger than the sum of the estimated bole wood ($14.5 \text{ Mg biomass ha}^{-1}$) and tree crowns ($9.5 \text{ Mg biomass ha}^{-1}$) which was estimated using an independent set of allometric equations [Ribeiro, 1996; Chambers *et al.*, 2004a].

3.3. Stem Diameter Increment After Logging

[28] The rates of stem growth increased markedly after logging (Table 1). The mean annual diameter increment increased from 0.19 ± 0.05 to $0.27 \pm 0.05 \text{ cm a}^{-1}$. The growth rate of small trees increased from 0.09 ± 0.02 to $0.26 \pm 0.01 \text{ cm a}^{-1}$, medium trees from 0.23 ± 0.04 to $0.31 \pm 0.03 \text{ cm a}^{-1}$, and large trees from 0.24 ± 0.07 to $0.26 \pm 0.05 \text{ cm a}^{-1}$. The average overall rate of wood production was $2.5 \text{ Mg biomass ha}^{-1} \text{ a}^{-1}$ before logging and $6 \text{ Mg biomass ha}^{-1} \text{ a}^{-1}$ after logging (Figure 4). The increase in production lagged the logging. The increase in diameter increment was first observed in early January, which was 3 to 4 months after the logging but coincident with the onset of the wet season. The annual wood production after logging was equivalent to 1.8% of the aboveground biomass, and indicates that the average annual turnover time of wood following logging was 55 to 60 years.

[29] The increase in production after logging was concentrated in the smaller size class (Figure 4 and Table 1). The total rate of production by trees with $10 \text{ cm} < \text{DBH} < 35 \text{ cm}$ increased from 1.5 to $3.5 \text{ Mg biomass ha}^{-1} \text{ a}^{-1}$, while the rate of production by medium size trees increased from 0.5 to $1.0 \text{ Mg biomass ha}^{-1} \text{ a}^{-1}$, and large trees increased from 0.5 to $1 \text{ Mg biomass ha}^{-1} \text{ a}^{-1}$. The smallest trees had the highest rates of wood production after logging, accounting for more than 60% of the total forest production. This increase in wood production was persistent, lasting throughout the period of observation, with no obvious decline after 3 years (Figure 4).

3.4. Logging Response by Proximity to a Gap

[30] The logging left a patchwork of intact forest and gaps (Figure 2). Most of the trees were within 40 m of the nearest gap created by logging (Figure 5). We compared the prelogging and postlogging growth rates of trees as a function of distance to the nearest logging gap (Figure 6). The postlogging data show the increments for trees binned

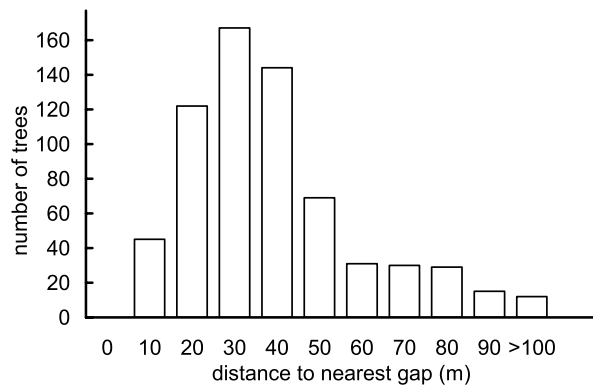


Figure 5. Distribution of trees with dendrometer bands after selective logging according to distance (m) to the nearest gap created by the logging.

by distance to nearest gap; the prelogging data show the increments for the same trees prior to logging.

[31] The increased growth by small trees that were not directly within a gap was only weakly related to gap proximity (Figure 6a). Small trees that were within 20-m of a gap increased from $0.08 \pm 0.03 \text{ cm a}^{-1}$ before logging to $0.33 \pm 0.03 \text{ cm a}^{-1}$ after logging, and small trees that were further than 20-m from a gap increased from $0.09 \pm 0.02 \text{ cm a}^{-1}$ to $0.23 \pm 0.02 \text{ cm a}^{-1}$. Small trees that were more than 50-m from the nearest logging gap showed significant, albeit weaker, increased growth. The medium size class trees showed a smaller overall increase in growth after logging; however, medium size trees close to gaps grew significantly faster than those further away (Figure 6b). Growth by medium trees that were within 20-m of the nearest gap increased from $0.14 \pm 0.09 \text{ cm a}^{-1}$ before logging to $0.46 \pm 0.08 \text{ cm a}^{-1}$ after logging (Figure 6b). Medium trees that were 30-m or further from the nearest gap showed no significant growth increase. The large tree class showed little overall response to logging (Table 1), and the rates of increment by large trees that were immediately adjacent to gaps did not increase, though the uncertainty in the large tree class is large due to the small number of trees (Figure 6c).

[32] The dendrometers installed after the logging were concentrated on small trees that were within or near the gaps created by logging. These trees had the highest average DBH growth rates measured ($0.44 \pm 0.03 \text{ cm a}^{-1}$, Table 1 and Figure 6a). The average growth rate of the gap trees was 76% larger than trees in the same size class within intact forest (Table 1 and Figure 7), similar to the results of Uhl *et al.* [1988]. The seasonality of gap tree growth was similar to that of trees in intact areas, with accelerated growth in the wet season (January–March, Figure 7).

3.5. Mortality After Logging

[33] Sixty-four trees with dendrometer bands within the 18-ha study area, or 10 percent of the 660 trees sampled, died during the 36 months after logging. This average annual mortality rate (3.2% per year) is higher than that reported for other forests in the Amazon, including the km-67 site (1.7% per year) [Rice *et al.*, 2004]. The high mortality observed at km-83 may indicate a delayed effect of logging on tree mortality.

[34] The mortality rate was similar among the three size classes: $3\% \text{ a}^{-1}$ of the small trees died, $3.3\% \text{ a}^{-1}$ of the medium trees died, and $3.7\% \text{ a}^{-1}$ of the large trees died. Field notes recorded the position of the dead trees: 74% (48 trees) remained standing, 15% (10 trees) fell to the ground, and 11% (7 trees) were snapped between 1 and 7 m above ground. We extrapolated these mortality rates to

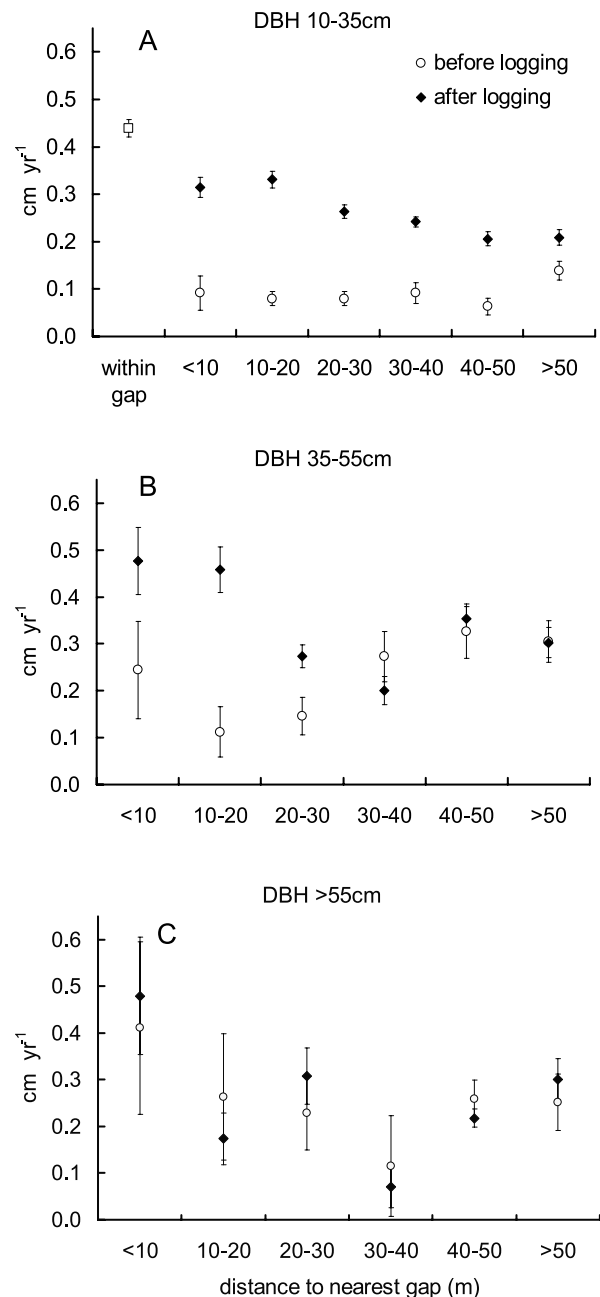


Figure 6. DBH growth rates (cm a^{-1}) versus distance to the nearest gap (m) before logging (November 2000 to August 2001, open circles) and after (September 2001 to November 2004, solid diamonds). (a) Small trees with $10 \text{ cm} < \text{DBH} \leq 35 \text{ cm}$ (also shown is the growth rate of trees within the logging gaps); (b) medium trees with $35 \text{ cm} < \text{DBH} \leq 55 \text{ cm}$; and (c) large trees with $\text{DBH} > 55 \text{ cm}$. The vertical bars represent the standard errors.

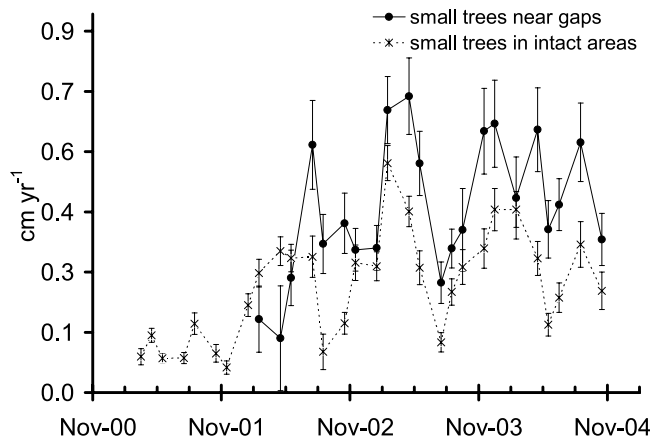


Figure 7. DBH increment (cm a^{-1}) of small trees ($10 \text{ cm} < \text{DBH} < 35 \text{ cm}$) with dendrometers that were directly within or adjacent to logging gaps (solid circles), and small trees with dendrometers installed before logging (crosses). The vertical bars represent the standard errors.

estimate absolute mortality rates of 10 small trees $\text{ha}^{-1} \text{a}^{-1}$ ($3 \text{ Mg biomass ha}^{-1} \text{a}^{-1}$), 0.8 medium trees $\text{ha}^{-1} \text{a}^{-1}$ ($1.5 \text{ Mg biomass ha}^{-1} \text{a}^{-1}$), and 0.7 large trees $\text{ha}^{-1} \text{a}^{-1}$ ($4.5 \pm 0.8 \text{ Mg biomass ha}^{-1} \text{a}^{-1}$).

3.6. Wood Carbon Use Efficiency

[35] The ratio of NPP to GPP can be used to assess the efficiency with which the forest allocated carbon to woody tissue. The total NPP at this site was estimated to be $7 \text{ Mg C ha}^{-1} \text{a}^{-1}$ in the year before logging (Table 2), and GPP from micrometeorological measurements was $33 \text{ Mg C ha}^{-1} \text{a}^{-1}$. The NPP:GPP ratio was $\sim 20\%$, which is slightly lower than that reported by *Chambers et al.* [2004b] for a central Amazon rain forest near Manaus (30%), and much lower than that reported for temperate forests ($\sim 50\%$) [*Waring et al.*, 1998].

[36] We calculated the ratio of dendrometer-based measurements of wood production to tower-based measurements of GPP to track changes in wood Carbon Use Efficiency (wood CUE) over time. This term differs from the more common use of CUE as the ratio of total NPP to GPP [cf. *Chambers et al.*, 2004b] (Table 2). Monthly wood CUE during the

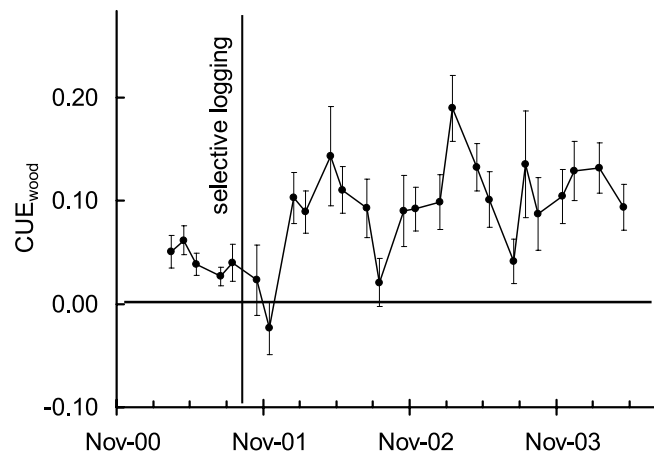


Figure 8. Wood carbon use efficiency (wood CUE) calculated as the ratio of biomass wood production ($\text{T C ha}^{-1} \text{a}^{-1}$) to GPP (gross primary production in $\text{T C ha}^{-1} \text{a}^{-1}$) at km-83 for the period from November 2000 to April 2004. Wood production was obtained by dendrometer measurements. GPP was obtained by micrometeorological measurements at the km-83 eddy flux tower over the same period. The vertical bars represent the standard errors.

period prior to logging was 0.04, indicating that only 4% of the carbon fixed by photosynthesis was stored in wood. Wood CUE increased to an average of 0.09 during the 19 months following logging (Figure 8).

[37] We considered the effects of changes in wood NPP and GPP on wood CUE. The change in GPP in the 24 months following logging was only 10%. This small decrease in GPP was consistent with the amount of canopy lost. Inter-annual variability may have also contributed to the change in GPP, though *Hutyra et al.* [2007] found interannual variation in GPP was small (less than 3%) over a 4-year period at the nearby km-67. In contrast, wood NPP more than doubled following logging (Figure 4).

3.7. Subcanopy PPFD

[38] The amount of light measured at the forest floor within a logging gap was an order of magnitude higher than measured in intact forest prior to logging. This increase in light was similar to *Denslow et al.* [1998], who found gap light levels 5–10 times larger than intact forest areas 1 year after gap creation. The light levels near the ground in the gap remained higher than those in the intact area for the duration of the measurements (more than 2 years). The near-ground light levels measured by both the gap and intact area sensors markedly decreased a year after the logging (October 2002), just prior to the beginning of the wet season, possibly associated with the creation of new leaves in anticipation of the rainy season [*Goulden et al.*, 2004; *da Rocha et al.*, 2004]. Other factors may have contributed to the measured light level decrease at the forest floor, including the growth of low-level vegetation within the gap that shaded the PPFD sensors mounted at 0.3 m height, and sensor degradation due to decreasing sensitivity and biofouling. Degradation/biofouling would be expected to occur steadily over time, and therefore the measured decrease in light levels in

Table 2. Annual Carbon Budget at km-83 Before Logging^a

Term	Value	Method
GPP	33	Annual u^* filtered eddy flux [<i>Goulden et al.</i> , 1996, 2004]
NPP _{wood}	1.3	Table 1
NPP _{leaf}	3	Annual litter fall [<i>Goulden et al.</i> , 2004]
NPP _{root}	2.5	Half the difference between annual soil respiration ($\sim 9 \text{ Mg C ha}^{-1} \text{a}^{-1}$) [<i>Goulden et al.</i> , 2004] and the sum of NPP _{wood} ($\sim 1.3 \text{ Mg C ha}^{-1} \text{a}^{-1}$) and NPP _{leaf} ($\sim 3 \text{ Mg C ha}^{-1} \text{a}^{-1}$) [<i>Raich and Nadelhoffer</i> , 1989]
NPP _{total}	7	
NPP _{total} /GPP	0.2	

^aUnits are in $\text{Mg C ha}^{-1} \text{a}^{-1}$, except NPP_{total}/GPP which has no units.

October 2002 was likely associated with the growth of new vegetation.

4. Discussion

4.1. Differential Effects of Logging on Tree Growth

[39] The woody increment at km-83 increased following logging (Figure 4). Changes in tree growth rates after logging varied among the size classes, with the increased growth most pronounced among trees in the small size class. By contrast, the overall growth rates of the medium and large trees were similar to prelogging rates. Increases in tree growth rates also varied according to tree location within the forest with respect to logging gaps, with (small) trees located within newly created gaps showing the largest growth rate increases of all trees (Figure 6 and Table 1). Enhanced growth rates were also found for trees that were near, but not within, logging gaps. Medium-sized trees showed the strongest growth rate dependence on proximity to a gap, with trees that were closer to gaps growing faster than those further away (Figure 6). Small trees near gaps also grew faster than those further away, though the dependence on proximity to a gap was weaker than for the medium trees (Figure 6). The large tree growth rates did not show a dependence on proximity to canopy gaps.

[40] These consistent patterns of growth response from before to after logging could not have been explained by interannual variations in climate, which we would expect to affect trees in a consistent manner independent of proximity to a newly created gap. We therefore attribute most of the changes we observed to the effects of logging, though we cannot exclude the possibility that some of the shifts were a result of natural interannual variability.

[41] The patterns of increased growth can be explained by shifts in the availability of light. Small trees in gaps experienced the greatest increase in light and, hence, the greatest increase in growth. The large trees experienced no change in light and no change in growth. The small and medium trees that were not directly in gaps experienced intermediate changes in light and intermediate changes in growth. The crowns of most medium trees were in the canopy, and logging would be expected to increase the direct-beam illumination on the sides of adjacent crowns that remained. Medium trees that were more distant from gaps likely experienced only modest changes in illumination. Most of the smaller trees had not yet achieved canopy status, and they relied to a greater extent on diffuse-beam illumination, which may have increased throughout the forest understory.

[42] The apparent increase in illumination for small trees that were distant from gaps may also reflect the generally dim conditions in the understory, since a small absolute increase in understory light would cause a large proportional increase in illumination. The amount of light reaching the forest floor within the intact area did not increase dramatically, as was the case within the gap. However, these sensors were installed close to the ground, and these data do not preclude increased light levels within the likely crown space (10–30 m above ground level) of the 10 cm < DBH < 35 cm trees. An increase in the growth of intact forest patches was also reported by *Chambers et al.* [2004a], who observed increased growth in control plots that were adjacent to selectively logged plots.

The differential response by size class is not consistent with increased water or nutrient availability, which would be expected to affect trees of all size classes.

4.2. Changes in Wood CUE

[43] The wood-production-based CUEs at km-83 increased markedly following logging (Figure 8). We considered whether this change in wood CUE was due to changes in the controlling factors (temperature or soil nutrients) that *Chambers et al.* [2004a] speculated are responsible for the low NPP-based CUEs found in tropical forest. The increase in wood CUE after logging was not related to a cooling of the local microclimate, as we previously reported slightly elevated subcanopy air temperatures following logging, presumably due to additional radiative heating at the forest floor in gaps [*Miller et al.*, 2007]. Likewise, *Olander et al.* [2005] found no increase in the availability of soil nutrients in logging gaps at the same site, implying that the increase in wood CUE was not a result of increased nutrient availability. Rather, we suspect the change in wood CUE with logging resulted from a shift in the relative contributions of the different tree size classes to GPP and NPP.

[44] We hypothesize that larger, dominant trees at km-83 have relatively low CUEs, which are constrained by intrinsic allocation patterns and low growth rates. This hypothesis is supported by observations that large tropical trees are not carbon limited [*Wurth et al.*, 2005]. Emergent tropical trees may not experience strong selection for continuing high growth rates, since their fitness is unlikely to improve if they become taller. We therefore suspect that the large trees at km-83 have relatively low CUEs. By contrast, many small trees are light limited, and would be expected to experience strong selection to maximize their growth rates, since their fitness will improve with increasing canopy access. We therefore suspect that the smaller trees at km-83 have relatively high CUEs. The logging at km-83 opened the canopy, which increased the proportion of production carried out by small trees (Figure 4). We hypothesize that the small trees used the increased carbon availability more efficiently than had been done by the taller trees, resulting in the observed increase in wood CUE (Figure 8).

[45] The doubling of wood growth rates following logging suggests that the overall CUE increased by roughly 20% if other components of NPP_{total} remain at prelogging levels (Table 2). We cannot exclude the possibility of changes in the other processes contributing to NPP_{total} . For example, changes in belowground carbon cycling could either increase or decrease total NPP and therefore CUE.

4.3. Changes in Aboveground Live Biomass Following Logging

[46] We used the measured and estimated biomass gains (tree growth, section 3.3 and Figure 4) and losses (logging, section 3.2; mortality, section 3.5) to construct a budget for aboveground biomass over the measurement interval (Figure 9). We note that tree recruitment into the smallest size class was neglected, and therefore the total wood production at km-83 may have been underestimated by $\sim 1 \text{ Mg biomass ha}^{-1} \text{ a}^{-1}$ or more [*Rice et al.*, 2004]. We previously reported [*Miller et al.*, 2004] that the km 83 site was close to carbon neutral during the year before the logging ($+0.8 \pm 2 \text{ Mg C ha}^{-1} \text{ a}^{-1}$). Compared to the

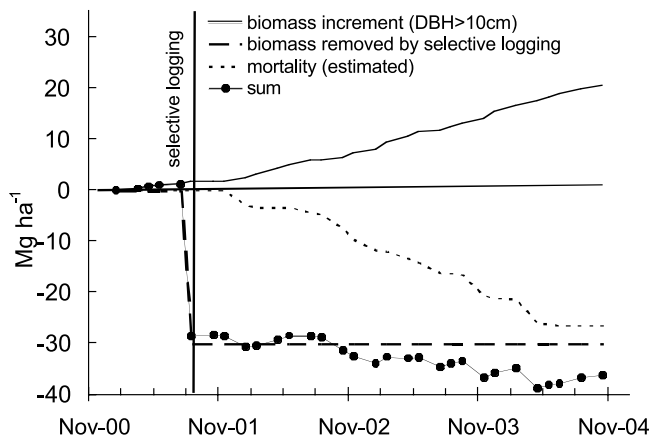


Figure 9. Aboveground live biomass (AGLB) gains and losses ($\text{Mg biomass ha}^{-1}$) in trees with $\text{DBH} > 10$ cm during the period from November 2000 to November 2004: biomass increment from the dendrometer bands (solid curve); biomass lost due to mortality (short dash); biomass removed by logging (long dash), and sum of gains and losses (solid curve with circles). The initial aboveground biomass was subtracted so that positive values correspond to biomass gains and negative values correspond to biomass losses.

prelogging total AGLB ($335 \text{ Mg biomass ha}^{-1}$), the forest biomass was $35 \text{ Mg biomass ha}^{-1}$ less at the end of the 36-month postlogging study interval (Figure 9). The direct removal and destruction of biomass by logging resulted in a sharp drop in biomass over a relatively short interval. In comparison, the biomass accumulation due to tree growth and loss due to mortality occurred at steady rates over the postlogging interval. The loss of biomass due to mortality ($-8 \text{ Mg biomass ha}^{-1} \text{ a}^{-1}$) was greater than the wood production ($+6 \text{ Mg biomass ha}^{-1} \text{ a}^{-1}$) following logging, such that the forest continued to lose AGLB throughout the study (Figure 9). While we did not measure mortality rates before logging, our postlogging mortality was greater than that reported for the nearby (unlogged) km 67 site [Rice *et al.*, 2004]. Logging potentially resulted in sustained higher rates of mortality relative to unlogged forest, due to lasting effects of mechanical damage, increased wind stress on trees adjacent to gaps and likelihood of wind throw, and damage to roots by heavy machinery.

[47] Our analysis focused on the effects of logging on the live biomass, and we did not consider the rates of heterotrophic respiration and the net ecosystem carbon balance. The logging left $5.5 \text{ Mg biomass ha}^{-1}$ of tree boles and $9.5 \text{ Mg biomass ha}^{-1}$ of tree crowns on the forest floor, which would be expected to decay over the next decade [Chambers *et al.*, 2004a]. It is likely that km-83 was a modest net carbon source for several years following disturbance [Sprugel, 1985]. The higher wood CUE following logging provides a mechanism for forest biomass recovery to prelogging levels. We expect that the site will recover biomass more rapidly as the logging-induced slash and tree boles decay and the mortality rate decreases to levels found in unlogged forest. Three issues will determine the future trajectory of net ecosystem carbon balance: (1) the rate that biomass lost during and after logging decays, (2) the rate that mortality

returns to its prelogging level, and (3) the rate that CUE returns to its prelogging level. A accurate prediction of future carbon balance will require a better understanding of the controls on tropical forest decomposition and tree mortality, and, particularly, carbon allocation and CUE by tropical forest trees.

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