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Coarse woody debris in undisturbed and logged forests in the eastern Brazilian Amazon

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Abstract

Coarse woody debris (CWD) is an important component of the carbon cycle in tropical forests. We measured the volume and density of fallen CWD at two sites, Cauaxi and Tapajós in the Eastern Amazon. At both sites we studied undisturbed forests (UFs) and logged forests 1 year after harvest. Conventional logging (CL) and reduced impact logging (RIL) were used for management on areas where the geometric volumes of logs harvested was about 25–30 $m^3 ha^{-1}$. Density for five classes of fallen CWD for large material ($>$10 cm diameter) ranged from 0.71 to 0.28 $Mg\,m^{-3}$ depending upon the degree of decomposition. Density of wood within large fallen logs varied with position relative to the ground and with distance from the center of the log. Densities for materials with diameters from 2 to 5 and 5 to 10 cm were 0.36 and 0.45 $Mg\,m^{-3}$, respectively. The average mass ($\pm$ SE) of fallen CWD at Cauaxi was 55.2 (4.7), 74.7 (0.6), and 107.8 (10.5) $Mg\,ha^{-1}$ for duplicate UF, RIL, and CL sites, respectively. At Tapajós, the average mass of fallen CWD was 50.7 (1.1) $Mg\,ha^{-1}$ for UF and 76.2 (10.2) $Mg\,ha^{-1}$ for RIL for duplicate sites compared with 282 $Mg\,ha^{-1}$ for live aboveground biomass. Small- and medium-sized material ($<$10 cm dia.) accounted for 8–18% of the total fallen CWD mass. The large amount of fallen CWD at these UF sites relative to standing aboveground biomass suggests either that the forests have recently been subjected to a pulse of high mortality or that they normally suffer a high mortality rate in the range of 0.03 per year. Accounting for background CWD in UF, CL management produced 2.7 times as much CWD as RIL management. Excess CWD at logging sites would generate a substantial CO_2 emission given the high rates of decay in moist tropical forests.

Key words: Amazon, coarse woody debris, reduced impact logging, selective logging, tropical forest, wood density

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Introduction

Coarse woody debris (CWD) is an important component in the carbon stock of mature tropical forests (Harmon *et al*., 1995; Chambers *et al*., 2000; Clark *et al*., 2002). In undisturbed, old growth, moist forests in the Brazilian Amazon, Chambers *et al*. (2000) and Gerwing (2002) found that CWD accounted for 6% and 18% of the aboveground live biomass at sites near Manaus and Paragominas. According to Rice *et al*. (in press), at the Tapajós National Forest, near Santarem, Pará, Brazil, CWD accounted for 25% of the aboveground carbon stock. Chambers *et al*. (2000, 2001b) found that CWD in forests near Manaus, decays with an instantaneous exponential rate of 0.13–0.17 per year (half-life from 4.1 to 5.3 years). The rapid decay of CWD accounts for a substantial carbon flux. Rice *et al*. (in press) estimated that respiration from CWD was approximately 6.3 $Mg\,C\,ha^{-1}\,yr^{-1}$; CWD respiration exceeded the average flux of fine litterfall (5.7 $Mg\,C\,ha^{-1}\,yr^{-1}$) at the site in the Tapajós National Forest, near Santarem. Aside from its important role in the carbon cycle, CWD

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contains important stocks of nutrients, in particular Mg and Ca (Fernandes *et al*., 1997; Keller *et al*., in press). CWD also provides habitats for a considerable diversity of life (e.g. MacNally *et al*., 2001; Nordén & Paltto, 2001).

Selective logging is a common management practice in tropical forests. The process of felling and bucking trees and then skidding the logs to decks (log landings) and roads leads to considerable mortality and damage to the forest (Verissimo *et al*., 1992; Pereira *et al*., 2002). In conventional logging (CL) in the eastern Brazilian Amazon, the construction of logging infrastructure such as decks and logging roads is also an important source of mortality, damage, and ground and canopy disturbance (Johns *et al*., 1996; Uhl *et al*., 1997; Pereira *et al*., 2002). Gerwing (2002) found that intact forests contained about 33 $Mg\,ha^{-1}$ of CWD (dry weight of biomass) above 10 cm diameter. CWD increased to 68 $Mg\,ha^{-1}$ at three 'moderate intensity logging' sites that had 28–48 $m^{-3}\,ha^{-1}$ of timber harvested using CL sampled 4–6 years after harvest.

Harvest practices designed to minimize damage to the residual forest stand while optimizing the harvest effort, are referred to as reduced impact logging (RIL). RIL employs pre-harvest mapping and inventory, and vine cutting. Inventory data are used to create harvest plans for directional felling. Skidding along planned trails uses wheeled skidders rather than crawler tractors. Several studies near Paragominas, Pará, in the eastern Brazilian Amazon investigated the effects of RIL compared with CL. RIL resulted in a reduction in residual stand damage and mortality (Verissimo *et al*., 1992; Johns *et al*., 1996). Comparisons of CL and RIL in eastern Pará, Brazil, show that RIL harvesting operations reduce ground and canopy damage by half compared with CL (Pereira *et al*., 2002). The decrease in biomass loss by RIL compared with CL was 44% for a forest in Sabah, Malaysia (Pinard & Putz, 1996). CWD generation by RIL compared with CL has not been quantified in the Brazilian Amazon.

RIL has the prospect to minimize carbon losses following logging in part through the reduction of CWD generation (Pinard & Putz, 1996). Under forest conditions in the Eastern Brazilian Amazon, RIL operations can harvest an equivalent volume of timber as CL without any increase in cost (Holmes *et al*., 2002). Should the avoidance of logging damage become allowable as a carbon offset practice under international agreement, then RIL operations should gain a competitive cost advantage over CL. The degree to which RIL conserves carbon compared with CL depends upon the generation of CWD, the decomposition of CWD, as well as on the rate of forest regeneration following logging.

In order to quantify the mass of CWD in forests of the eastern Brazilian Amazon and to quantify the generation of CWD by both CL and RIL management, we worked at two sites, near the towns of Santarem and Paragominas, which have active timber industries. We report on the volume, densities, and mass of fallen CWD. We made a detailed estimate of the density of CWD and analyzed the errors related to both density and volume sampling.

Site description

We worked at two sites that we refer to as Cauaxi and Tapajós. At the Cauaxi site, we studied undisturbed forest (UF), and forests harvested using CL and RIL. At Tapajós, only UF and RIL were studied. Sampling units, whether logged or unlogged ranged in size from 50 to 100 ha.

The Fazenda Cauaxi in the Paragominas Municipality, Pará, has hosted RIL demonstration and training by the Fundação Floresta Tropical since 1995 in collaboration with the property owners CIKEL Brasil Verde SA. A centrally located camp (3.73°S, 48.29°W) serves as a base for these activities. Prior to current logging operations, there is no historical record of land use or collection of non-timber forest products, although there are indicators of indigenous activity. Ranchers and loggers first entered the area in 1976 through the Rio Capim and the Rio Surubiju. There were no roads in the area until the 1980s.

The climate at Fazenda Cauaxi is humid tropical. Total annual precipitation averages about 2200 mm (Costa & Foley, 1998). Soils in the area are classified mainly as dystrophic yellow latosols according to the Brazilian system (RADAMBRASIL 1983). The topography is flat to mildly undulating. The forest at Fazenda Cauaxi is classified as tropical dense moist forest (IBGE 1988). Stand basal area is approximately 26 $m^2\,ha^{-1}$ for trees greater than 10 cm diameter at breast height (DBH). The most common timber species that were harvested during 5 years of forest operations were *Manilkara huberi*, *M. paraensis*, *Protium pernevatum*, *Dinizia excelsa*, and *Piptadenia suaveolens*. The most common tree species found are *Licania* sp., *M. huberii*, *Astronium lecointei*, *Eschweilera odorata*, and *Parkia* spp. At Cauaxi, we studied six forest blocks (50–100 ha each) including duplicates of UF, CL, and RIL treatments. All blocks were measured in 2001 and the logged blocks had been harvested about 1 year earlier in 2000. Harvest volumes for the RIL blocks were recorded in detail and ranged from 25 to 30 $m^3\,ha^{-1}$. Detailed records are not available for the CL blocks but interviews, observations, and market conditions all suggest that harvest volumes were similar on all blocks.

At Cauaxi, RIL caused only about half as much ground and canopy damage compared with CL. The ground damage, defined as the area affected by machines, was 11.2% of CL blocks vs. 4.6% for RIL blocks. Canopy damage, defined as the gap fraction measured approximately 1 year following logging was 21.6% for CL vs. 10.9% for RIL (Pereira *et al.*, 2002).

The Tapajós National Forest is located south of the city of Santarem in Pará state. The study site is located near km 83 on the BR-163 (Santarem-Cuiaba) Highway (3.04°S, 54.95°W). The region receives approximately 2000 mm of precipitation per year and has an annual mean temperature of 25 °C (Silver *et al.*, 2000). The study site is located on an old, nearly flat, erosional remnant plateau with well-drained soils. Our studies were located mainly on a clay-textured Oxisol (80% clay, 18% sand, 2% silt). A limited number of transects crossed a sand-loam-textured Ultisol (60% sand, 38% clay, 2% silt) (Silver *et al.*, 2000). Vegetation at the site is evergreen, tropical dense moist forest with a total aboveground live biomass (dry weight) of about 282 Mg ha^{-1} (Keller *et al.*, 2001). The most common timber species harvested during 2000 were *M. huberi*, *Carapa guianensis*, *Couratari guianensis*, *Licaria brasiliensis*, and *Nectandra rubra*. The most common tree species ($>$35 cm DBH) found are *Pouteria* sp., *M. huberi*, *C. guianensis*, *Eschweilera* sp. and *Sclerolobium melanocarpum*. We studied four forest blocks ($\sim$100 ha each) including duplicate UF and RIL treatments. CWD was sampled in 2001 approximately 1 year following harvest.

Methods

We used line-intercept sampling (also termed planar intercept sampling) to quantify CWD volume (e.g. Brown, 1974; De Vries, 1986; Ringvall & Stahl, 1999). Three or more lines were selected at random locations along an edge of each rectangular study block. Parallel lines separated by at least 100 m ran perpendicular to the block edge. In the case of logging blocks, we oriented the lines so that they crossed logging roads at approximately right angles. As we have shown previously, damage is concentrated along the roads and log storage decks bordering the roads (Pereira *et al.*, 2002). The sampling lines were thus oriented to cross both high and low damage areas in order to avoid a sampling bias. We sampled between 2500 and 3400 m of line for each study block (Table 1) with a total of nearly 29 km of transect reported for the entire study.

We defined CWD as fallen dead woody material with diameter greater than 2 cm. We did not measure standing dead material. We divided the material into three classes according to diameter: 2–5, 5–10, and $>$10 cm. Each transect was divided into 50 m segments. A measuring tape was used to demarcate the transects. In each 50 m segment, a 10 m sub-sample was selected at random and the small and medium classes (2–5 and 5–10 cm dia.) were counted only in that segment. Diameter was measured to the nearest centimeter for all pieces of CWD greater than 10 cm. This material was classified according to its decomposition state into five classes (Harmon *et al.*, 1995). The classes 1–5 from freshest to most rotten were defined according to the following criteria. Class 1 material was newly fallen solid wood with some leaves and/or fine twigs still attached. Material in class 2 was still solid and had intact bark but no fine twigs or leaves. Class 3 material resembled class 2 except that bark for this class was rotten or sloughing. Class 4 material is somewhat rotten and could be broken when kicked. Class 5 material was rotten and friable and it could be broken apart with bare hands.

Table 1 Sites sampled for fallen coarse woody debris for three treatments

Code	Site	Treatment	Line sampled (m)	CWD volume (m^3 ha^{-1})	Std. error (m^3 ha^{-1})
CUF1	Cauaxi	UF	3100	103	14
CUF2	Cauaxi	UF	2830	115	15
CRIL1	Cauaxi	RIL	3120	146	30
CRIL2	Cauaxi	RIL	2760	136	15
CCL1	Cauaxi	CL	2810	205	19
CCL2	Cauaxi	CL	2700	171	15
TUF1	Tapajos	UF	3050	105	7
TUF2	Tapajos	UF	3000	112	15
TRIL6	Tapajos	RIL	2310	179	11
TRIL9	Tapajos	RIL	3000	130	18

UF, undisturbed forest; RIL, reduced impact logging; CL, conventional logging. The volume error is a standard error of the mean following Eqn (1) for all CWD volume. The codes are mnemonic. The first letter refers to the location Cauaxi (C) or Tapajós (T) and the next letters refer to the treatments as described above. The number gives the replicate block number.

We determined densities from a sampling of logs ($n = 479$) from the Tapajós National Forest from all five decay classes. We stratified the sample inversely according to the frequencies of the diameter classes that we encountered in our volume sampling. We randomly selected CWD pieces from more populated classes and sampled all pieces encountered for less populated classes. Cylindrical radial sections were cut from the selected sample of the downed material. We removed cylindrical plugs from the radial sections using a power drill equipped with plug and tenon extractor bits (9.525, 12.7, and 19.05 mm dia.). Plugs were removed along one of eight randomly selected radii at 5 cm intervals from the center of each cylinder (Fig. 1a). We cut the ends of the plugs flush to facilitate fresh volume estimation. For heavily decayed (class 5) CWD, we used the power drill and tenon extractor exclusively to sample 29 of 60 pieces. For 11 pieces of CWD in class 5 that were too friable to sample with the power drill, we instead inserted a clear plastic cylinder to a known depth and removed all material that filled the cylinder. Both the plastic cylinder and the power drill methods were used on 10 pieces of CWD from decay class 5. The cylindrical plugs ($n = 634$ from logs >10 cm) were oven dried at 65 °C and wood density was calculated as oven dry mass divided by fresh volume.

Radial sections were photographed digitally. We separated void space from solid wood by visual interpretation (Fig. 1b, c). The binary classes of wood and void were summed to allow a determination of a proportional void space for each radial section. The final density for each sampled piece of wood was calculated by multiplying the averaged wood density of the plugs by the proportion of space that was not void.

We also sampled 103 and 87 randomly selected individual pieces of CWD in the 2–5 (small) and 5–10 cm (medium) diameter classes, respectively. Fresh volume was estimated by calculating the volume of a cylinder corresponding to the length and diameter of each piece. In some cases, the tenon extractor was used to remove one to two plugs from medium-sized pieces of CWD. The pieces were cut to manageable sizes (generally less than 10 cm length) for oven drying (65 °C).

Error and statistical analysis

Mean CWD volume for a given decay class was calculated as the average of CWD volume for each sample transect weighted by transect length. We report standard errors of the mean for volume and density measurements. The variances of the mean for volume (σ^2, Eqn (1)) are also weighted by transect lengths (L_j)

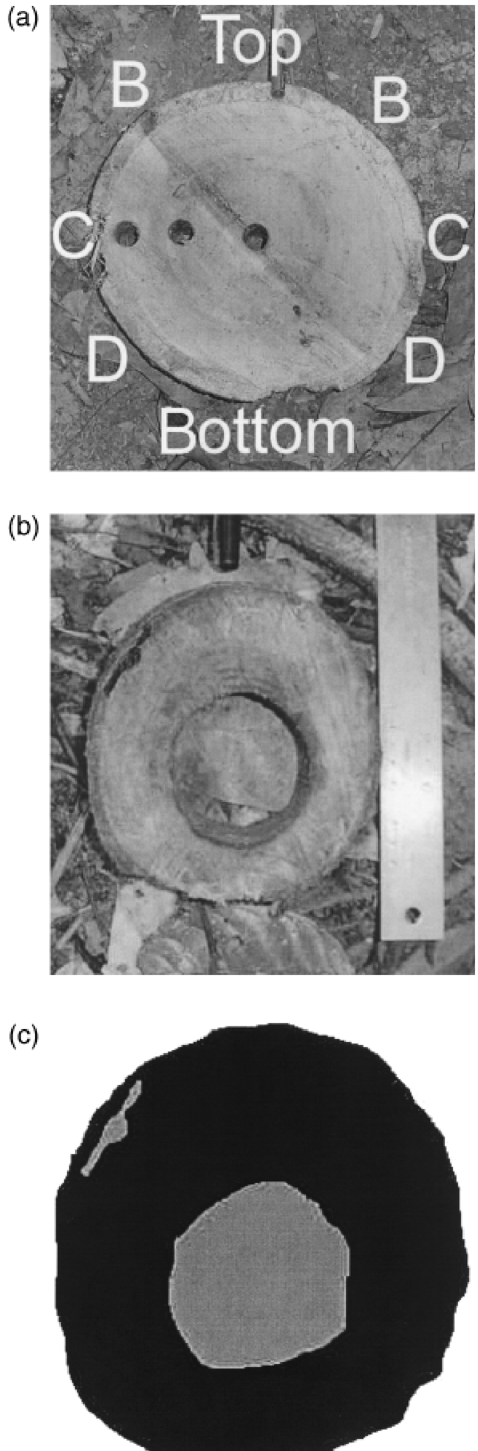

Fig. 1 (a) A cylindrical section of a piece of fallen CWD after removal of plugs for density sampling. The groups of sampling radii are marked top (0°), B (45° + 315°), C (90° + 270°), D (135° + 225°) and bottom (180°). (b) A cylindrical section of a piece of fallen CWD showing void space. (c) Binary visual interpretation of the void space. Solid wood is shown in black and void is shown in gray.

for n transects, as recommended by DeVries (1986, p. 256), prior to calculation of the standard errors for volumes:

$$\sigma^2 = \frac{\left[\sum L_j (V_j - \bar{V})^2\right]}{\left[(n-1) \cdot \sum L_j\right]} \quad (1)$$

The mass of CWD (M_i) for class $i = 1$–7 (decay classes 1–5 for large debris and small and medium debris) was calculated from the product of the volume of material (V_i) and the respective density for the material class (Δ_i):

$$M_i = \rho_i \cdot V_i \quad (2)$$

Therefore, the error on each M_i (E_M) was calculated by:

$$E_M = E_\rho \cdot V + \rho \cdot E_V \quad (3)$$

where E_ρ and E_V represent the errors in density and volume, respectively. Eqn (2) is valid when V and Δ are not correlated. Our analysis (data not shown) indicated no significant correlation ($r^2 = 0.00$) between volume of the CWD pieces sampled and density for all decay classes. The mass for a given decay class is not necessarily independent of the mass for another decay classes. Therefore, we estimated the total error in mass conservatively for all material classes as the simple sum of the component errors in mass.

We only measured densities at the Tapajós site and we applied these densities to mass calculations at both sites. Although Tapajós and Cauaxi sites share many species in common, it is possible that the CWD densities will vary somewhat between these sites. This possible difference in densities between sites represents an unknown potential bias in the reporting of CWD mass for Cauaxi.

We compared mean fallen CWD volume and mass across sites and treatments (UF and RIL) using a two-way ANOVA with a site × treatment interaction term. We also compared mean mass and volume for three treatments (UF, CL, and RIL) at Cauaxi using a one-way ANOVA. The density across five decay classes and two smaller size classes of CWD material and the effect of the radial sampling direction were also compared using a one-way ANOVA.

Results

The total volume of CWD ranged from 102 to 205 $m^{-3} ha^{-1}$ across the 10 blocks sampled (Table 2). In a two-way ANOVA, taking into account site and treatment effects (UF, RIL), we found no significant difference between the Cauaxi and Tapajós sites,

Table 2 Mean CWD volume (± SE) for 10 sampled blocks of undisturbed forest, reduced impact, and conventional logging at Cauaxi and Tapajós

Code	Class 1 ($m^3 ha^{-1}$)	Class 2 ($m^3 ha^{-1}$)	Class 3 ($m^3 ha^{-1}$)	Class 4 ($m^3 ha^{-1}$)	Class 5 ($m^3 ha^{-1}$)	Small ($m^3 ha^{-1}$)	Medium ($m^3 ha^{-1}$)	Total ($m^3 ha^{-1}$)
CUF1	2.6	10.4	32.7	25.9	15.0	7.7	8.6	102.9
	(1.4)	(3.9)	(4.3)	(6.7)	(2.1)	(1.2)	(1.6)	(21.1)
CUF2	2.1	11.0	55.6	19.5	8.8	7.8	9.6	114.5
	(1.1)	(3.8)	(10.4)	(3.7)	(2.4)	(1.0)	(1.7)	(24.1)
CRIL1	3.1	29.4	37.8	25.6	19.5	13.6	16.9	145.8
	(1.6)	(10.4)	(8.2)	(5.2)	(11.8)	(2.5)	(3.3)	(43.0)
CRIL2	16.1	23.7	56.9	14.3	5.6	9.4	10.2	136.2
	(5.0)	(4.0)	(7.0)	(5.5)	(1.5)	(1.6)	(1.4)	(26.1)
CCL1	15.5	53.9	87.7	15.5	2.1	14.4	15.6	204.8
	(4.8)	(14.8)	(18.9)	(7.2)	(0.6)	(2.3)	(2.1)	(50.7)
CCL2	44.1	28.6	57.1	18.2	1.6	10.3	11.1	171.0
	(6.7)	(8.9)	(15.5)	(5.0)	(0.3)	(1.6)	(0.9)	(38.9)
TUF1	2.5	8.5	30.3	29.9	23.3	4.3	6.6	105.5
	(2.2)	(6.0)	(6.9)	(2.6)	(5.7)	(0.7)	(2.1)	(26.2)
TUF2	4.4	5.8	26.4	36.2	21.5	6.5	11.3	112.0
	(2.4)	(1.2)	(0.9)	(6.9)	(6.3)	(1.0)	(1.9)	(20.5)
TRIL6	4.3	17.5	47.7	27.5	40.6	18.6	22.1	178.2
	(2.7)	(6.8)	(9.2)	(6.6)	(12.2)	(0.5)	(3.4)	(41.6)
TRIL9	5.6	15.5	28.2	25.2	22.4	10.6	22.5	130.1
	(2.9)	(6.0)	(11.8)	(2.9)	(1.6)	(0.2)	(4.0)	(29.6)

The errors for five decays classes of large material (> 10 cm dia.) and small (2–5 cm) and medium (5–10 cm) material are standard errors of the mean. The error for the total is a simple sum of the individual errors. Site codes are defined in Table 1.

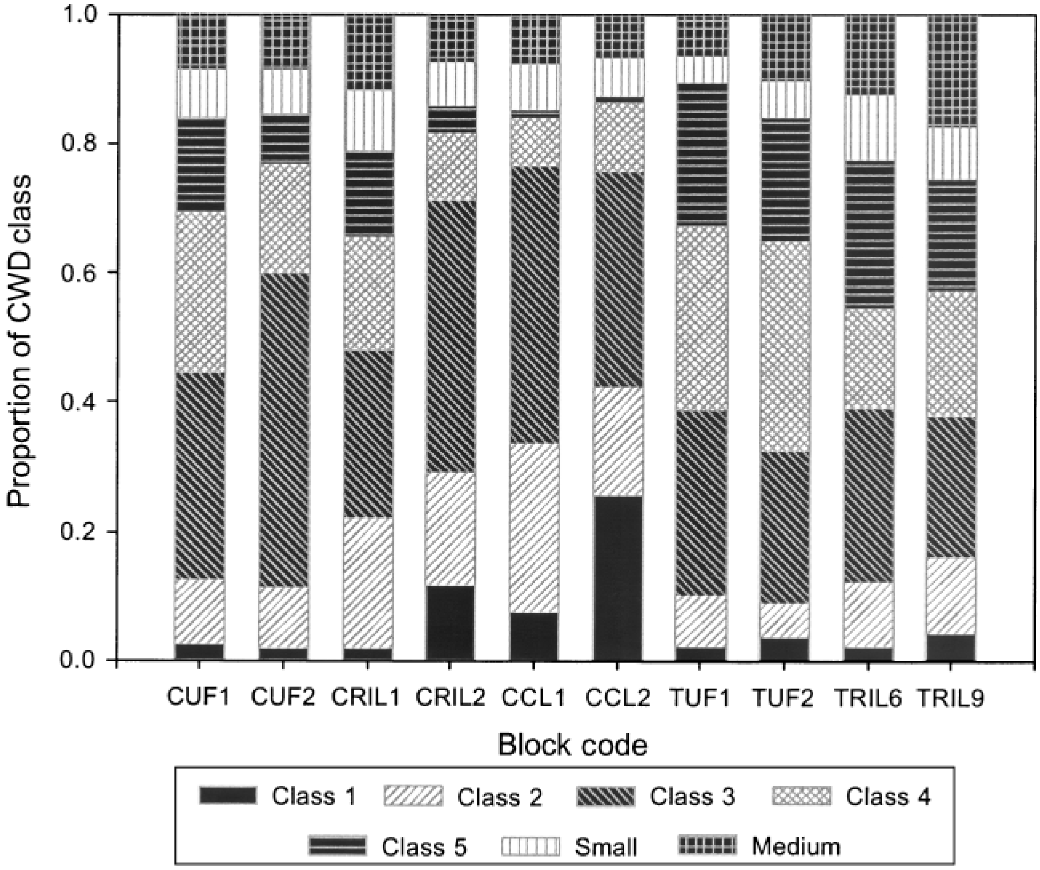

Fig. 2 A stacked bar graph showing the proportions of CWD mass by decay class for diameter > 10 cm and for small and medium material. Class 1 material was newly fallen solid wood with some leaves and/or fine twigs still attached. Material in class 2 was still solid and had intact bark but no fine twigs or leaves. Class 3 material resembled class 2 except that bark for this class was rotten or sloughing. Class 4 material is somewhat rotten and could be broken when kicked. Class 5 material was rotten and friable and it could be broken apart with bare hands. Small and medium material had diameters from 2–5 cm and 5–10 cm respectively. Small and medium material was not further classified for decay status. Site codes are defined in Table 1.

although there was a significant difference between the UF and RIL treatments ($P<0.05$). There was no site × treatment interaction. Comparing three treatments (UF, RIL, CL) at Cauaxi, we found that the CWD volume among logging treatments was significantly different (ANOVA, $P<0.05$). Large debris (> 10 cm dia.) represents 72–92% of the total CWD volume (Fig. 2). Class 3 (partly decayed) material, was the modal volume class for all sampled sites accounting for 22–49% of CWD volume, with the exception of one UF block at Tapajós (TUF2) where class 4 material represented 32% of CWD volume. As expected, relatively fresh material (classes 1 and 2) represented a greater proportion of the CWD volume in recently logged sites, with up to 43% in one conventionally logged site (CCL2).

Density of large CWD (> 10 cm dia.) corrected for void space differed significantly among decay classes (ANOVA, $P<0.001$) (Table 3). Density tended to decrease with the increasing level of decay for classes 1–5. Curiously, decay class 1, the freshest material was on average less dense than the slightly more decayed material in class 2.

The amount of void space also varies significantly among the decay classes (ANOVA, $P<0.001$). Void space was minimal for classes 1 and 2. Void space increases progressively with the level of decay for classes 1–4. Material in class 5 was generally highly fragmented. In class 5, 39 of 60 pieces collected had no macroscopic void space. Evidently, these pieces of CWD were fragments of larger pieces that had decayed. For those pieces of CWD in class 5 where the original form of the log could be identified, the proportion of void space was 0.27 (± 0.04) consistent with the trend of increasing void space with increasing decay class.

Small (2–5 cm dia.) and medium (5–10 cm dia.) materials were not classified according to decay conditions. On average this material had mean densities

Table 3 Mean (S. E.) wood plug densities, void proportions, and corrected densities for 5 decay classes of CWD (dia. >10 cm) and medium (5–10 cm) and small (2–5 cm) debris

Debris class	Plug density (Mg m^{-3})	Void proportion	Corrected density (Mg m^{-3})	Number of pieces sampled
1	0.61 (0.02)	0.02 (0.01)	0.60 (0.02)	88
2	0.71 (0.03)	0.02 (0.01)	0.70 (0.03)	35
3	0.63 (0.02)	0.08 (0.02)	0.58 (0.03)	48
4	0.58 (0.03)	0.21 (0.03)	0.45 (0.03)	52
5	0.32 (0.03)	0.09 (0.02)	0.28 (0.03)	60
Medium(5–10 cm)			0.45 (0.02)	86
Small (2–5 cm)			0.36 (0.01)	103

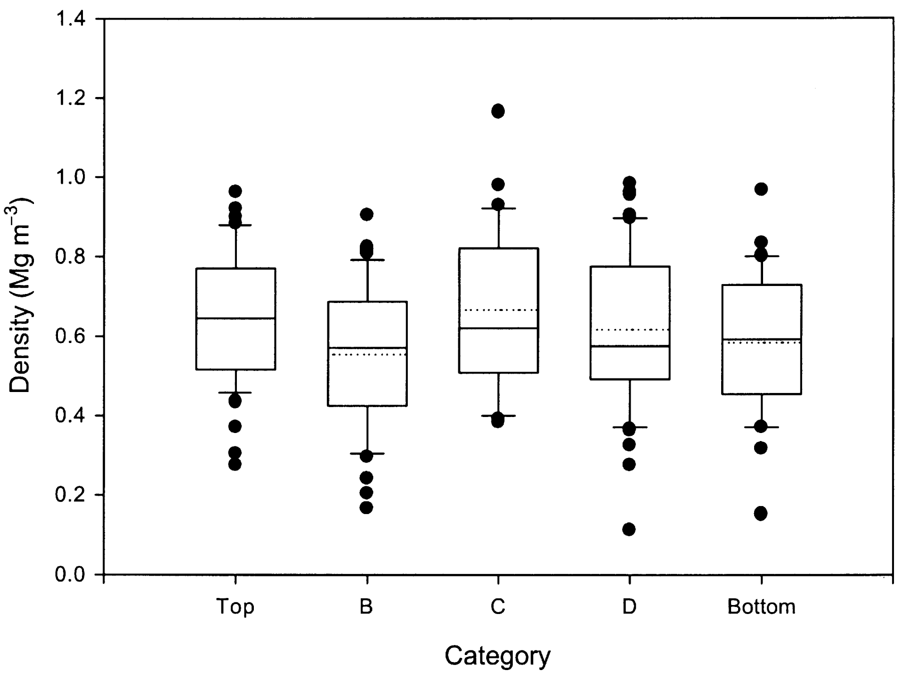

Fig. 3 Box-and-whisker plot of wood plug density vs. direction sampled. Box labels represent 5 categories of directions (top, bottom, B (45° + 315°), C (90° + 270°) and D (135° + 225°)) as illustrated in Fig. 1a. Boxes mark the upper and lower quartiles of the data. Whiskers indicate the 10th and 90th percentiles. Outliers are indicated by bold points. A thick line represents the median and a dotted line the mean. A total of 215 CWD pieces sampled for the radial direction were analyzed.

(0.36–0.45 Mg m^{-3}) between those of classes 4 and 5. Field observations suggested that much of the material in the small and medium size classes was from vines, particularly in the logged plots. We did not quantify the origin of vine- vs. tree-derived debris.

We checked for potential biases related to our density sampling approach. First, as noted above, we found no significant correlation between the corrected density and the size of the debris pieces sampled for large CWD (>10 cm dia.). We examined whether the wood density of plugs varied with the position of the randomly selected radius in fallen logs. For this analysis we grouped the eight randomly selected radii according to the symmetry through a plane perpendicular to the ground from the top (0°) to the bottom position (180°) of the log. The eight radii collapse into five categories: top; bottom; B (45°+315°); C (90°+270°); and D (135°+225°) as illustrated in Fig. 1a. Radial position had a significant effect (ANOVA, $P<0.05$) (Fig. 3). We also examined the possibility that wood density for extracted plugs varied by distance from the center of the logs. When wood density for individual plugs was normalized to the average for each radial section, we found an inverse correlation ($r^2 = 0.55$) between plug density and the distance from the center of the fallen log (Fig. 4).

The mass of CWD in individual blocks varied from 51 to 118 Mg ha^{-1} (Table 4). A comparison of CWD mass in RIL logging and UF treatments at both Cauaxi and

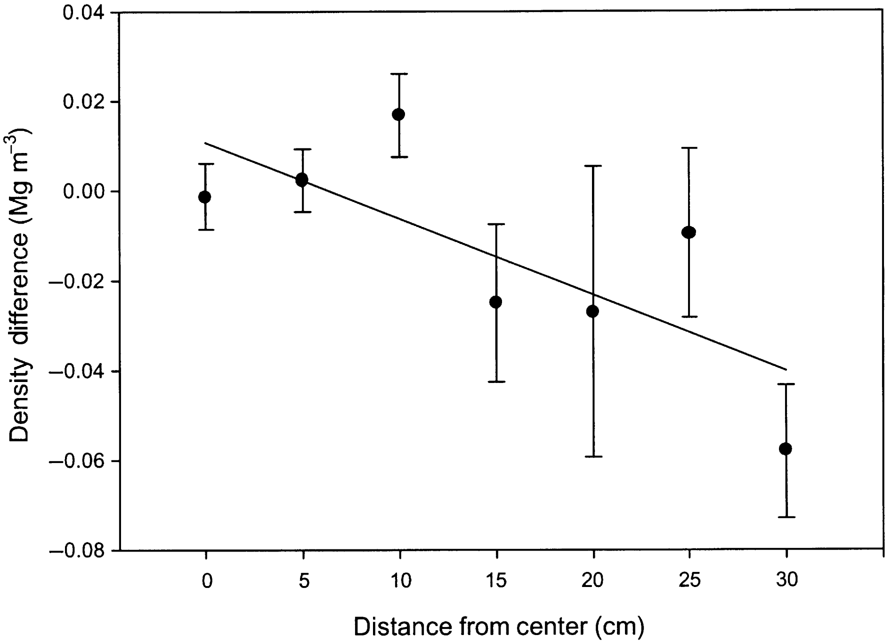

Fig. 4 Averages (± standard error) of the differences in density for plugs at distance from the center of a piece of CWD compared with the average plug density for the same piece of CWD. The linear regression is $y = 0.0109–0.00170x$ ($r^2 = 0.556$). Only CWD pieces with at least two samples per piece ($n = 192$) were used for this analysis. The analysis was truncated beyond a distance of 30 cm because of the paucity of samples.

Table 4 Mean (± propagated error) fallen CWD mass for 10 sampled blocks of undisturbed forest, reduced impact, and conventional logging at Cauaxi and Tapajós for five decays classes of large debris (>10 cm dia.) and small (2–5 cm) and medium (5–10 cm) debris

Code	Class 1 (Mg ha^{-1})	Class 2 (Mg ha^{-1})	Class 3 (Mg ha^{-1})	Class 4 (Mg ha^{-1})	Class 5 (Mg ha^{-1})	Small (Mg ha^{-1})	Medium (Mg ha^{-1})	Total (Mg ha^{-1})
CUF1	1.6	7.3	19.1	11.6	4.2	2.8	3.9	50.5
	(0.9)	(3.0)	(3.4)	(3.7)	(1.0)	(0.5)	(0.9)	(13.4)
CUF2	1.3	7.7	32.5	8.8	2.5	2.8	4.4	59.9
	(0.7)	(3.0)	(7.6)	(2.1)	(0.9)	(0.5)	(1.0)	(15.8)
CRIL1	1.8	20.6	22.1	11.5	5.5	4.9	7.7	74.0
	(1.0)	(8.1)	(5.8)	(3.0)	(3.9)	(1.1)	(1.9)	(24.8)
CRIL2	9.7	16.6	33.2	6.4	1.6	3.4	4.6	75.5
	(3.3)	(3.5)	(5.6)	(2.9)	(0.6)	(0.7)	(0.9)	(17.4)
CCL1	9.3	37.8	51.2	7.0	0.6	5.2	7.1	118.2
	(3.2)	(11.9)	(13.4)	(3.6)	(0.2)	(1.0)	(1.3)	(34.7)
CCL2	26.5	20.1	33.4	8.2	0.4	3.7	5.0	97.3
	(4.7)	(7.1)	(10.6)	(2.7)	(0.1)	(0.7)	(0.7)	(26.6)
TUF1	1.5	6.0	17.7	13.4	6.5	1.6	3.0	49.7
	(1.4)	(4.5)	(4.9)	(1.9)	(2.2)	(0.3)	(1.1)	(16.3)
TUF2	2.6	4.1	15.4	16.2	6.0	2.3	5.1	51.8
	(1.5)	(1.0)	(1.2)	(4.0)	(2.4)	(0.4)	(1.1)	(11.7)
TRIL6	2.6	12.3	27.8	12.3	11.4	6.7	10.1	83.1
	(1.7)	(5.3)	(6.7)	(3.7)	(4.6)	(0.5)	(2.1)	(24.4)
TRIL9	3.4	10.9	16.5	11.3	6.3	3.8	10.2	62.4
	(1.9)	(4.7)	(7.7)	(2.0)	(1.1)	(0.2)	(2.3)	(19.8)

Site codes are defined in Table 1.

Table 5 Average density of fallen CWD and average mass (SE) of CWD for five site × treatment combinations

	Cauaxi UF	Cauaxi RIL	Cauaxi CL	Tapajos UF	Tapajos RIL
Average density ($Mg\,m^{-3}$)	0.51	0.53	0.57	0.47	0.47
Average mass ($Mg\,ha^{-1}$)	55.2	74.8	107.8	50.8	72.8
Standard error ($Mg\,ha^{-1}$)	4.7	0.7	10.5	1.1	10.4

Standard errors are calculated from $n = 2$ blocks per site.

Tapajós, showed a significant effect of treatment (ANOVA, $P < 0.05$) with no significant effect of site and no site × treatment interaction. At Cauaxi, fallen CWD mass varied significantly among treatments (ANOVA, $P < 0.05$).

Average density of CWD calculated for the various sites and logging treatments, gives an integrated view of the CWD composition (Table 5). At Cauaxi, the average density of CWD tended to follow the degree of disturbance; average density for CL ($0.57\,Mg\,m^{-3}$) exceeded that for RIL ($0.53\,Mg\,m^{-3}$), which in turn exceeded the average density in the UF ($0.51\,Mg\,m^{-3}$). Density did not vary between UF and RIL sites at Tapajós. Tapajós RIL sites had a relatively high proportion of CWD volume in small and medium classes compared with other sites. These relatively low-density classes offset the increase in fresh material compared with UF.

Discussion

Comparison of mature forest sites

The mass of fallen CWD (>10 cm dia.) for the Tapajós and Cauaxi sites is surprisingly similar (46 and $50\,Mg\,ha^{-1}$, respectively). This assumes that the Tapajós and Cauaxi forests have similar CWD densities because we only measured density at Tapajós. We believe this is a reasonable assumption given that there is a strong overlap in the species composition at these sites. Our values for fallen CWD mass (>10 cm) are greater than those found for most forest sites measured in the Amazon region. Brown *et al*. (1995) found $30\,Mg\,ha^{-1}$ for a forest in Rondonia. Gerwing (2002) reported $33\,Mg\,ha^{-1}$ for forest sites near Paragominas. Chambers *et al*. (2000) estimated $21\,Mg\,ha^{-1}$ of fallen CWD (>10 cm) and $30\,Mg\,ha^{-1}$ of 'coarse litter' (Chambers *et al*., 2001a) for forest near Manaus. In contrast, Rice *et al*. (in press) measured fallen CWD of $70\,Mg\,ha^{-1}$at a site only 20 km away from ours at Tapajós.

The fallen CWD (dia. >10 cm) at the Tapajós site contained about 16% as much mass as the aboveground live biomass (Keller *et al*., 2001), while Rice *et al*. (in press) found 24% at a Tapajós site 20 km distant. These proportions are large compared with the results by Chambers *et al*. (2000, 2001a) near Manaus, Gerwing (2002) near Paragominas, and Brown *et al*. (1995) (6–9%, 11%, and 11%, respectively).

We do not believe that the difference among sites was an artifact of the methods used. Brown *et al*. (1995), Chambers *et al*. (2000), and Rice *et al*. (in press) used plot-based methods, while Gerwing (2002) and our study use line-intercept sampling. However, Rice *et al*. (in press) compared their plot-based method with line-intercept measurements using the approach described above and found no difference within the errors of the respective methods. Despite the comparable methods, Rice *et al*., found a much greater mass of CWD. Apparently, forest dynamics and mortality can vary significantly on a spatial scale of kilometers and it is likely, as Rice *et al*. (in press) contend, that their site has recently suffered a considerable pulse of mortality. Rice *et al*. (in press) have speculated that the severe El Niño related droughts of 1997 and 1998 may have provoked the pulse in mortality.

Is CWD at steady state in these mature forests?

Given the large quantity of CWD found at the Tapajós forest in our study, is it reasonable to assume that UFs at our study sites are close to steady state? We consider a simple compartment model for the forest,

$$dB/dt = G - \mu B \quad (4)$$

and

$$dN/dt = \mu B - kN \quad (5)$$

Biomass (B) and necromass (N) change according a fixed growth rate (G) and first-order mortality (μ) and decay of necromass (k). For our purposes, we consider B to be only woody aboveground biomass and N to be CWD. Therefore G is the growth rate of aboveground wood. At steady state, $\mu B = kN$. For Tapajós ($B = 282\,Mg\,ha^{-1}$, $N = 51\,Mg\,ha^{-1}$), if we assume a range of decay rates (k) estimated by Chambers *et al*. (2000, 2001b) of 0.13–0.17 per year, then at steady state the instantaneous mortality rate (μ) (*sensu* Sheil *et al*., 1995) ranges from 0.024 to 0.031 per year. If we increase the CWD pool (N) by 20% to account for standing dead (Rice *et al*., in press), then the instantaneous mortality rates would rise to 0.028–0.037 per year. These rates are at the high end of the range of mortalities compiled by Phillips *et al*. (1994), but consistent with the mortality coefficient derived from measurements in permanent plots in the Tapajós National Forest (0.032 per year) (Alder & Silva, 2000; Keller *et al*., in press). A steady-state interpretation cannot be ruled out by our measurements.

The CWD flux resulting from mortality includes not only tree death but also branch fall. Branch fall has received limited attention in tropical forest studies (Clark *et al*., 2001). Chambers *et al*. (2001c) estimated that branch fall accounted for $0.9\,\mathrm{Mg\,ha^{-1}\,y^{-1}}$ for tropical moist forest outside Manaus. Other biomass components, such as vines and small trees, not normally included in long-term mortality studies may also contribute a significant flux of CWD. Given these other sources of mortality, when considering the CWD pool, the high mortality rates calculated above appear to be reasonable.

Effects of logging on CWD stocks

We studied logged sites where $25–30\,\mathrm{m^3\,ha^{-1}}$ of timber had been harvested. This level of harvest falls between intermediate and high intensity for current logging in the Brazilian Amazon (Nepstad *et al*., 1999). Fallen CWD increased by 35–43% above background levels in RIL treatments and by 95% in CL treatments. This finding is consistent with the 106% increase in fallen CWD observed by Gerwing (2002) for 'moderately logged' sites near Paragominas. Those sites had $28–48\,\mathrm{m^3\,ha^{-1}}$ of timber removed 4–6 years prior to sampling. If we subtract a background level of $55\,\mathrm{Mg\,ha^{-1}}$ fallen CWD for Cauaxi, then the CL treatment produced 2.7 times as much CWD as RIL for the same volume of timber harvested. In paired high intensity (54 to $175\,\mathrm{m^3\ ha^{-1}}$) RIL and CL logging operations in Sabah, Malaysia, Pinard & Putz (1996) found that CL operations produced 77% more necromass than did RIL (including roots, and wood waste at the mill).

The production of CWD following logging will strongly influence the carbon balance of logged sites. The carbon content of CWD created for RIL blocks is about equal to the carbon in timber extracted while in CL blocks, about 2.5 times as much carbon goes to CWD as goes to the sawmill. Assuming the instantaneous decay constant estimated by Chambers *et al*. (2000) of 0.17 per year, we would expect CWD at the RIL and CL sites at Cauaxi to emit about $1.5–4.5\,\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$ in the year after they were sampled. This represents a substantial portion of the gross primary production ($26\,\mathrm{Mg\,C\,ha^{-1}\,y^{-1}}$) for UF at the Tapajós site (Goulden *et al*., in press).

In recently logged sites, we would expect some increase of net primary productivity (NPP) resulting from opening of the canopy and liberation of the suppressed understory species (Silva *et al*., 1995). The balance between added respiration from CWD following logging and possible increases of NPP from liberation has not been measured. Recent model results based on the Tapajós Forest site that we studied, suggest that over 200 years of logging at $30\,\mathrm{m^3\,ha^{-1}}$ with 30 years cutting cycles, about $29\,\mathrm{Mg\,C\,ha^{-1}}$ would be lost from CL managed sites and $16\,\mathrm{Mg\,C\,ha^{-1}}$ would be lost from RIL managed forest (Keller *et al*., in press). However, results from the CAFOGROM stand projection model (Alder & Silva, 2002; Keller *et al*., in press) suggest that CL logging would not be commercially sustainable over 200 years.

Analysis of errors

In order to estimate the mass of CWD we had to measure both volume and density of the fallen material. The volume estimates were made using line-intercept sampling, a standard method that is considered highly efficient (De Vries, 1986). Even in logged forest, a practiced three-person team could measure fallen CWD on 3000 m of transect per day. Errors in sampling CWD volume arise primarily from the highly uneven spatial distribution of the CWD. Our within-block errors (6–21% expressed as standard error of the mean) for all fallen CWD volume were similar to within treatment errors at a given site (3–16%) (Table 1). Proportionally, within site errors in volume estimates were similar for both logged and UF sites and the greatest variation was found between logging sites. This variation probably resulted from differences in harvest management.

We counted several thousand ($n = 9527$) individual pieces of CWD. It was impractical to determine density for this large sample. Therefore, we randomly subsampled fallen CWD to measure density. We found that the proportional errors in density ranged from 3% to 10% of the mean density and the most highly decayed material (class 5) had the greatest proportional variation in density (Table 3).

When estimating mass, we applied a specific density estimate to each material class. In order to estimate the overall error in mass, we conservatively summed the errors for individual classes. Using data from all 10 blocks, error in volume accounted for 69% of the error in mass determination and the error in density accounted for the remaining 31%. Many other recent estimates of CWD mass in tropical forests only accounted for the errors in volume measurement (e.g. Gerwing, 2002; Grove, 2001). Therefore, they substantially underestimated the uncertainty in their measurements.

Our results suggest that the wood in outer portions of fallen logs has a lower density than wood at the core of fallen logs (Fig. 4). We did not attempt to correct the volume-weighted density for this effect because of the complications that the apparently anisotropic distribution of void space would impose on such a correction.

The average volume-weighted density of CWD for UF at the Tapajós site (0.47 Mg m^{-3}) was high compared with values measured in other tropical forests. For example, in a wet forest in Costa Rica, Clark et al. (2002) found that mean density was 0.45 Mg m^{-3} for 'sound' debris, 0.35 Mg m^{-3} for 'partially decomposed' debris, and 0.25 Mg m^{-3} for 'fully decomposed' debris. In the Daintree lowland rain forest in Australia, Grove (2001) found a volume weighted density of 0.26 Mg m^{-3}.

Gerwing (2002) applied densities of 0.7 Mg m^{-3} to 'sound' fallen CWD with the exception of debris from *Cecropia* sp. where a density of 0.3 Mg m^{-3} was applied. This value is taken from the average density of fresh wood from Amazonian trees as compiled by Fearnside (1997). For the 'intermediate' and 'rotten' categories, Gerwing (2002) used factors of 0.88 and 0.60 multiplied by the value for 'sound' debris giving densities of 0.62 and 0.42 Mg m^{-3} for non-*Cecropia* species. These estimated densities appear quite high compared with our measured values. Therefore, we suspect that Gerwing (2002) overestimated CWD mass.

We sampled CWD approximately 1 year following logging at CL and RIL sites. Presumably, most CWD is generated immediately following logging. However, tree mortality may remain elevated compared with background levels for several years following logging. The time history of flux of CWD falling to the ground following logging has not been quantified in a tropical forest site.

Conclusion

The old growth forest sites at Cauaxi and Tapajós contained an average (SE) of 53.0 (2.3) Mg ha^{-1} fallen CWD. At Tapajós, this CWD pool is 18% as large as the aboveground biomass. Taking into account the best current estimates for decomposition of CWD in the Amazon, this large pool size implies that either our site at Tapajós was subject to a recent disturbance or that it normally has a high instantaneous mortality rate in the range of 0.03 per year. Mortality in this case would include branch fall, a flux that is rarely measured.

Volume weighted density of all fallen CWD at the Tapajós site (0.47 Mg m^{-3}) is greater than the density of fallen CWD measured at other tropical forest sites. It is plausible that this greater density results from a predominance of more recently fallen material at Tapajós. However, the densities for individual decomposition classes appear to be greater at Tapajós than at other sites. Density of CWD has been measured infrequently in tropical forests. Error in the density measurements in our study accounted for about 18% of the overall estimated error in CWD mass in a study block. In most studies, this density error is not quantified and therefore the error in CWD stock is underestimated.

Density of woody material within the large fallen logs varied significantly both with regard to position relative to the ground and with distance from the center of the log. Void space within fallen logs ranged from about 2% for fresh material (classes 1 and 2) to 27% for relatively intact logs in the most rotten material (class 5). An unbiased density sampling method must account for the anisotropy in wood density and the haphazard distribution of void space.

Logging significantly increases the fallen CWD pools. Fallen CWD mass at our two sites sampled 1 year following logging averaged 75 and 108 Mg ha^{-1} for RIL and CL management, respectively. Accounting for background CWD in UF, CL management produced 2.7 times as much CWD as RIL management. Decay of CWD in the logged sites we studied would emit about 1.5–4.5 Mg C ha^{-1} y^{-1} about 1 year following logging.

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References

Alder D, Silva JNM (2000) An empirical cohort model for management of Terra Firme forests in the Brazilian Amazon. *Forest Ecology and Management*, **130**, 141–157.

Alder D, Silva JNM (2002) Sustentabilidade da produção volumétrica: Um estudo de caso na Floresta Nacional do Tapajós com o auxílio do modelo de crescimento

CAFOGROM. In: *Silvicultura na Amazônia Oriental: Resultados do Projeto EMBRAPA/DFID* (eds Silva JNM, de Carvalho JOP & Yared J). EMBRAPA Amâzonia Oriental, Belém, Brasil.

Brown IF, Martinelli LA, Thomas WW *et al*. (1995) Uncertainty in the biomass of Amazonian forests: an example from Rondonia, Brazil. *Forest Ecology and Management*, **75**, 175–189.

Brown JK (1974) *Handbook for Inventorying Downed Woody Material*. USDA Forest Service, Ogden, Utah.

Chambers JQ, Higuchi N, Schimel JP *et al*. (2000) Decomposition and carbon cycling of dead trees in tropical forests of the central Amazon. *Oecologia*, **122**, 380–388.

Chambers JQ, Higuchi N, Tribuzy ES *et al*. (2001a) Carbon sink for a century. *Nature*, **410**, 429.

Chambers JQ, Schimel JP, Nobre AD (2001b) Respiration from coarse wood litter in central Amazon forests. *Biogeochemistry*, **52**, 115–131.

Chambers JQ, Santos J, Ribeiro RJ, Higuchi N (2001c) Tree damage, allometirc relationships, and above-ground net primary production in a dense tropical forest. *Forest Ecology and Management*, **152**, 73–84.

Clark DA, Brown S, Kicklighter DW *et al*. (2001) NPP in tropical forests: an evaluation and synthesis of the existing field data. *Ecological Applications*, **11**, 371–384.

Clark DB, Clark DA, Brown S *et al*. (2002) Stocks and flows of coarse woody debris across a tropical rain forest nutrient and topography gradient. *Forest Ecology and Management*, **164**, 237–248.

Costa MH, Foley JA (1998) A comparison of precipitation datasets for the Amazon basin. *Geophysical Research Letters*, **25**, 155–158.

De Vries PG (1986) *Sampling Theory for Forest Inventory. A Teach-Yourself Course*. Berlin, Springer-Verlag.

Fearnside PM (1997) Wood density for estimating forest biomass in Brazilian Amazonia. *Forest Ecology and Management*, **90**, 59–87.

Fernandes ECM, Biot Y, Castilla C *et al*. (1997) The impact of selective logging and forest conversion for subsistence agriculture and pastures on terrestrial nutrient dynamics in the Amazon. *Ciencia e Cultura Journal of the Brazilian Association for the Advancement of Science*, **49**, 34–47.

Gerwing JJ (2002) Degradation of forests through logging and fire in the eastern Brazilian Amazon. *Forest Ecology and Management*, **157**, 131–141.

Goulden ML, Miller SD, Menton MC *et al*. (in press) Physiological controls on tropical forest CO_2 exchange. *Ecological Applications*.

Grove SJ (2001) Extent and composition of dead wood in Australian lowland tropical rainforest with different management histories. *Forest Ecology and Management*, **154**, 35–53.

Harmon ME, Whigham DF, Sexton J (1995) Decomposition and mass of woody detritus in the dry tropical forest of the Northeastern Yucatan Peninsula, Mexico. *Biotropica*, **27**, 305–316.

Holmes TP, Blate GM, Zweede JC *et al*. (2002) Financial and ecological indicators of reduced impact logging performance in the eastern Amazon. *Forest Ecology and Management*, **163**, 93–110.

Johns JS, Barreto P, Uhl C (1996) Logging damage during planned and unplanned logging operations in the eastern Amazon. *Forest Ecology and Management*, **89**, 59–77.

Keller M, Palace MW, Hurtt G (2001) Biomass estimation in the Tapajós National Forest, Brazil. Estimation of sampling and allometric uncertainties. *Forest Ecology Management*, **154**, 371–382.

Keller M, Silva JMN, Asner GP *et al*. (in press) Sustainability of selective logging of upland forests in the Brazilian Amazon: carbon budgets and remote sensing as tools for evaluation of logging effects. In: *Working Forests in the American Tropics: Conservation Through Sustainable Management?* (eds Zarin DJ, Alavalapati J, Putz FE, Schmink M), Colombia University Press, New York.

MacNally R, Parkinson A, Horrocks G *et al*. (2001) Relationships between terrestrial vertebrate diversity, abundance and availability of coarse woody debris on south-eastern Australian floodplains. *Biological Conservation*, **99**, 191–205.

Nepstad DC, Verissimo A, Alencar A *et al*. (1999) Large-scale impoverishment of Amazonian forests by logging and fire. *Nature*, **398**, 505–508.

Nordén B, Paltto H (2001) Wood-decay fungi in hazel wood: species richness correlated to stand age and dead wood features. *Biological Conservation*, **101**, 1–8.

Pereira R, Zweede JC, Asner GP *et al*. (2002) Forest canopy damage and recovery in reduced impact and conventional logging in eastern Para, Brazil. *Forest Ecology and Management*, **168**, 77–89.

Phillips OL, Gentry AH (1994) Increasing turnover through time in tropical forests. *Science*, **263**, 954–958.

Pinard MA, Putz FE (1996) Retaining forest biomass by reducing logging damage. *Biotropica*, **28**, 278–295.

Rice AH, Pyle EH, Saleska SR *et al*. (in press) Carbon balance and vegetation dynamics in an old-growth Amazonian forest. *Ecological Applications*.

Ringvall A, Stahl G (1999) Field aspects of line intersect sampling for assessing coarse woody debris. *Forest Ecology and Management*, **119**, 163–170.

Sheil D (1995) Evaluating turnover in tropical forests. *Science*, **268**, 894–895.

Silva JNM, Carvalho JPO, de Lopes JCA *et al*. (1995) Growth and yield of a tropical rainforest 13 years after logging. *Forest Ecology and Management*, **71**, 267–274.

Silver WL, Neff J, McGroddy M *et al*. (2000) Effects of soil texture on belowground carbon and nutrient storage in a lowland Amazonian forest ecosystem. *Ecosystems*, **3**, 193–209.

Uhl C, Barreto P, Verissimo A *et al*. (1997) Natural resource management in the Brazilian Amazon. *Bioscience*, **47**, 160–168.

Verissimo A, Barreto P, Mattos M (1992) Logging impacts and prospects for sustainable forest management in an old Amazonian frontier: the case of Paragominas. *Forest Ecology and Management*, **55**, 169–199.