Wood density and stocks of coarse woody debris in a northwestern Amazonian landscape

Kuo-Jung Chao, Oliver L. Phillips, and Timothy R. Baker

Abstract: Coarse woody debris (CWD) is a rarely studied component of the carbon cycle. We report the first measurements of both CWD wood density and necromass in humid, lowland northwestern Amazonia, using both line-intersect and plot-based methods. Average CWD densities were not significantly different between clay-rich and white sand unflooded forests, but lower in floodplain forest ($p \leq 0.001$). Necromass of CWD lying on the ground was also lower in the floodplain (10.3 ± 6.1 $\mathrm{Mg \cdot ha^{-1}}$, mean ± 1 SE) than in the clay-rich (30.9 ± 5.4) and white sand (45.8 ± 7.3) forests ($p \leq 0.001$, using the line-intersect method). These patterns are likely driven by disturbance history, species composition, and decomposition rates. Plot-based data showed that standing and fallen CWD together accounted for 6.4%–15.4% of total coarse aboveground vegetative mass (trees ≥10 cm diameter). Across humid, lowland neotropical forests, we show that wood densities of intact and partially decayed CWD are significantly related with live wood density at the same site ($p = 0.026$ and 0.003, respectively). We show that these relationships can be applied generally to estimate CWD wood density for humid, lowland neotropical forests wherever destructive sampling is not possible.

Résumé : Les débris ligneux grossiers (DLG) constituent une composante rarement étudiée du cycle du carbone. Nous présentons les premières mesures tant de la densité du bois des DLG que de leur nécromasse dans les basses terres humides du nord-ouest de l'Amazonie en utilisant des méthodes basées sur l'intersection de lignes et sur des placettes-échantillons. La densité moyenne des DLG n'était pas significativement différente dans les forêts non inondées établies sur un sol de sable blanc ou sur un sol argileux mais elle était plus faible dans la forêt établie dans la plaine inondable ($p \leq$ 0,001). La nécromasse des DLG au sol était aussi plus faible dans la plaine inondable (10,3 ± 6,1 $\mathrm{Mg \cdot ha^{-1}}$; moyenne ± 1 ET) que dans les forêts sur un sol argileux (30,9 ± 5,4) ou dans les forêts sur un sol de sable blanc (45,8 ± 7,3) ($p \leq$ 0,001, avec la méthode basée sur l'intersection de lignes). Cette situation est probablement due à l'historique des perturbations, à la composition en espèces et aux taux de décomposition. Les données basées sur les placettes-échantillons révèlent qu'ensemble, les DLG debout et tombés au sol représentent 6,4 à 15,4% de la masse végétale aérienne grossière (arbres ≥ 10 cm de diamètre). Dans les forêts néotropicales humides sur les basses terres, nous montrons que la densité du bois des DLG intacts et partiellement décomposés est significativement reliée à la densité des arbres vivants au même endroit ($p =$ 0,026 et 0,003 respectivement). Nous montrons que ces relations peuvent généralement être appliquées pour estimer la densité du bois des DLG dans les forêts néotropicales humides sur les basses terres partout où il n'est pas possible d'effectuer un échantillonnage destructif.

[Traduit par la Rédaction]

Introduction

Coarse woody debris (CWD), one of the key components of the carbon pool (Harmon et al. 1986), is still rarely studied in neotropical forests (Clark et al. 2002; Keller et al. 2004; Palace et al. 2007), which account for a third of vegetative carbon found in forest ecosystems (Dixon et al. 1994). Published studies demonstrate that stocks of CWD (necromass) represent 6%–25% of total aboveground living and dead vegetative mass (Delaney et al. 1998; Clark et al. 2002; Nascimento and Laurance 2002; Rice et al. 2004). However, most plot-based estimates of carbon balance typically focus only on the living aboveground biomass (e.g., Phillips et al. 1998; Baker et al. 2004*a*).

This study aims to improve estimates of the carbon stocks and balances of lowland Amazonian forests. In particular, in western Amazonia few detailed studies of forest carbon pools have been conducted. Western Amazonia accounts for one quarter of the total 6 × 10^6 $\mathrm{km^2}$ Amazonian rainforest, if defined conservatively as the Amazon basin forests of Colombia, Ecuador, Peru, Bolivia, and Acre (Brazil) (data adapted from Food and Agricultural Organization of the United Nations 2000). It is also likely to include 20 Pg of carbon of aboveground live woody biomass (Malhi et al. 2006). To our knowledge, in the humid lowland forests of this region, there is only one study of necromass in southern Peru (Baker et al. 2007) and one of CWD volume in Ecuador (Gale 2000). Here, we report the first values for CWD wood density and stocks in humid, lowland northwestern Amazonian forests.

In contrast with well-established protocols for measuring CWD volume such as line-intersect sampling (Warren and Olsen 1964; van Wagner 1968), there is no standard proto-

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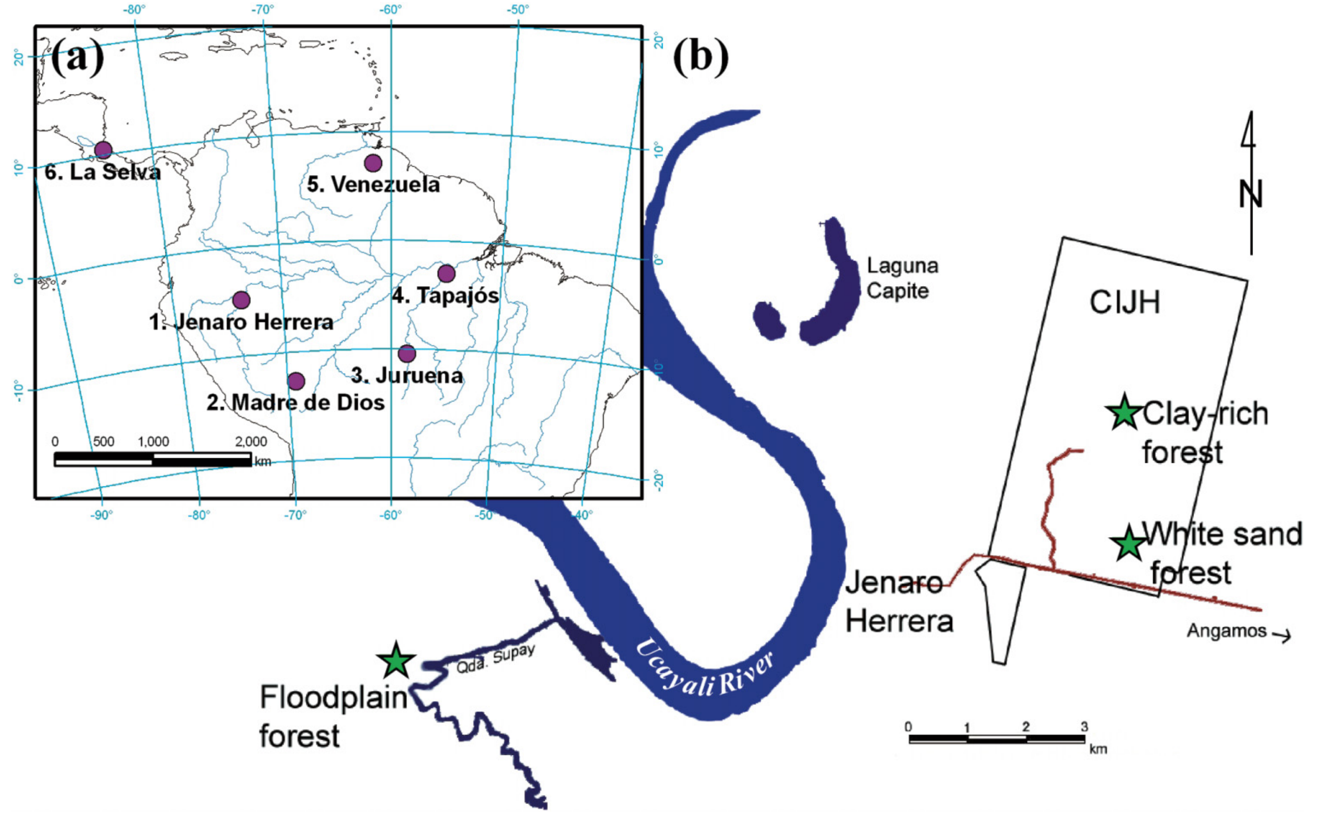
Fig. 1. (*a*) Locations of published coarse woody debris (CWD) wood density studies that report direct measurements with three decay classes, in humid lowland forests in the neotropics. 1, This study; 2, Baker et al. (2007); 3, Palace et al. (2007); 4, Keller et al. (2004); 5, Delaney et al. (1998); 6, Clark et al. (2002). (*b*) Plot locations of this study (star symbols). Modified from drawing by Eurídice Honorio, Centro de Investigaciones Jenaro Herrera (CIJH), Peru.



col for sampling the density of CWD. For example, Gerwing (2002) assumed that the densities of intact, partially decayed, and rotten logs are 100%, 88%, and 60% that of living trees, respectively, whereas Brown et al. (1995) used a random sample of 20 pieces of CWD to parameterize their wood density estimates. Most humid, lowland neotropical studies use a subjective classification of the degree of CWD decay (e.g., Kauffman et al. 1988; Keller et al. 2004), with two to six classes, depending on the researchers' definitions. In these studies, the density of each class is calibrated by direct density measurement of subsamples (Kauffman et al. 1988; Delaney et al. 1998; Clark et al. 2002; Keller et al. 2004). Overall, there are only five other CWD density studies in the neotropics that use a direct sampling method to produce at least three decay classes, and none are located in northwestern Amazonia (Fig. 1*a*). Also, direct sampling is a destructive method that is not suitable for some protected reserves. An indirect, nondestructive method is urgently needed to allow rapid assessment of CWD stocks from measurements of CWD volume, and especially for regions where at present only measurements of CWD volume are available (e.g., Gale 2000).

We conducted an investigation of CWD densities and stocks in three forest types at Jenaro Herrera in Amazonian Peru. The line-intersect method (also known as line-intercept; Warren and Olsen 1964; van Wagner 1968) was applied to sample CWD pieces for wood density and volume in this landscape. Additional plot-based (Harmon and Sexton 1996) measurements were made to measure the quantities of both standing and fallen CWD, and also to compare directly the carbon pools of CWD and living trees in the same area.

Specifically, we ask: (*i*) What are the CWD wood densities and stocks in the northwestern Amazonia? (*ii*) Are there differences in the CWD wood densities and stocks between forest types in this region?

Methods

Study sites

Fieldwork was undertaken in northern Peru at the Centro de Investigaciones de Jenaro Herrera (4°55′S, 73°44′W), located 200 km upstream of Iquitos, and administered by the Peruvian Institute for Amazonian Research (IIAP) (Fig. 1*b*). Annual rainfall in this landscape ranges from 2500 to 2700 mm, with mean monthly precipitation from 140 to 309 mm, and mean annual temperature between 26 and 27 °C (Spichiger et al. 1996; Kvist and Nebel 2001). CWD densities and stocks were studied in one seasonally flooded and two unflooded lowland forests. The unflooded forests are located on clay-rich (terra firma) and white sand soils, and the floodplain forest is located in high restinga forest, which on average is inundated for 1 month per year (Kvist and Nebel 2001). The sampling area is close to some permanent plots that were established in the different forest types (Fig. 2). In the unflooded forest, two 1 ha plots, established by the RAINFOR project (Malhi et al. 2002; Peacock et al. 2007; www.

geog.leeds.ac.uk/projects/rainfor/index.html), were randomly located in mature forest on two different soil types: clay-rich (RAINFOR code: JEN-11) and white sand soil (JEN-12). Every living individual tree ≥10 cm in diameter in the plots was measured, tagged, and identified in March 2005. In the seasonally flooded forest, two 1 ha plots were established in 1993 by Nebel et al. (2001*b*) (plot 2 and plot 3, coded JEN-02 and JEN-03, respectively).

Line-intersect based CWD measurements

We located two to four transects using the line-intersect method (van Wagner 1968) in March 2005 in the three types of forests (Fig. 2). Each transect (*i*) was started at least 10 m away from the corner of each permanent plot to avoid possible anthropogenic impacts, (*ii*) was oriented in parallel to the two perpendicular border directions of each plot to reduce any effect of orientation bias (Bell et al. 1996), and (*iii*) was at least 100 m away from the others (except for a 50 m transect, which was used for wood density sampling but not for volume estimation). Transect length depended on the patch size of the selected forest type. When the selected angle was unsuitable for transect setup (e.g., the line would cross a stream, trail, or enter a different forest type), the transect line orientation was shifted by 20° if possible. When a trail could not be avoided, the transect stopped 20 m before and started 20 m after, continuing in the same direction. In total, we inventoried 800 m of transect in the forest on clay-rich soils, 610 m in white sand forest, and 470 m in floodplain forest, encountering a total of 249 pieces of fallen CWD.

CWD is defined as all dead woody material, including lianas and palm trees, with diameter ≥10 cm. For every piece of CWD, we measured diameter, recorded decay class (see the next section: Wood density of CWD), and sampled part of the log for further density calibration. All CWD diameter measurements from the transects were used to estimate total CWD volume and necromass in each forest, except for data from the short (50 m) transect in the white sand forest. CWD volume was calculated as:

$$[1] \qquad V = \frac{(\pi^2 \Sigma D_i^2)}{8L}$$

where V is the CWD volume per unit area (m^3·ha^{-1}), D_i is the diameter (cm) of log i, and L (m) is the length of the transect line (van Wagner 1968). The variance of the volume (σ^2) for n transects was weighted by transect lengths (L_j), as recommended by De Vries (1986, p. 256, cited in Keller et al. 2004):

$$[2] \qquad \sigma^2 = \frac{\Sigma L_j (V_j - \overline{V})^2}{(n-1)\Sigma L_j}$$

Wood density of CWD

Density samples were taken from the cross-section of CWD intersected by the transect lines, and five standing dead trunks adjacent to the transects. If a tree was intersected more than once by a sampling line, only one branch from the tree was sampled to avoid pseudo-replication of individual trees. Sampling methods depended on softness of logs. For hard pieces, a chain saw was used to cut a cylindrical radial section, and rectangular or cylindrical solid wood plugs were taken from each radial section by a machete (Fig. 3*a*). Power drill sampling methods (Keller et al. 2004) were not suitable in this region, because most samples disintegrated before extraction, possibly because of the relatively soft wood in western Amazonia (Baker et al. 2004*b*). Samples were removed randomly in one of the three radii through a plane perpendicular to the ground (upper vertical, 0°; middle horizontal, 90°/270°; lower vertical, 180°), and at

Fig. 2. The relative position of transect lines and permanent plots in Jenaro Herrera, Peru. (*a*) clay-rich forest (plot size: 1 ha; 100 × 100 m^2), (*b*) white sand forest (plot size: 1 ha; 40 × 250 m^2), and (*c*) floodplain forest (size of each plot is 1 ha; 100 × 100 m^2). The line-intersect method of measuring CWD was conducted in all forest types, whereas the plot-based method was only conducted in the clay-rich and white sand plots.

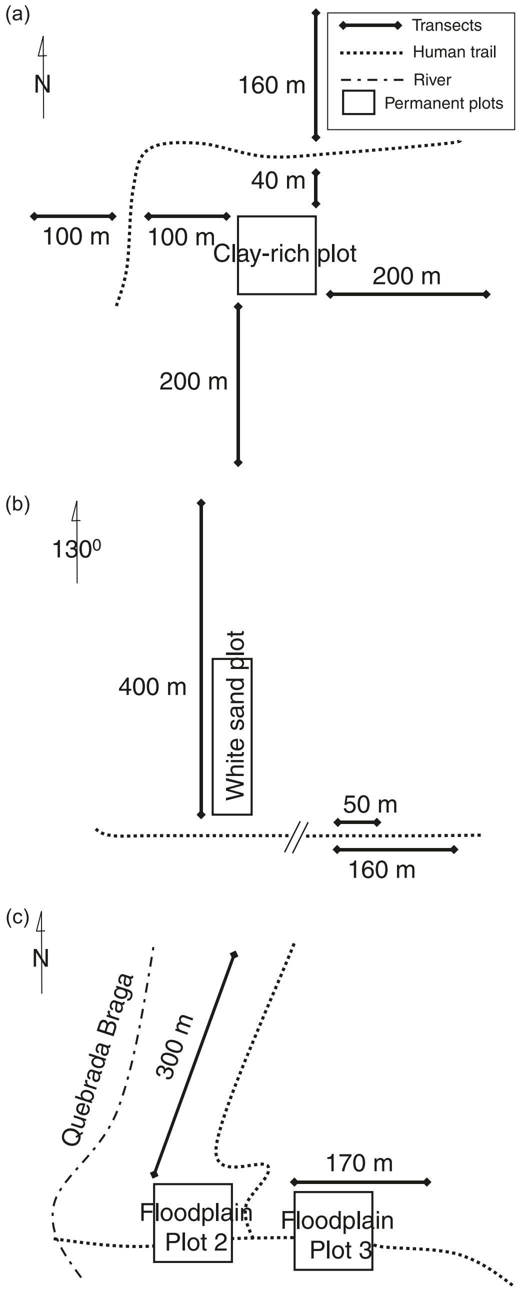


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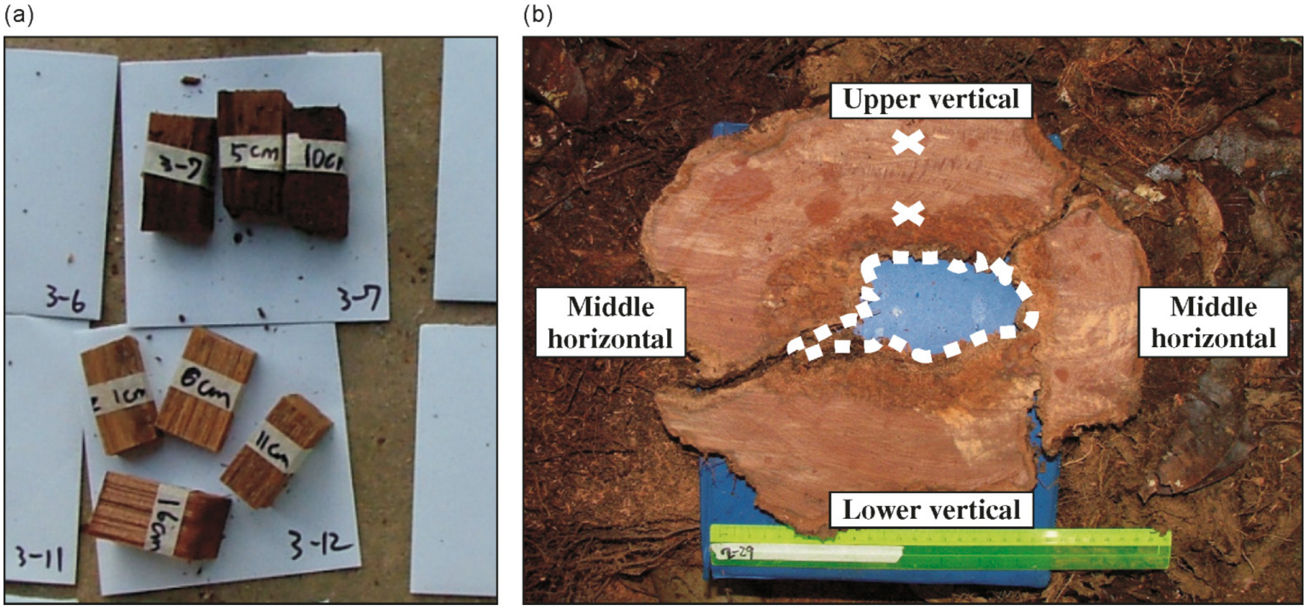
Fig. 3. Wood density samples of coarse woody debris. (*a*) Rectangular solid samples for density measurements. (*b*) A dead wood section from a log. Wood samples were removed randomly in one of the three radii through a plane perpendicular to the ground (upper vertical, middle horizontal, and lower vertical). Wood densities were taken at approximately 5 cm intervals, indicated by crosses. Void space, indicated by dotted circle, was measured by counting digital pixels of the photo.



5 cm intervals outwards from the centre of each wood section (Fig. 3*b*) (Keller et al. 2004).

For heavily decayed pieces, we collected a portion of the material by filling a known-volume (7 cm^3) clear plastic cylinder ($n = 68$). The contents of each cylinder were removed to a known-weight envelope to permit measurement of dry mass in the laboratory. In some cases, the material was too fragile to extract a coherent rectangular shape by machete, but too solid to use the plastic cylinder method. Here, irregular-shaped wood samples were taken. Where the decay classes of bark and heartwood were different, both parts were sampled. Digital photos were taken for each woody radial section (a ruler was included in each photo) to calculate void space proportion for the log (Fig. 3*b*).

Fresh volumes were determined by calipers in three length dimensions (l_1, l_2, and l_3) for a rectangular solid shape, or radius (r) and length (l) for a cylindrical sample. Volumes of irregular-shaped samples were determined by water displacement measurement inside a graduated plastic cylinder to the nearest 0.5 mm. All samples ($n = 381$, from 252 sampled trees) were then oven-dried at 60 °C. Dry mass was measured using a Oertling HB 63 2/3 db balance. Density was calculated as ovendry mass divided by fresh volume (Fearnside 1997).

The density of wood blocks in each decay class ("original density") was calculated by averaging the density samples within each log, and then averaging these densities within the same decay class. Void space in a wood section can affect CWD volume and therefore density calculations. In our study, we defined void space as hollows surrounded by solid wood and determined it by counting digital pixels of field photos using ImageJ (rsb.info.nih.gov/ij/). The density value of wood including voids in each decay class ("revised density") was calculated by adjusting the original density value by average percentage of void space in each decay class. Except where specified, "density" of CWD in this study indicates the "revised density" (Keller et al. 2004).

Decay classes of CWD were originally categorized into five classes, modified after Keller et al. (2004). Class 1 material was recently dead with more than 75% of the wood intact and hard, and sometimes still with fine twigs attached. Class 1.5 material was solid wood with slightly damaged bark. Material in class 2 was damaged, the log had experienced some decay, between the decay degree of class 1.5 and 2.5, and was also applied to pieces of wood where the bark had gone but the heartwood remained solid. Class 2.5 was applied to somewhat rotten material, with part of the wood friable and easily broken when kicked. Class 3 material was at least 75% soft and rotten, which a machete blade could enter easily, and which collapsed when stepped on. Where the state of decay of the bark and heartwood were very different, decay classes were attributed separately. To facilitate comparison within our landscape and with published studies, we also collapsed the "five decay class" results into three major decay classes, by combining class 1.5 with class 1, and class 2.5 with class 3.

As the sample size in "decay class 1" ($n = 1$) of the original "five decay class" classification design was insufficient, mean stand-level living wood density values were applied for this class (to account for stand-level variations in wood density composition across Amazonian forests (Baker et al. 2004*b*)). Living wood density averages were estimated on a basal-area basis, rather than on a per-stem basis, because larger trees are likely to be disproportionately present in the CWD pool, as they contribute relatively larger stocks of wood (Chambers et al. 2001*a*) and have slower decomposition rates (Chambers et al. 2000). There was no such sample size problem in the "three decay class" classification, so our actual measurements were used.

Average living wood density ($\rho_{\mathrm{BA}j}$), weighted by basal

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area, was estimated using the species composition data of nearby permanent plots (Fig. 2) (Nebel et al. 2001*b*; Peacock et al. 2007) and a species wood density database (Baker et al. 2004*b*; Chave et al. 2006; Lopez-Gonzalez et al. 2006). Wood density data were matched to the plot data on a tree-by-tree basis. In cases where species wood density was unavailable, the average for the genus (25% of 11 252 individuals), or family (5%) was used. For unidentified trees, or individuals in families lacking wood density data, the average wood density of the available species in the plot, on a per-stem basis, was used (1%).

Plot-based CWD measurements

We also quantified CWD volume in March 2005 using the plot-based method (Harmon and Sexton 1996) within the two unflooded permanent plots, but not in the floodplain forest because of time limitation. We recorded diameter, length, and decay class (see section Density of CWD) of every piece of CWD (≥10 cm diameter), whether standing or prone, in the whole clay-rich plot and half of the white sand plot. CWD lying on the ground was classified as "fallen CWD", and both standing dead trees and stumps were classified as "standing CWD". For fallen CWD, diameters at both ends were estimated by two perpendicular directions to the nearest centimetre. Where accessible because of hollowing, the thickness of bark was recorded and used to adjust the volume of CWD. For "standing" stumps, the diameters of smaller ends and the length (height) were visually estimated. For logs tapering to <10 cm diameter, measurements were only made up to the point of 10 cm diameter. For buttressed trunks, diameters were taken above the buttresses.

The volume (v, m^3) of each CWD piece by the plot-based method was calculated using Smalian's formula (Phillip 1994):

$$[3] \qquad v = \frac{\pi}{8} L_{\mathrm{CWD}}(D_1^2 + D_2^2)$$

where L_{CWD} (m) is the length of the CWD piece, and D is the geometric mean of trunk diameter measurements (m) at either end 1 or 2. For CWD with bark thickness measurements, volumes were calculated by subtracting the inner volume from the outer volume.

Stocks of CWD and biomass

Stocks of CWD are termed as necromass. Necromass (N) in each decay class d was calculated as the product of the volume (V_d, by either the plot-based or intersect-based method) and the density (ρ_d) for all material in that class in each forest type.

The sampling standard error (E_N) of necromass N_d (d = 1 to 3) by the line-intersect method was calculated as:

$$[4] \qquad E_N = E_\rho V_d + \rho_d E_V$$

where E_ρ and E_V represent the standard errors in density (ρ_d) and volume (V_d), respectively. This is a conservative approach that accounts for the possible interaction between errors in CWD density and volume (Taylor 1997). The total error in the necromass was estimated by summing the component errors in each decay class.

AGB$_{\mathrm{coarse}}$ (Mg) is defined as aboveground living trunks or branches ≥10 cm in diameter within plots. It is estimated by multiplying aboveground biomass (AGB, kg) by a coarse wood correction factor of 0.85 (N. Higuchi, unpublished data, cited in Chambers et al. 2000), to account for woody trunks >10 cm diameter only.

$$[5] \qquad \mathrm{AGB}_{\mathrm{coarse}} = \frac{0.85\,\mathrm{AGB}}{1000}$$

Estimates of AGB of the two unflooded forests (clay-rich and white sand plots) were derived from two different allometric models. The first is based on a one-site neotropical study, developed from trees >5 cm in diameter at 1.3 m or above buttresses, n = 315, near Manaus, Brazil (Chambers et al. 2001*a*). We adjusted the equation using species-level wood density values following Baker et al. (2004*b*).

$$[6] \qquad \mathrm{AGB} = \frac{\rho_i}{0.67}\exp[0.333(\ln D_i) + 0.933(\ln D_i)^2 - 0.122(\ln D_i)^3 - 0.370]$$

where ρ_i (g·cm^{-3}) is the species-level wood density of each individual i, and D_i (cm) is the diameter at 1.3 m of the same tree.

The second model is a multi-site pan-tropical "moist forest" (n = 15) study, included all available biomass measurements of trees >5 cm (Chave et al. 2005).

$$[7] \qquad \mathrm{AGB} = \rho_i \exp[2.148(\ln D_i) + 0.207(\ln D_i)^2 - 0.0281(\ln D_i)^3 - 1.499]$$

AGB of the floodplain forest was estimated as the average of biomass results, reported by Malhi et al. (2006) for JEN-02 and JEN-03, multiplied by the 0.85 correction factor. In Malhi et al. (2006), biomass was calculated using known plot basal area and structural conversion factors. The structural conversion factors were interpolated using distance-weighted kriging and soil-type weighted methods.

Results

Wood density of CWD

Revised CWD densities showed significant differences among decay classes and forest types (Table 1), both for the five class classification (two-way ANOVA (ln-transformed for a normal distribution), decay class, $F_{[3,239]}$ = 15.2, $p \le 0.001$; forest type, $F_{[2,239]}$ = 5.9, p = 0.003; no interaction, p = 0.109) and the three class classification (decay class, $F_{[2,243]}$ = 19.8, $p \le 0.001$; forest type, $F_{[2,243]}$ = 7.6, $p \le 0.001$; no interaction, p = 0.063). Density declined monotonically with increasing decay classes (Table 1). However, the densities of decay classes 1 and 2 in the floodplain forest were similar, which is likely to be due to the small sample size in decay class 1. Densities of CWD were indistinguishable between forests on clay-rich soil and on the white sand, but both were significantly higher than densities of the floodplain forest (Table 1).

More than one fifth (21.3%) of the sampled pieces had a void space in the wood, but the void area means were only 3%–4% in each decay class (Table 1). There were no significant effects of diameter size class (class 1, 10∼20 cm; class 2, 20∼40 cm; and class 3, ≥40 cm) on CWD densities

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Table 1. Densities (mean ± 1 SE, g·cm^{-3}) of coarse woody debris in three forest types in Jenaro Herrera, northern Peru.

			Revised density*				
Decay class*	Original density	Void proportion	Clay-rich^{a}	White sand^{a}	Floodplain^{b}	Overall	$n^{\dagger}$
Five‡							
1	—	—	0.67 (±0.01)	0.70 (±0.00)	0.51 (±0.00)	—	—
1.5^{a}	0.55 (±0.03)	0.03 (±0.01)	0.55 (±0.04)	0.58 (±0.04)	0.29 (±0.03)	0.53 (±0.03)	65
2^{b}	0.42 (±0.02)	0.04 (±0.02)	0.42 (±0.03)	0.48 (±0.03)	0.22 (±0.02)	0.41 (±0.02)	74
2.5^{c}	0.30 (±0.02)	0.04 (±0.02)	0.30 (±0.03)	0.28 (±0.03)	0.26 (±0.05)	0.28 (±0.02)	71
3^{d}	0.21 (±0.02)	—	0.25 (±0.04)	0.19 (±0.02)	0.14 (±0.02)	0.21 (±0.02)	41
Three							
1^{a}	0.57 (±0.04)	0.03 (±0.01)	0.58 (±0.06)	0.59 (±0.04)	0.26 (±0.05)	0.55 (±0.04)	43
2^{b}	0.42 (±0.02)	0.03 (±0.01)	0.43 (±0.03)	0.46 (±0.03)	0.24 (±0.02)	0.41 (±0.02)	126
3^{c}	0.24 (±0.02)	0.03 (±0.02)	0.27 (±0.03)	0.20 (±0.02)	0.17 (±0.03)	0.23 (±0.01)	83

*Results of Tukey's HSD tests are labelled by lowercase letters a, b, c, and d.

†Samples were regrouped from "five decay classes" into three major decay classes, by combining class 1 with 1.5, and class 2.5 with 3. Some logs were classified in between defined classes, e.g., 1.5–2 or 2–2.5, in the field. In the "five decay class" scheme, class 1.5–2 was grouped to class 1.5, and class 2–2.5 was grouped to class 2.5. In the "three decay class" scheme, both classes 1.5–2 and 2–2.5 were grouped into class 2.

‡In the five class classification, the sample size in decay class 1 was not enough, so this class was not used for Tukey's HSD test and the value is the is living tree density weighted by basal area in the nearby permanent plot. Wood in class 3 was too fragile, so the void proportion was not included.

Table 2. Necromass (average ± 1 SE, Mg·ha^{-1}) of fallen CWD in three forest types in Jenaro Herrera, northern Peru, based on the line-intersect method.

	Forest type*		
Decay class*	Clay-rich^{a}	White sand^{a}	Floodplain^{b}
Class 1^{a}	8.7 (±1.2)	16.0 (±3.0)	3.0 (±0.7)
Class 2^{b}	16.5 (±2.6)	23.9 (±3.1)	6.9 (±5.1)
Class 3^{a}	5.8 (±1.6)	6.0 (±1.2)	0.4 (±0.2)
Total	30.9 (±5.4)	45.8 (±7.3)	10.3 (±6.1)

*Results of Tukey's HSD tests are labelled by lowercase letters a, b, c, and d.

Table 3. Necromass (Mg·ha^{-1}) of both standing and fallen CWD in two unflooded forests in Jenaro Herrera, northern Peru, based on the plot-based method.

	Forest type					
	Clay-rich			White sand		
Decay class	All	Fallen	Standing	All	Fallen	Standing
Class 1	7.7	5.3	2.4	20.0	14.1	5.8
Class 2	9.8	6.9	2.9	19.0	12.3	6.7
Class 3	2.9	2.2	0.6	2.2	1.6	0.6
Total	20.3	14.4	5.9	41.1	28.1	13.1

among the decay classes (ln-transformed CWD densities, two-way ANOVA, diameter class, $F_{[2,239]} = 0.2$, $p = 0.787$ for the five classes; $F_{[2,243]} = 0.2$, $p = 0.800$ for the three classes). Moreover, the density of fallen wood was not affected by either radial position (Kruskal–Wallis test, $p = 0.995$), or by the distance from centre (linear regression, difference in density with the piece in the central of the same log against its distance from the centre, $r^2 = 0.001$, $p = 0.723$).

Because the three decay class classification method revealed comparable patterns to the five class classification and is less susceptible to potential problems of small sample sizes, hereafter we only report results from the three class classification.

Stocks of CWD

Volume of CWD varied between forest types and decay classes using the line-intersect method estimation (two-way ANOVA, forest type, $F_{[2,15]} = 3.8$, $p = 0.046$; decay class, $F_{[2,15]} = 5.9$, $p = 0.013$; no interaction, $p = 0.920$). There was no detectable difference in volume between forests on clay-rich soils (74.7 ± 5.7 m^{3}·ha^{-1}) and white sand (108.8 ± 3.4 m^{3}·ha^{-1}), but volume was significantly lower in the floodplain forest (42.8 ± 20.1 m^{3}·ha^{-1}).

Similar to the results of CWD volume and density, necromass also varied between forest types and decay classes using the line-intersect method estimation (two-way ANOVA, forest type, $F_{[2,15]} = 11.3$, $p \leq 0.001$; decay class, $F_{[2,15]} = 13.2$, $p \leq 0.001$; no interaction, $p = 0.423$). There was no detectable difference in necromass between forests on clay-rich soils (30.9 Mg·ha^{-1}) and white sand (45.8 Mg·ha^{-1}), but necromass was significantly lower in the floodplain forest (10.3 Mg·ha^{-1}) (Table 2). Also, necromass in decay class 2 was significantly greater than in classes 1 and 3 (Table 2).

By the plot-based methods, the quantity of total necromass, including both fallen and standing CWD was 20.3 Mg·ha^{-1} in the clay-rich forest, and 41.1 Mg·ha^{-1} in the white sand forest (Table 3). Necromass of standing CWD accounted for 29%–32% of total necromass. In other words, the necromass of standing CWD was almost half as much (41%–47%) as the necromass of fallen CWD. The quantities of fallen necromass measured by the plot-based method were generally lower than those measured by the line-intersect method.

As the plot-based method for standing CWD was not used in the floodplain forest, we applied the average proportion of standing CWD (44%), derived from the unflooded forests, as a preliminary estimate of total CWD in the floodplain forest. As a proportion of $\mathrm{AGB}_{\mathrm{coarse}}$ in the three forests, CWD contributes proportionally most in the white sand for-

Table 4. Biomass (Mg·ha^{-1}) and necromass (Mg·ha^{-1}, both standing and fallen) in three forest types in Jenaro Herrera, northern Peru.

Stock	Unflooded forest*				Floodplain forest†	
	Clay-rich		White sand			
AGB$_{coarse}$‡	Chambers	Chave	Chambers	Chave	Kriging-based	Soils-based
Census 1	253.2	261.4	231.0	226.1	214.8	211.5
Census 2	254.8	263.5	236.6	231.8	—	—
Necromass	20.3	20.3	41.1	41.1	14.8	14.8
Total	273.5	281.7	272.1	267.2	229.7	226.4

*Biomass estimated using two allometric models (Chambers et al. 2001*a*; Chave et al. 2005) for censuses 2005 and 2006. Necromass estimated by the plot-based methods.

†Biomass interpolated by Malhi et al. (2006), using distance-weighted kriging and soil-type weighted methods, for census 2001. Note that necromass estimated by the line-intersect method with 44% added to account for standing coarse woody debris.

‡Coarse aboveground biomass.

est (17.8%–18.2%), followed by the clay-rich forest (7.8%–8.0%), and least in the floodplain forest (6.8%–6.9%; Table 4). As a proportion of total coarse aboveground vegetative mass, CWD contributes 15.1%–15.4% in the white sand forest, 7.2%–7.4% in the clay-rich forest, and 6.4%–6.5% in the floodplain forest (Table 4).

Discussion

Stocks of CWD

CWD stocks were lowest in the floodplain forest and greatest in the white sand forest (Table 4). Baker et al. (2007) reviewed other neotropical rainforest studies and showed that CWD stocks range from 96.1 Mg·ha^{-1} on a disturbed, nutrient-poor oxisol forest, Brazil (Rice et al. 2004) to only 2.5 Mg·ha^{-1} on a spodosol forest (white sand), Venezuela (Kauffman et al. 1988), and the average value is about 35 Mg·ha^{-1}. The floodplain forest in this study is located at the lower end of this range, whereas the unflooded forests, on clay-rich and white sand soils, are mid-range. The broad range of CWD reported for the neotropical forests implies large local and regional variations in disturbance history, decomposition rates, and (or) input rates (i.e., mortality and branch fall), and may also be affected by differences in sampling methods used by researchers.

The low stocks of CWD in the floodplain forest probably result from flood disturbance, which can relocate CWD stocks and influence decomposition rates. A plot-based study in white-water floodplain forests (várzea) in Brazil showed that flooding redistributed CWD from higher to lower forests, and that the cycle of wetting and drying enhanced the rate of decomposition (Martius 1997). In that study, dead wood stock was also relatively insignificant, and represented an even lower proportion of vegetative mass than that found in this study (2.7% of the living wood mass). Low necromass in our study is also driven by low CWD density in this forest type (Table 1), as necromass is a product of the volume and density of CWD.

Quantities of CWD were not significantly different between the two unflooded forests, but CWD represented a higher proportion of AGB$_{coarse}$ in the white sand than in the clay-rich forest. This phenomenon could be explained by either higher rates of CWD input, or lower decomposition rates of CWD in the white sand forest. Longer-term observations, including mortality inputs, direct measurements of decomposition rates, and flooding disturbance effects are needed to better interpret the necromass balance of this landscape.

The ratios of standing to fallen CWD are 0.41–0.47 in our northwestern forests, 0.32 in southwestern Amazonian forests in Baker et al. (2007), 0.80 in northeastern Amazonian forests in Delaney et al. (1998), and 0.14–0.17 in eastern Amazonian forests in Palace et al. (2007). These variations suggest that it is essential to account for standing dead trees when estimating the stocks of CWD.

Wood density of CWD

Void space was not an important feature of CWD in this study. By contrast, a study in eastern Brazilian Amazonia reported that the void area of CWD ranged from 1% to 26% (Keller et al. 2004; Palace et al. 2007), and Fearnside (1997) suggested that about 20%–30% of living trees (≥10 cm diameter) in Brazil have a hollow space in the centre. One reason for this lack of void space phenomenon in NW Amazonia could be the smaller average tree size (Malhi et al. 2002) and faster turnover rates and consequent shorter life spans (Phillips et al. 2004) in this region. Thus, trees in western Amazonia may simply not grow large enough or live long enough to develop void space, perhaps via termite infestation (e.g., Apolinário and Martius 2004). These differences in hollow space proportions across Amazonia could affect both biomass and necromass estimates. Studies based on allometric equations from eastern Amazonia, where the proportion of hollow section is larger, could underestimate the biomass of trees in these northwestern Amazonian forests.

Our study shows that within a relatively small area, the floodplain forest has significantly lower wood density of CWD than the clay-rich and white sand forests. A plausible explanation of this is the distinctive species composition differences between floodplain forests and other forest types (Terborgh and Andresen 1998; ter Steege et al. 2000). At Jenaro Herrera, the dominant families in the floodplain forest are Moraceae, Fabaceae, and Arecaceae (Nebel et al. 2001*a*), with mean wood density of 0.60, 0.73, and 0.43 g·cm^{-3}, respectively (Lopez-Gonzalez et al. 2006). In the nearby clay-rich forest, the dominant families are Fabaceae (0.73 g·cm^{-3}), Lecythidaceae (0.63 g·cm^{-3}), and Sapo-

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taceae (0.75 g·cm^{-3}) (Lopez-Gonzalez et al. 2006; Peacock et al. 2007). In the white sand forest, the dominant families also differ, including Fabaceae (0.73 g·cm^{-3}), Clusiaceae (0.66 g·cm^{-3}), and Euphorbiaceae (0.61 g·cm^{-3}) (Lopez-Gonzalez et al. 2006; Peacock et al. 2007). As wood density is a phylogenetically conserved trait (Baker et al. 2004*b*) and the floodplain forest is composed of families with relatively low wood density, variation in species composition explains the landscape-scale live wood density differences and therefore potentially the CWD density differences.

However, the question remains, why should density of living trees be lower in the floodplain forest? Soil fertility gradients may affect stand level wood density values. For example, higher fertility may favour low wood density species that grow fast, whereas low soil fertility slows tree growth and favours high wood density, longer-lived species (Muller-Landau 2004). Pan-Amazonian terra firma (unflooded) forest research shows that wood density is typically lower on the more fertile soils in western Amazonia than on the less fertile soils in central and eastern Amazonia (Baker et al. 2004*b*). At Jenaro Herrera, the floodplain forest grows on a fertile soil (concentration of cations (ECEC) = 20.9 cmol^{+}·kg^{-1} in horizon A, Nebel et al. 2001*b*), while the clay-rich (oxisols, Spichiger et al. 1996) and the white sand forests (ECEC = 1.84 cmol^{+}·kg^{-1} in horizon A, unpublished RAINFOR data) are located on much poorer soils. Together, the poorer soil fertility and therefore higher living wood density could explain why CWD densities were higher in the unflooded forests.

Wood densities of CWD and living forest in the neotropics

Available humid, lowland neotropical studies show that wood density of CWD in decay class 1 on average (±1 SE) is 82% ± 6% of $\rho_{\mathrm{BA}j}$, in decay class 2 is 66% ± 4% of $\rho_{\mathrm{BA}j}$, and in decay class 3 is 46% ± 6% of $\rho_{\mathrm{BA}j}$ (Table 5), where ρ_{BAj} is the mean wood density of living trees of plot *j*, weighted by basal area. To explore how important living wood density may be in determining CWD density, we constructed regression models for humid, lowland, neotropical forests from available data (Table 5, except for Juruena, Mato Grosso, Brazil, where living wood density data were not available). We found significant relationships between wood densities of living trees ($\rho_{\mathrm{BA}j}$, weighted by basal area) and CWD, both in decay class 1 ($\rho_{d=1}$, r^2 = 0.661, p = 0.026) and 2 ($\rho_{d=2}$, r^2 = 0.860, p = 0.003), but not for decay class 3 (p = 0.324) (Fig. 4). The equations are as follows.

$$[8] \qquad \rho_{d=1} = 1.17\rho_{\mathrm{BA}j} - 0.21$$

and

$$[9] \qquad \rho_{d=2} = 1.17\rho_{\mathrm{BA}j} - 0.31$$

where $\rho_{\mathrm{BA}j}$ (g·cm^{-3}) is the mean wood density of living trees weighted by basal area of plot *j*, and $\rho_{d=1}$ and $\rho_{d=2}$ (g·cm^{-3}) represent the CWD densities in decay classes 1 and 2, respectively. We recommend applying these relationships for mature, humid, lowland neotropical forests where average living wood densities ($\rho_{\mathrm{BA}j}$) are within 0.51–0.74 g·cm^{-3}. CWD wood density in decay class 3, which contributes relatively little to necromass, may be influenced more strongly

Table 5. Mean densities (± 1 SE, g·cm^{-3}) of living and CWD (diameter ≥10 cm) in humid, lowland neotropical forests (rainfall ≥2000 mm·year^{-1}).

					CWD (ρ_d)			
No.	Location	Rainfall	Soil type	Living ($\rho_{\mathrm{BA}j}$)	Intact (d = 1)	Partially decayed (d = 2)	Rotten (d = 3)	Reference
1	Jenaro Herrera, Peru							
	Clay-rich, JEN-11	2521	Oxisols	0.67±0.01*	0.58±0.06	0.43±0.03	0.27±0.03	This study
	White sand, JEN-12	2521	White sand	0.70±0.00*	0.59±0.04	0.46±0.03	0.20±0.02	This study
	Floodplain, JEN-02/03	2715	Entisols	0.51±0.01*	0.26±0.05	0.24±0.02	0.17±0.03	This study
2	Madre de Dios, Peru	2200	Ultisols	0.56±0.00*	Average: 0.54 (0.54±0.01; 0.53±0.04)	Average: 0.39 (0.40±0.04; 0.37±0.03)	0.38±0.03	Baker et al. (2007)
3	Juruena, Mato Grosso, Brazil	2200	Oxisols and (or) Ultisols	—	Average: 0.70 (0.71±0.02; 0.69±0.04)	Average: 0.52 (0.60±0.04; 0.59±0.06)	0.33±0.05	Palace et al. (2007)
4	Tapajós UF, Brazil	2000	Oxisols with some Ultisols	0.69±0.00*	Average: 0.65 (0.60±0.02; 0.70±0.03)	Average: 0.52 (0.58±0.03; 0.45±0.03)	0.28±0.03	Keller et al. (2004)
5	Venezuela	2500–3200	Inceptisols and (or) Ultisols†	0.74±0.01*	0.58±0.02	0.59±0.03	0.50±0.13	Delaney et al. (1998)
6	La Selva, Costa Rica	4000	Inceptisols and (or) Ultisols	0.54±0.11‡	0.45±0.003	0.35±0.007	0.25±0.011	Clark et al. (2002)
	Mean ratio of ρ_d / $\rho_{\mathrm{BA}j}$				0.82±0.06	0.66±0.04	0.46±0.06	

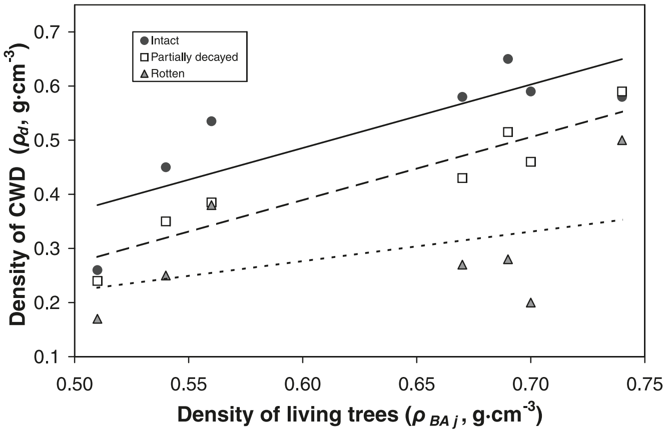
Note: Living wood density ($\rho_{\mathrm{BA}j}$) is the plot-level average of living trees, weighted by basal area. CWD densities (ρ_d) are classified into three decay classes (d), including intact (d = 1), partially decayed (d = 2), and rotten (d = 3).

*Plot and wood density data are the best available to the first author at the time of final data checking (8 February 2007).

†Carey et al. (1994).

‡$\rho_{\mathrm{BA}j}$ (±SD) of individuals with diameter ≥30 cm (Muller-Landau 2004).

Fig. 4. Relationships between average wood densities of living trees (ρ_{BAj}) and CWD (ρ_d) in humid lowland neotropical forests. Sites are as in Table 5, except for site No. 3, where ρ_{BAj} was not available. Solid line is the linear regression for the intact CWD ($\rho_{d=1}$ = 1.17 ρ_{BAj} – 0.21, r^2 = 0.661, p = 0.026), broken line is for the partially decayed CWD ($\rho_{d=2}$ = 1.17 ρ_{BAj} – 0.31, r^2 = 0.860, p = 0.003), and dotted line is for the rotten CWD (r^2 = 0.193, p = 0.324).



by other factors such as moisture condition, presence of decomposers, and wood components and structures (Harmon et al. 1986). Since this class is not related to living wood density, the average value across humid, lowland neotropical studies (0.29 g·cm^{-3} (±0.04, 1 SE)) may be applied. As Fig. 4 shows, plot-average densities (ρ_{BAj}) between 0.57 and 0.66 g·cm^{-3} are not represented in available neotropical studies, so investigations within this range are needed to gain a better understanding of the overall relationships.

Measurement of CWD density

Although decay classes of CWD are classified subjectively, the direct measured densities related with that of live trees, which suggests cross-site comparison between classes is feasible. Besides, based on our results, the three class classification has similar patterns to the five class classification method and is less susceptible to sample size problems. When using the five class classification, the fallen necromass was estimated as 31.5 ± 6.6 Mg·ha^{-1} in the clay-rich forest, 45.3 ± 13.2 in the white sand forest, and 10.7 ± 6.1 in the floodplain forest. All of these values are within the standard error ranges of the results using the three class classification. Thus, we believe that the three class classification is sufficient for necromass estimation.

Careful examination of decay class in dead wood is also important. For example, the densities of the intact and partially decayed CWD are indistinguishable in the Venezuelan plots (Delaney et al. 1998) (Table 5). Delaney et al. (1998) suggest that this pattern is because logs classified as partially decayed to rotten in their study still had relatively sound heartwood or sapwood. Therefore, when the decay classes of heartwood and sapwood are different we recommend recording them separately. Besides, a comparison of wood density in standing and fallen CWD is needed. Our study was not designed to make such a comparison, but an eastern Amazonian study (Chambers et al. 2001*b*) showed that the decomposition rates of standing CWD are likely to be different from fallen CWD. Since standing CWD can account for a substantial proportion of total CWD, future studies should take wood density of standing CWD into consideration.

The densities in fallen CWD in our study did not vary significantly with radial positions and distance from centre. Keller et al. (2004) found that CWD density was significantly higher on the upper compared with the lower part of the log, and declined with distance from the log centre. These patterns are probably due to microbe availability and activity, which vary within a log depending on moisture content and the substrate (Harmon et al. 1986). Our “insignificant” results may be caused by a mixture of species-specific decomposition mechanisms. For example, the centres of palm boles decompose more quickly than the exterior parts, whereas the sapwood of many dicotyledonous species appears to decompose faster than heartwood. A chronosequence study of wood decomposition in boreal forests of Russia (Yatskov et al. 2003) suggests that there are four types of CWD density decay patterns. (*i*) Decreasing linearly with decay classes. (*ii*) No density change until late decay stages because of decay-resistant heartwood. (*iii*) Decreasing rapidly in density at early decay stages, but then levelling off because of a high sapwood-to-heartwood ratio or intermediate decay-resistant heartwood. (*iv*) Complex decomposition processes proceeding simultaneously from both the outside and inside due to heart rot. In the tropics, the activities of wood decomposers, such as termites (Apolinário and Martius 2004), may also influence patterns of wood decay. Therefore, to examine the effects of radial position and distance to the centre, a better method would be to sample the same logs of known species at different radial positions and distances from the centre, rather than comparing these effects using different logs from unknown species.

Clark et al. (2002) showed that to estimate the true mean of CWD wood density within ±20%, it is necessarily to have 8, 14, and 26 samples, respectively, for each decay class. For both the clay-rich and the white sand forests, the sampled numbers of logs for all decay classes are higher than the criteria. However, in the floodplain forests, the available logs were relatively few and we had relatively small sample sizes — we tried to elongate the transects, but failed because of the restricted area of the forest type. Wood density and stocks of CWD in floodplain forest may also have seasonal patterns due to flood-redistribution of wood (Martius 1997), and longer-term observation of CWD patterns here is especially needed. With the relationships found in Fig. 4, we provide an alternate way to estimate CWD wood density when direct measurement is not practical, based on the average wood density of the living forest.

Conclusions

This study provides the first estimates of CWD for a large part of Amazonia. Both density and stocks of CWD vary among forest types within the northwestern Amazonian landscape. CWD wood density and stocks in the floodplain forest are relatively low, apparently because of the distinctive composition of low-density-wood species, and possibly the flooding regime itself. Values for both CWD wood density and necromass are indistinguishable between the two nonflooded forests. In the broader context of humid, lowland neotropical forests, CWD wood densities in decay classes 1 and 2 were significantly related to the wood density of the living forest, and differences in species composition appear to provide a generally applicable explanation for the regional-scale variation in wood density of CWD. Therefore, for areas where destructive measurements are not possible, necromass values may be estimated simply on the basis of the dead wood volume in each class, and the stand's live wood density for CWD wood density in decay classes 1 and 2 (eqs. 8 and 9). As for CWD wood density for the decay class 3, the mean value across the humid, lowland neotropical forest studies (0.29 g·cm^{-3}) can be applied.

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