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Necromass in undisturbed and logged forests in the Brazilian Amazon

Michael Palace [a,*], Michael Keller [a,b], Gregory P. Asner [c], Jose Natalino M. Silva [d], Carlos Passos [e]

[a] *Complex Systems Research Center, Morse Hall, University of New Hampshire, Durham, NH 03824, USA*
[b] *International Institute of Tropical Forestry, USDA Forest Service, Rio Piedras, PR 00928-5000, USA*
[c] *Department of Global Ecology, Carnegie Institution, Stanford University, Stanford, CA 94305, USA*
[d] *EMBRAPA Amazônia Oriental, PO Box 48, 66095-100 Belém, Pará, Brazil*
[e] *UFMT, Universidade Federal do Mato Grosso, Av Fernando Correa da Costa sn, Cuiabá MT 78060-900, Brazil*

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Abstract

Necromass is an important stock of carbon in tropical forests. We estimated volume, density, and mass of fallen and standing necromass in undisturbed and selectively logged forests at Juruena, Mato Grosso, Brazil (10.48°S, 58.47°W). We also measured standing dead trees at the Tapajos National Forest, Para, Brazil (3.08°S, 54.94°W) complementing our earlier study there on fallen necromass. We compared forest that was selectively logged using reduced-impact logging methods and undisturbed forest. We estimated necromass density accounting for void volume for necromass greater than 10 cm diameter at Juruena for five decay classes that ranged from freshly fallen (class 1) to highly decayed material (class 5). Average necromass density adjusted for void space (±S.E.) was 0.71 (0.02), 0.69 (0.04), 0.60 (0.04), 0.59 (0.06), and 0.33 (0.05) Mg m^{-3} for classes 1 through 5, respectively. Small (2–5 cm) and medium (5–10 cm) size classes had densities of 0.52 (0.02) and 0.50 (0.04) Mg m^{-3}, respectively. The average dry mass (±S.E.) of fallen necromass at Juruena was 44.9 (0.2) and 67.0 (10.1) Mg ha^{-1} for duplicate undisturbed and reduced impact logging sites, respectively. Small and medium sized material together accounted for 12–21% of the total fallen necromass at Juruena. At Juruena, the average mass of standing dead was 5.3 (1.0) Mg ha^{-1} for undisturbed forest and 8.8 (2.3) Mg ha^{-1} for forest logged with reduced impact methods. At Tapajos, standing dead average mass was 7.7 (2.0) Mg ha^{-1} for undisturbed forest and 12.9 (4.6) Mg ha^{-1} for logged forest. The proportion of standing dead to total fallen necromass was 12–17%. Even with reduced impact harvest management, logged forests had approximately 50% more total necromass than undisturbed forests.

Keywords: Amazon; Coarse woody debris; Necromass; Standing dead; Reduced impact logging; Tropical; Forest; Wood density

1. Introduction

The death and subsequent decomposition of trees is an important component in forest ecosystem carbon cycling (Denslow, 1987; Harmon and Franklin, 1989). Dead trees or portions of dead trees are termed necromass. Necromass in tropical forests is rarely studied although it contributes a large proportion of the total carbon pool in tropical forests (Clark et al., 2002; Chambers et al., 2000; Keller et al., 2004a). Necromass is important in nutrient cycling and it serves as habitat for some organisms (MacNally et al., 2001; Nordén and Paltto, 2001).

Necromass or coarse woody debris (CWD) is often divided into two categories: (1) fallen or downed necromass and (2) standing dead wood (snags) (Harmon et al., 1986). In the Brazilian Amazon, previous estimates of CWD mass in undisturbed upland (*terra firme*) forests have ranged from 42.8 Mg C ha^{-1} (Summers, 1998 as cited by Rice et al., 2004) to 15 Mg C ha^{-1} (Brown et al., 1995). Brown (1997) estimated that necromass accounts for 5–40% of the total carbon in a tropical forests, exclusive of soil carbon. In the Tapajos National Forest near Santarem, Brazil, the ratio of necromass to biomass ranged from 18 to 25% (Keller et al., 2004a; Rice et al., 2004). For tropical forested areas outside of the Brazilian Amazon, researchers have found CWD ranging from 3.8 to 6.0 Mg C ha^{-1} in Jamaica (Tanner, 1980), 22.3 Mg C ha^{-1} in Costa Rica (Clark et al., 2002) and 22.5 Mg C ha^{-1} in Malaysia (Yoda and Kira, 1982). Estimates of standing dead necromass

* Corresponding author.
E-mail address: michael.palace@unh.edu (M. Palace).

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are infrequent in tropical forests. Rice et al. (2004) found standing dead mass to be 8.6 Mg C ha^{-1} or 18% of the total necromass, while Clark et al. (2002) found 3.1 Mg C ha^{-1} or 12% of the total necromass.

The Amazon region contains the largest continuous expanse of tropical forest in the world and is important to carbon cycling on a global scale (Keller et al., 2004b). Selective logging is a widespread practice in the Brazilian Amazon (Asner et al., 2005). Although still uncommon in the Amazon region of Brazil, reduced impact logging (RIL) is a method of selective logging that limits the damage to the forest by use of tree surveys, vine cutting, road planning, articulated wheeled skidders, and planned directional felling (Pereira et al., 2002). Canopy damage in RIL is about half that in conventional logging (Pereira et al., 2002; Asner et al., 2004). At the Fazenda Cauaxi in Para State, Brazil, Keller et al. (2004a) estimated that conventional logging created 2.7 times more fallen necromass than that of RIL.

The mass of fallen CWD may be calculated from the product of measured volumes and estimates of CWD density (Keller et al., 2004a). A difficulty in determining necromass density in tropical forests is the large number of tree species. Past studies in the tropics have estimated CWD density using the average density of living trees or samples of decayed wood to estimate necromass density (Gerwing, 2002; Chambers et al., 2000). Division of necromass into decay classes based on field inspection has been used to improve the quantification of CWD mass in forests (Harmon et al., 1995; Eaton and Lawrence, 2006). Average density stratified by decay class facilitates the calculation of mass from necromass volume (Keller et al., 2004a). Decay classes are easily recorded during measurements of volume and are critical for an accurate estimation of CWD mass because decayed logs have lower density than freshly fallen CWD (Harmon et al., 1995). Void spaces in logs must be accounted for in density measurements either by using large pieces of necromass (e.g., Chambers et al., 2000; Clark et al., 2002) or by separately quantifying void space (Keller et al., 2004a).

We measured fallen CWD volume and density at undisturbed and logged sites in Juruena, Mato Grosso, Brazil and compared these data to measurements from the Tapajos National Forest using identical methods (Keller et al., 2004a). For this study, we measured the standing dead pool at both Juruena and Tapajos. For both sites, we examined the effect that reduced impact logging had on necromass pools. We include detailed error estimates for both densities and masses.

2. Methods

2.1. Sites

We measured density, void space, and volume of fallen and standing necromass at Juruena, Mato Grosso, Brazil (10.48°S, 58.47°W). We also measured standing necromass at Juruena and Tapajos National Forest, Para, Brazil (3.08°S, 54.94°W). Biomass estimates were conducted in undisturbed forests (UF) at Juruena and compared with biomass estimates at Tapajos (Keller et al., 2001). For the study of necromass we examined two forest types: areas that were selectively logged using RIL methods and undisturbed forest. A detailed site description for Tapajos is found in Keller et al. (2004a). A comprehensive description of the Juruena forest is presented in Feldpausch et al. (2005), although logging practices at our study sites were not identical to those described by Feldpausch et al. (2005).

Sample units at both sites were approximately 100 ha blocks with no historical clearing. The forest at Tapajos had suffered limited felling of *Manilkara huberi* for latex extraction about 25 years prior to our study. At Juruena, it is likely that some mahogany (*Swietenia macrophylla*) had been harvested in the last two decades. Logging took place about 1 year prior to our measurements. The amount of timber extracted, at Tapajos was between 20 and 30 $m^3\,ha^{-1}$, while only about 6.4–15.0 $m^3\,ha^{-1}$ were harvested at Juruena (Feldpausch et al., 2005).

Measurements of CWD volume and subsequent mass estimates were compared between the new site, Juruena, and the Tapajos site (Keller et al., 2004a). Density estimates for Tapajos were presented in Keller et al. (2004a) and are included in this paper for comparison with Juruena density estimates. Standing necromass results for Tapajos and Juruena are both presented for the first time in this paper.

2.2. Density and void space estimation

Necromass density was determined using a plug extraction technique for large CWD (>10 cm diameter) in November 2003. This plug extraction method (Keller et al., 2004a) uses a plug and tenon extractor attached to a portable power drill. Plugs were extracted every 5 cm from the center of a disk cut from a log in one of eight directions, 0°, 45°, 90°, 135°, 180°, 225°, 270°, and 315° selected randomly.

Each piece of CWD greater than 10 cm diameter (*large* CWD) was classified into one of five decay classes. These decay classes ranged from newly fallen necromass (class 1) to highly decayed material that could be broken apart by hand (class 5) (Harmon et al., 1995; Keller et al., 2004a). Decay class 1 material included newly fallen solid wood with leaves and/or fine twigs still attached. Necromass in decay class 2 was solid and had intact bark but no fine twigs or leaves. Decay class 3 necromass resembled class 2 except the bark was rotten or sloughing. Decay class 4 material was rotten and could be broken when kicked. Decay class 5 necromass was highly friable and rotten and it could be broken apart with bare hands. For pieces of CWD >2 and <10 cm, we did not assign decay classes. Sampling of these *small* (2–5 cm dia.) and *medium* (5–10 cm dia.) pieces was done either by plug extraction or by cutting with a knife. All necromass pieces were randomly selected along a transect with stratified probabilities to allow us to collect a sufficient sample number based on size, decay class, and treatment (RIL versus UF).

For large fallen CWD, decay class, diameter, and other features such as large voids and the presence of termites or fungi were noted. We sketched each sample cross-section for comparison to digital images (see below). We measured plug lengths and calculated volume for the cylindrical plugs. Plugs were stored in plastic bags and transported to the laboratory where they were dried at 60 °C until reaching constant weight (up to 3 months). Plugs were then weighed and density was determined based on fresh volume and dry mass.

Void space was measured from digital images of each disk sampled for density. For each image we digitized the areas of wood and void. The smallest identified voids had diameters of ~5 mm. The proportion of void space was used to calculate the adjusted density for void space.

2.3. Fallen CWD estimation

Line intercept sampling for fallen CWD volume was conducted at Juruena in November 2003 and in June 2004 (Brown, 1974; De Vries, 1986; Ringvall and Stahl, 1999). Most logged sites were sampled about 6 months following logging operations. CWD was separated into the same three diameter groups used in density estimation. Woody material with diameter <2 cm was disregarded as it is normally included in litterfall studies. A tape was used to measure distance and then left on the ground to create the transect line. All wood pieces, with a diameter greater then 10 cm, intersecting the transect line, were recorded for diameter. Each transect was divided into 50 m segments. For each 50 m segment, a 10 m sub-sample was selected at random and the smaller classes (2–5 and 5–10 cm) were tallied. Large CWD was classified by decay class using identical criteria as those used in density estimates. A median diameter (3.5 cm for small necromass pieces and 7.5 cm for medium necromass pieces) was used to calculate volume for the small and medium size classes. Use of median diameters for these two classes expedited estimates by allowing tallies of the numerous pieces on a line intersect transect using a go-no-go gauge (Brown, 1974).

Volume (V) ($m^3\ ha^{-1}$) of CWD for an individual transect was determined using the following equation:

$$V = \frac{\pi^2 \sum (d_n)^2}{8 \times L} \tag{1}$$

where d_n is the diameter of a piece of necromass at the line intercept and L is the length of the transect used in sampling. For each decay class, we determined the mean fallen CWD volume for each treatment that we sampled, with the contribution of each transect weighted based on its length (De Vries, 1986, p. 256; Keller et al., 2004a). We sampled four forest blocks with three randomly located 1 km transects per block for a total of 12 km of line intercept sampling at Juruena.

2.4. Strip plot sampling (snags)

Measurements of standing dead trees (snags) were conducted in July 2002 and June 2004 at Tapajos and Juruena, respectively. We measured standing dead trees along 10 m wide strip plots that followed the line transects for fallen CWD. We used the same five-group decay classification and the associated densities for each decay class for mass calculations. A laser ranger finder with built-in clinometer was used to measure the heights of snags (Impulse-200LR, Laser Technology Inc., Englewood, Colorado). A tape was used to measure diameter at breast height (dbh, 1.3 m). If the snag was shorter than 1.3 m, the diameter was measured at the highest point. We estimated volume for snags by disk integration of a taper function around the vertical axis of the snag with height and diameter measurements. The taper function was

$$D_h = 1.59 \times \text{dbh} \times (h^{-0.091}) \tag{2}$$

where D_h is the diameter at a specific height based on the dbh (diameter at breast height = 1.3 m) and height (h) of the snag (Chambers et al., 2000). Mass was calculated using the decay class density multiplied by snag-volume. Snags with buttresses were measured above the buttress whenever possible, otherwise we estimated diameter from two perpendicular positions.

The total area of strip plots sampled for standing dead was 11.1 ha for Tapajos and 12 ha for Juruena. At Tapajos, we sampled duplicate blocks of UF and RIL treatments with a transect sampling design similar to the one in Juruena (Keller et al., 2004a). The areas of the strip plots were approximately evenly divided between UF and RIL treatments.

2.5. Biomass plots

We estimated biomass at Juruena in undisturbed forests using the same strip plots used for standing necromass sampling. We sampled areas 5 m on either side of the line intersect transects for all trees greater than 30 cm dbh. Every 50 m along the strip, a 10 m section was chosen randomly for sampling trees greater than 10 cm dbh. Final biomass estimates were adjusted for area sampled. dbh was recorded for all trees sampled. We estimated biomass for each tree using the allometric relation for tropical moist forests developed by Brown (1997)

$$B = \frac{42.69 - 12.80 \times \text{dbh} + 1.242 \times \text{dbh}^2}{1000} \tag{3}$$

where B is the biomass (kg) for a given dbh (cm) for each individual tree measured in the field.

2.6. Mass calculations and estimation of error

Fallen CWD mass and standing dead mass (M_i) were each determined from the product of the volume of material (V_i) and the respective density for the material class (ρ_i)

$$M_i = \rho_i V_i \tag{4}$$

Transect necromass mean estimates were weighted based on the length of each line intercept transect, as done in De Vries (1986). We calculated the standard error using weighted means from each block (Keller et al., 2004a).

2.7. Statistical analysis

Plug density and density adjusted for void space were compared by one-way analysis of variance (ANOVA) across seven classes of material (five decay classes for large material and medium and small size classes). A Wilcoxon/Kruskal–Wallis Rank Sum test was conducted to examine void space at Juruena across the five decay classes. This non-parameteric test was used because many of the necromass pieces had no void space and thus the data was not normally distributed nor could it be easily transformed. Because we performed multiple tests on density data, we conservatively selected the probability of $\alpha = 0.01$ as a threshold for significance for differences in density.

We examined plug density and adjusted density for void space using a two-way analysis of variance (ANOVA) with categories for decay/size class and site (Juruena and Tapajos). Void space was compared between sites for each decay class using a Wilcoxon/Kruskal–Wallis Rank Sum test.

CWD was sampled for density from a disk cut from a log along eight radii (0°, 45°, 90°, 135°, 180°, 225°, 270°, and 315°) and then reduced to five different groups: top (0°), bottom (180°), B (45° + 315°), C (90° + 270°) and D (135° + 225°). We tested the effect of this radial position on a residual plug density with a one-way ANOVA. We defined the residual plug density as the density of a plug minus the average density of all plugs taken from the disk. A one-way ANOVA was also used to test the residual plug density based on the distance from the center of each sampled disk.

We conducted a series of two-way ANOVAs for the variables of volume and mass according to the categories of site (Juruena, Tapajos), treatment (UF, RIL), and site by treatment interaction for the pools that we measured (small, medium and large size classes, total fallen CWD, standing dead, and total necromass). Mass and volume tests all used $\alpha = 0.05$ for indication of significant differences.

Overall density for both fallen and standing necromass for each site-treatment combination was calculated from total mass divided by total volume. Overall density was compared using two-way ANOVAs that examined site, treatment, and site by treatment interaction. We also examined the proportion of decay classes 1–3 mass to total fallen mass, as well as small and medium size class mass to total fallen mass using two-way ANOVAs that examined site, treatment, and site by treatment interaction.

Orthogonal linear regression (JMP IN 5.1) was used to examine the relation between standing dead and fallen CWD for site and treatment. This regression uses an estimate of the ratio of variance of the two variables including analytical and sampling uncertainties (Tan and Iglewicz, 1999). The variance ratio is different for each sampled block. We tested the sensitivity of the orthogonal regression to variance ratio using maximum, mean, and minimum values.

2.8. Simple model of necromass

We used a simple compartment model for the necromass of undisturbed forests at Tapajos and Juruena. This model was parameterized using data from this study and from other research conducted at Tapajos and Juruena. The model uses estimates of biomass and necromass pools, literature estimates for mortality (Rice et al., 2004) and decay (Chambers et al., 2000, 2001b), and the assumption of steady state (Table 4). The basic model is

$$\frac{dM}{dt} = -kM + F \tag{5}$$

where M is the necromass pool (Mg), F is the rate of necromass creation (Mg year^{-1}), and k is the instantaneous decay rate (year^{-1}). By definition at steady state $kM = F$. The residence time (τ) for necromass at steady state is M/F.

3. Results

3.1. Density and void space

For necromass density and void space at Juruena we sampled 273 disks and removed 609 plugs. In addition, 113 small (2–5 cm dia.) and 43 (5–10 cm dia.) medium sized pieces of CWD were sampled for necromass density. Plug densities for large pieces of CWD at Juruena, were significantly different by decay class, with a decreasing density for increasing decay classes (ANOVA, $p < 0.001$) (Table 1). Void space was significantly different across decay classes with decay classes 1 and 2 having little void space and 4 and 5 having the most (Wilcoxon test, $p < 0.001$) (Table 1). We found no relation between the diameter of the larger CWD and density. On average small and medium size classes had densities similar to decay class 4, with densities of 0.52 Mg m^{-3} for the small size class and 0.50 Mg m^{-3} for the medium size class. We found no significant difference among relative densities based on the distance from the log center or among the radial directions.

Comparison within decay classes between the two sites, Juruena and Tapajos, found that decay classes 1 had a significant difference between sites (ANOVA, $p < 0.0407$). The small size class also had a significantly different plug density (not adjusted for void space) between Tapajos and Juruena (ANOVA, $p < 0.0024$). No significant difference was found for void space within each decay class compared between sites. Adjusted density for void space was found to have a significant difference between decay class 1 (ANOVA, $p < 0.0024$) and the small size class between sites (ANOVA, $p < 0.001$).

3.2. Volume and mass

We measured a total of 1093 snags at the two sites, 640 at Tapajos and 453 at Juruena. Standing dead volume estimates by block ranged from 9.3 to 22.4 m^3 ha^{-1} and standing dead mass ranged from 5.3 to 13.9 Mg ha^{-1} for all blocks sampled at Juruena and Tapajos. Comparison of standing dead volume or mass yielded no significant differences for site or treatment although RIL treatments had a slightly greater standing dead mass (Table 2).

At Juruena, we sampled a total of 2650 pieces of necromass for volume estimation using line intercept sampling. Of these,

Table 1
Comparison of density and void space by site and decay class

Site	Decay class	Number sampled	Plug density (Mg m^{-3})		Void proportion (%)		Density adjusted for void (Mg m^{-3})	
Juruena	1	31	0.72	(0.03)*	0.01	(0.00)	0.71	(0.02)*
	2	26	0.70	(0.04)	0.02	(0.01)	0.69	(0.04)
	3	24	0.66	(0.04)	0.08	(0.03)	0.60	(0.04)
	4	18	0.67	(0.07)	0.12	(0.04)	0.59	(0.06)
	5	18	0.44	(0.05)	0.20	(0.04)	0.33	(0.05)
	Small	113	0.52	(0.02)*	NA	NA	0.52	(0.02)*
	Medium	43	0.50	(0.04)	NA	NA	0.50	(0.04)
Tapajos	1	88	0.61	(0.02)*	0.02	(0.01)	0.60	(0.02)*
	2	35	0.71	(0.03)	0.02	(0.01)	0.70	(0.03)
	3	48	0.63	(0.02)	0.08	(0.02)	0.58	(0.03)
	4	52	0.58	(0.03)	0.21	(0.03)	0.45	(0.03)
	5	21	0.46	(0.05)	0.26	(0.04)	0.34	(0.05)
	Small	103	0.36	(0.01)*	NA	NA	0.36	(0.01)*
	Medium	86	0.45	(0.02)	NA	NA	0.45	(0.02)

Tapajos DC 5 differs from Keller et al. (2004a,b) because some pieces of necromass in DC 5 were not included in this analysis. In Keller et al. (2004a,b) we sampled small highly friable pieces of CWD to examine if these differed from whole logs classified as DC 5. We excluded these small DC 5 pieces in this analysis to be consistent with our methods using at Juruena. Numbers in parentheses are standard errors of the mean.

* Indicates significant difference between decay classes or size class between sites (t-test).

49% (n = 1298) were in the large size class and 51% (n = 1352) were in the small and medium size classes. Total fallen CWD volume estimates for Juruena were 90.6 (1.6) m^3 ha^{-1} for UF and 121.1 (19.5) m^{-3} ha^{-1} for RIL treatments. We found no significant difference for total fallen CWD volume for treatment, site or site × treatment interaction. Total fallen CWD mass was 44.9 (0.2) Mg ha^{-1} for UF treatments at Juruena, and 67.0 (10.1) Mg ha^{-1} for RIL. Total fallen CWD mass showed a significant difference by treatment, but no significant difference for site or site × treatment interaction (ANOVA, $p < 0.0384$) (Table 2). Total necromass combining fallen CWD and standing dead for UF treatments was 50.2 (1.2) Mg ha^{-1} at Juruena and 58.4 (0.9) Mg ha^{-1} at Tapajos (Table 2). We estimated total necromass at RIL treatments to be 75.9 (7.8) Mg ha^{-1} for Juruena and 86.5 (14.9) Mg ha^{-1} for Tapajos. Total necromass for all components showed a significant difference for treatment, but not for site or site × treatment interaction (ANOVA, $p < 0.03854$). Fallen CWD and standing dead mass showed a clear proportional relation independent of site and treatment (Fig. 1). The relation between fallen CWD and standing dead across sites and treatments was examined using orthogonal linear regression. Although the relation was not statistically significant, there was a high coefficient of determination ($r^2 = 0.84$, $p < 0.0862$). The orthogonal regression was not sensitive to the variance ratio when we used maximum, mean, and minimum values of variance.

We estimated that aboveground biomass at Juruena was 281 (32) Mg ha^{-1} for undisturbed forest for trees greater then 10 cm dbh, 263 (34) Mg ha^{-1} for trees greater then 15 cm, and 186 (20) Mg ha^{-1} for trees greater then 35 cm dbh. The number of trees greater than 35 cm dbh was 63 (10) ha^{-1}. Basal area for trees greater then 10 cm dbh was 25 (3) m^2 ha^{-1}.

Total standing density of necromass, derived from standing dead mass divided by standing dead volume showed no significant difference between site, treatment, or site × treatment interaction. Total fallen necromass density showed a significant difference for site, treatment, and site × treatment interaction (ANOVA, $p < 0.0036$). Density for all necromass was also found to be significant for site, treatment and site × treatment interaction (ANOVA, $p < 0.0101$). The proportion of small and medium size classes to total fallen necromass was found to be only significantly different for site × treatment interaction (ANOVA, $p < 0.0263$).

Table 2
Comparison between treatments and sites for necromass pool components

Site treatment measurement	Juruena RIL (Mg ha^{-1})		Tapajos RIL (Mg ha^{-1})		Juruena UF (Mg ha^{-1})		Tapajos UF (Mg ha^{-1})		Stats (s, t, t × s)
Standing dead	8.8	(2.3)	12.9	(4.6)	5.3	(1.0)	7.7	(2.0)	
Total fallen	67.0	(10.1)	72.6	(10.4)	44.9	(0.2)	50.7	(1.1)	t
Fallen small	3.6	(1.0)	5.3	(1.4)	3.3	(0.3)	1.9	(0.4)	
Fallen medium	5.0	(1.2)	10.0	(0.1)	3.7	(0.6)	4.0	(1.0)	s, t
Fallen large	58.5	(7.9)	57.4	(9.0)	37.9	(0.6)	44.7	(0.4)	
Total all necromass	75.9	(7.8)	85.5	(14.9)	50.2	(1.2)	58.4	(0.9)	t

All estimates are in Mg ha^{-1}. Numbers in parenthesis are standard errors of the mean. Significant differences found by ANOVA are indicated by s: site; t: treatment; and t × s: treatment site interaction.

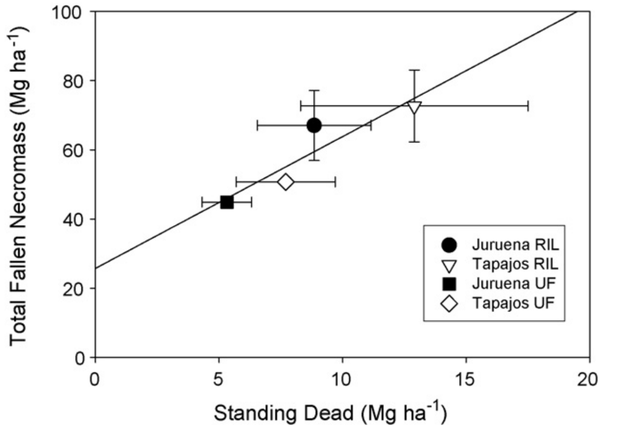

Fig. 1. Fallen vs. standing necromass for sites and treatments. Error bars represent standard errors.

4. Discussion

4.1. Density sampling and void space estimation

We found that plug density, void space, and density adjusted for void space decreased with higher decay classes and were significantly different between decay classes at Juruena. This finding agrees with results at Tapajos (Keller et al., 2004a). In our sampling design, we randomized the radial position for extraction of plugs. Our previous study at Tapajos had shown that radial position had a significant influence on plug density (Keller et al., 2004a). Interestingly, this was not the case in Juruena. We had observed in the field that wood soundness was highly variable within a fallen log. At Tapajos, there was a significant correlation between plug density and distance from the fallen log center (Keller et al., 2004a), whereas we found no difference at Juruena.

The densities of necromass decay classes are quite similar for Juruena and Tapajos. Comparison across sites showed significant differences only for decay class 1. In the case of class 1, initial live tree density may be an important influence. Recent studies have discussed the importance of spatial variation in density to biomass estimates (Baker et al., 2004; Nogueira et al., 2005). We lack data for live biomass average density estimates for Tapajos and Juruena, but comparison with such data might aid in understanding the differences in the density of decay class 1 between our two study sites. All other decay classes show no significant difference between our two sites. Density for the small size class also differed significantly between sites. Because the small size class decays rapidly, the density of small material may vary seasonally.

Seasonal variability in decomposition is likely to be greatest for fine as opposed to coarse material because of its shorter lifetime, lower initial density, and easier decomposer access to interior portions of the wood. Variation in wood moisture content tends to be greater in small diameter size classes, likely influencing the rate of decomposition (Silva, 2005). In the varzea forest in the Brazilian Amazon, the time that the wood falls influences its immediate and longer term decomposition (Martius, 1997). Tapajos samples were collected at the beginning of the dry season. Fine litter decomposition in tropical moist forests is limited by moisture (Goulden et al., 2004). We believe that the small and medium sized material collected at the beginning of the dry season had been exposed to a long period of optimal decay conditions and therefore tended to be less dense at Tapajos than similar material collected at Juruena.

The division of CWD into classes must bring some arbitrary divisions because decay is a continual process. However, as long as densities are matched with the decay classification at a given site, the classification will be useful for mass determination. The densities determined for Juruena are very similar to densities found at Tapajos. It is possible that our density estimates can be used in other areas of the Amazon with similar vegetation types although we caution that the necromass densities found in this study will not be applicable to all forest types in Amazonia. In particular, they would be inappropriate for secondary forests or forests of the western Amazon where the density of live wood is considerably less than in old growth forests of the eastern Amazon (Baker et al., 2004).

4.2. Fallen and standing necromass

In the two undisturbed forests, the proportion of necromass to aboveground biomass (>15 cm dbh) is 26% at Tapajos and 19% at Juruena. This is similar to results from Rice et al. (2004), where necromass account for 25% of the aboveground estimate. We lack biomass measurements for the logged forest, but obviously the proportion of necromass would be higher, since the logging occurred less than 1 year prior to our field work.

Our estimates for fallen CWD created by logging in the Juruena RIL areas were greater than those reported by Feldpausch et al. (2005) for the same field site, although we conducted field work in areas that were logged during different years. Rohden Industria Lignea, the company that owns and manages the site, had been adopting RIL techniques in preparation for FSC certification. Possibly, we encountered more damage because our measurements were made only at the beginning of the company's conversion from conventional to RIL practice prior to the study by Feldpausch et al. (2005). In addition, we note that we measured CWD and snag volume directly for entire logged blocks converting volume to biomass based on our intensive study of CWD densities. Feldpausch et al. (2005) used an indirect method. They measured ground damage (decks, skids, and treefall gaps) by line intercept sampling. CWD creation in treefall gaps was measured only for single tree gaps whereas we observed that multiple treefall gaps were common in the field. Necromass creation in the damaged skid and deck areas was estimated based on average biomass calculated from belt transects. The total biomass loss estimate depended upon multiplication of these two factors. The approach taken by Feldpausch et al. (2005) necessarily compounds errors, and may have led to underestimation of total necromass creation.

For fallen necromass, we found a significant difference between treatments, but no difference between sites and site × treatment interaction. There were no significant differences for standing dead mass or large fallen necromass. The total necromass component was different between treatments, but not for site or site × treatment interaction. Despite the lack of significance for standing dead, it still increases roughly in proportion with fallen necromass for all site-treatment combinations studied. While this may be a chance result, we think the lack of significance is simply an artifact of our sampling intensity. We measured five times as many pieces of fallen necromass as we did snags.

The proportion of necromass in decay classes 1, 2 and 3 is higher in RIL treatments than the undisturbed treatments, though not significantly different (Table 3). Immediately following logging, less decayed wood was present on the forest floor. The density of total fallen necromass and all necromass components were both significantly different for site, treatment, and site × treatment interaction. This indicates that fallen necromass decay classes are different between sites and treatments, and are likely to indicate different disturbance histories and possible difference in future decomposition rates.

Reports of the mass of standing dead trees are rare in tropical forests. We found that standing dead made up 12–17% of the total necromass (Table 3). This estimate is similar to that found by Rice et al. (2004) and Clark et al. (2002). We did not measure attached dead wood or dead coarse roots. We are not aware of any measurements of these pools in tropical forests.

Small and medium size classes make up about 12–21% of total fallen necromass (Table 3). The portion of small and medium size classes to total fallen necromass were significantly different for site × treatment interaction and are likely related to the seasonal timing of sampling. Another study in the Amazon region estimated that smaller diameter (<10 cm) fallen necromass (<10 cm) to accounted for 12% of the total fallen necromass (Rice et al., 2004). Our findings are slightly higher than other estimates in the literature and we stress the importance of including smaller necromass size classes in pool estimates.

Much small and medium sized material may not be accounted for if mortality alone is used to estimate necromass creation. Many tree mortality studies only examine trees larger than 10 cm dbh, and thus do not include smaller stems that were an important component of coarse woody debris in our study. Contribution to the necromass pool by fallen branches may be an important component of necromass that is missed using mortality-based estimates. Trees may lose branches through several processes that do not lead to whole tree mortality. For example, shaded lower branches may be shed and physical damage may result from crown interactions or animal activity. Chambers et al. (2001a,b) considered limb-loss in a moist tropical forest outside Manaus. He estimated branch-fall to be 0.9 Mg ha^{-1} year^{-1} based upon a comparison of field measured allometries and an optimized model tree structure based on the hydraulic constraints to tree architecture.

4.3. Simple model of necromass

If we assume that the forest necromass pool is in steady state then we can estimate both the creation and decay of necromass to evaluate its role in the forest carbon budget. The assumption of steady state for the necromass pool is reasonable for old growth forests when a large area is sampled except for the case of infrequent very large disturbances such as blow-downs (Nelson et al., 1994). Gap formation and other local perturbations will be averaged over a large sampling area. We used a dbh cutoff of 15 cm for live biomass to accommodate the data available at our two sites. Disregarding small trees in the live aboveground biomass pool creates a bias that tends to emphasize the role of necromass. Studies at other tropical sites suggest that trees less than 15 cm dbh and lianas contribute about 20% of the aboveground biomass (Keller et al., 2001). We acknowledge this bias and attempt to capture only the general pattern of the necromass cycle for the ecosystems. Greater biomass estimates would result in greater modeled rates of necromass creation and decay at steady state.

We calculated that necromass creation (F) was 8.5 Mg ha^{-1} year^{-1} at Tapajos and 7.9 Mg ha^{-1} year^{-1} at Juruena (Table 4) using mortality rates of 0.03 (Silva et al., 1995; Rice et al., 2004). Although that mortality rate used is at the upper end of the range for old-growth tropical forests (Phillips and Gentry, 1994), it yields results consistent with known decay rates for CWD. Decay rates (k) were estimated to be 0.14 year^{-1} at Tapajos and 0.16 year^{-1} at Juruena, with corresponding residence times (τ) of 6.9 and 6.4 years (Table 4). If one uses an estimate of about 30 Mg C ha^{-1} year^{-1} for total ecosystem respiration (Chambers et al., 2004), our estimates of necromass decay are approximately 15% of the total ecosystem

Table 3
Comparison of site and treatments for average site densities generated from total site volume and total site mass

Site treatment	Juruena RIL		Tapajos RIL		Juruena UF		Tapajos UF		Stats (s, t, t × s)
Total fallen density	0.55	(0.01)	0.47	(0.01)	0.50	(0.01)	0.47	(0.00)	s, t, t × s
Standing dead density	0.61	(0.02)	0.56	(0.03)	0.56	(0.04)	0.57	(0.00)	s, t, t × s
Average density all necromass	0.56	(0.01)	0.48	(0.00)	0.50	(0.01)	0.48	(0.01)	
Proportion of standing dead vs. total fallen necromass	0.14	(0.06)	0.17	(0.04)	0.12	(0.02)	0.15	(0.04)	
Proportion of small and medium size classes vs. total fallen necromass	0.13	(0.01)	0.21	(0.01)	0.16	(0.02)	0.12	(0.03)	t × s
Proportion of DC 1–3 vs. total fallen necromass	0.65	(0.16)	0.78	(0.02)	0.42	(0.03)	0.59	(0.02)	t

Proportions of necromass components are also compared. Numbers in parentheses are standard errors of the mean. Significant differences found by ANOVA are indicated by s: site; t: treatment, and t × s: treatment site interaction.

Table 4
Estimation of pools and fluxes of necromass for an undisturbed forest assuming steady state

Site	Mortality rate of 0.03		Mortality rate of 0.01	
	Tapajos	Juruena	Tapajos	Juruena
Biomass[a]	282[d]	263[c]	282[d]	263[c]
Mortality (%)	0.03[f]	0.03[f]	0.01	0.01
Estimated creation of CWD and snags[b]	**8.46**	**7.89**	**2.82**	**2.63**
Standing dead	7.7[c]	5.3[c]	7.7[c]	5.3[c]
Fallen CWD	50.7[e]	44.9[c]	50.7[e]	44.9[c]
Necromass pool (fallen and snags)[a]	58.4[c]	50.2[c]	58.4[c]	50.2[c]
Estimated decay rate if at steady state	**0.14**	**0.16**	**0.05**	**0.05**
Residence time (year)	**6.90**	**6.36**	**20.71**	**19.09**
Estimate creation if $k = .13$ and steady state[b]	**7.59**[g]	**6.53**[g]	**7.59**[g]	**6.53**[g]
Estimate Creation if $k = .17$ and steady state[b]	**9.93**[h]	**8.53**[h]	**9.93**[h]	**8.53**[h]

Bold numbers are estimated from the steady state model.
[a] All pool estimates in Mg ha^{-1}.
[b] Assuming decay amount equals creation amount.
[c] Field data from this paper (≥15 cm dbh).
[d] Field data from Keller et al. (2001) (≥15 cm dbh).
[e] Field data from Keller et al. (2004a,b).
[f] Field data from Rice et al. (2004).
[g] Field data from Chambers et al. (2000).
[h] Field data from Chambers et al. (2001a,b).

respiration (Chambers et al., 2004). This estimate of necromass respiration is similar to those found in Chambers et al. (2004) and Rice et al. (2004).

Estimates for decay rates from our steady state model using a mortality rate of 0.01 were more common for old-growth forests in the Eastern Amazon, but were not consistent with literature values for CWD decay rates (Table 4). The mortality rate of 0.03 used in our simple model is at the high end of disturbances rates from the Amazon (Phillips and Gentry, 1994), although it is derived from field data from Tapajos (Silva et al., 1995; Rice et al., 2004). A high mortality rate (0.03) partly compensates for the underestimation of biomass caused by exclusion of trees <15 cm dbh, and the exclusion of other potential CWD inputs such as branchfall and partial tree disturbance. Estimates of decay rates using a 0.03 mortality rate are similar to field estimates by Chambers et al. (2000, 2001b) (Table 4).

Ideally field estimates of the necromass creation would divide pools into small, medium and large size classes improving model accuracy and flux estimates. Chambers et al. (2000) showed that diameter influences decay rates. We lacked data for inputs or specific decay rates for individual size classes, therefore, for simplicity, we grouped small, medium and large diameter size classes into one necromass pool.

We can also examine necromass creation using the necromass pool data and decay rate estimates. The estimates of CWD creation and resulting residence time of necromass calculated from literature decay rates, and our necromass pool, are similar to our estimates of the model parameters when biomass and mortality rates are used in the modeling exercise (Table 4). This suggests that our assumptions of steady state, pool estimate, and use of mortality and decay rates are reasonable.

Disturbances that cause tree mortality and create necromass function on different temporal and spatial scales. An understanding of the mortality patterns and age structure of a forest and its variation in time and space can aid in estimation of the creation of necromass. Although rainforest mortality is driven by many factors (includes large scale blowdowns), on the individual tree level mortality is influenced by competition, for nutrients and light (Prance et al., 1985; Martinez-Ramos et al., 1988; Lieberman et al., 1989). Field estimates of necromass creation would provide an understanding of necromass carbon dynamics. Field measurements of necromass decay rates would also help us to constrain carbon fluxes.

Our model does not include a separate standing dead necromass cycle and creation of smaller necromass that may result from branch-fall rather than tree mortality. Standing dead material is likely to have a lower decay rate in moist tropical forest compared to large fallen CWD due to the lack of contact with the soil and periodic shortages of moisture. Contact with the soil allows fungi to transmit nutrients from the soil to the necromass promoting decomposition. Frey et al. (2003) found that fungal mycelia extended from the soil to CWD and translocated nutrients via the mycelia from soil to decaying wood. In addition, necromass on the forest floor is likely to have higher moisture content (Goulden et al., 2004). Decay of smaller litter is rapid compared to larger CWD (Mackensen et al., 2003). Small and medium size classes of necromass probably decay more quickly than larger fallen logs or snags and therefore contribute disproportionately to the carbon dioxide emission from the forest ecosystem. Smaller diameter necromass decay more quickly due to lower initial density, (Nogueira et al., 2005) and easier access of decomposers to the interior wood (Mackensen et al., 2003).

5. Conclusions

We examined necromass density, volume, and mass at two sites in the Brazilian Amazon. Necromass represents about

19–26% of the aboveground carbon for undisturbed forests at these sites. With RIL harvest management, logged forests had approximately 1.5 times as much total necromass as undisturbed forests. Density and void space estimates for decay classes were similar at the two sites, indicating that these measurements may be usefully applied for necromass studies conducted in similar forest types in Amazonia. Proportions of standing dead and fallen small, medium, and large CWD size classes were similar across sites within treatments (RIL versus UF). Decay class proportions were also similar across sites within treatments. RIL treatments showed a proportionate increase in both fallen and standing necromass across sites compared to UF. Small and medium size classes make up about 12–21% of total fallen necromass. Standing dead made up 12–17% of the total necromass. Comprehensive studies of necromass in tropical forests need to include both standing dead and smaller size class measurements (<10 cm diameter) because collectively these contribute a large proportion of the overall necromass pool. A simple compartment model with the assumption of steady state for undisturbed forests indicates that necromass at our two study sites has a residence time of about 7 years in the forests studied. The rapid decay of this necromass suggests that the flux of carbon dioxide from necromass may account for approximately 15% of the gross CO_2 efflux from these undisturbed forests.

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