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Low stocks of coarse woody debris in a southwest Amazonian forest

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Abstract The stocks and dynamics of coarse woody debris (CWD) are significant components of the carbon cycle within tropical forests. However, to date, there have been no reports of CWD stocks and fluxes from the approximately 1.3 million km^2 of lowland western Amazonian forests. Here, we present estimates of CWD stocks and annual CWD inputs from forests in southern Peru. Total stocks were low compared to other tropical forest sites, whether estimated by line-intercept sampling (24.4 ± 5.3 Mg ha^{-1}) or by complete inventories within 11 permanent plots (17.7 ± 2.4 Mg ha^{-1}). However, annual inputs, estimated from long-term data on tree mortality rates in the same plots, were similar to other studies (3.8 ± 0.2 or 2.9 ± 0.2 Mg ha^{-1} year^{-1}, depending on the equation used to estimate biomass). Assuming the CWD pool is at steady state, the turnover time of coarse woody debris is low (4.7 ± 2.6 or 6.1 ± 2.6 years). These results indicate that these sites have not experienced a recent, large-scale disturbance event and emphasise the distinctive, rapid nature of carbon cycling in these western Amazonian forests.

Keywords Decomposition rate · Net flux · Carbon balance · Permanent plot · Tropical forest

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Introduction

Characterising the stocks and fluxes of carbon in tropical forests is important for understanding the global carbon cycle. In tropical regions, uncertainty about how much carbon is stored in biomass is an important limitation of regional-scale estimates of carbon flux (Houghton et al. 2001; Houghton 2005), and improving these estimates requires field studies of both above- and belowground biomass stocks. The most commonly studied compartment is the aboveground biomass of living trees, as living trees usually represent the largest fraction of total stand biomass (Nascimento and Laurance 2002). Large (≥10 cm diameter) pieces of standing and fallen dead wood (coarse woody debris, CWD) can also comprise a significant fraction of the total stocks, but information on the quantity and dynamics of carbon stored in the necromass in these ecosystems is relatively sparse.

Estimates of CWD stocks in tropical forests vary widely from 0 to >60 Mg ha^{-1}, and can comprise up to 33% of the biomass of trees ≥10 cm in diameter (Fig. 1; Clark et al. 2002; Rice et al. 2004). Values reported from lowland Amazonian forests encompass the entire range, from very low stocks in forests on white sand soils in Venezuela (bana and caatinga vegetation, Kauffman et al. 1988), to

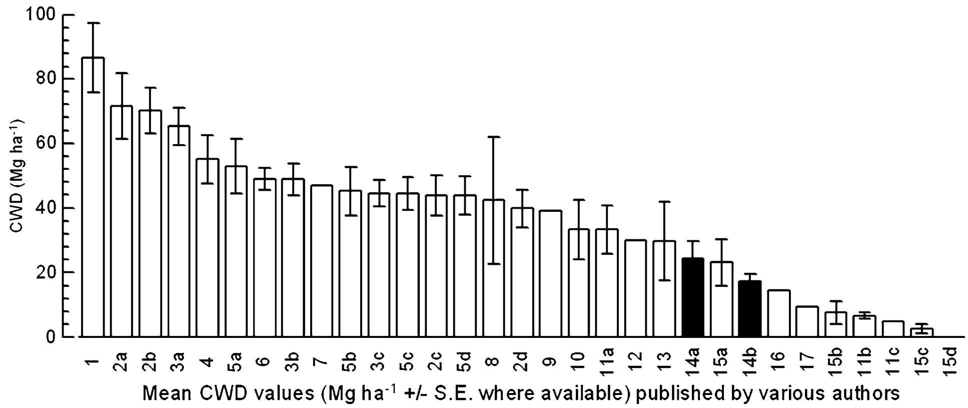

Fig. 1 Coarse woody debris (CWD, Mg ha^{-1}) ≥10 cm in diameter unless stated, in lowland (<1,000 m.a.m.s.l) tropical forests. Studies using both plot-based and line-intercept methods are included; forests affected by known major disturbances such as hurricanes or fires, secondary forests, and seasonally flooded forests are excluded. Data from: *1* Rice et al. (2004); *2* Gale (2000), ≥20 cm, estimated from empirical, cross-study relationship between CWD volume (m^3 ha^{-1}) and CWD mass (Mg ha^{-1}), Mass = (0.55 × Volume) –13.5: *a* Hoja Blanca, Ecuador, *b* Andalau, Borneo, *c* Belalong, Borneo, *d* Danum, Borneo; *3* Clark et al. (2002): *a* steep ultisol, *b* flat ultisol, *c* flat inceptisol; *4* Gerwing (2002); *5* Keller et al. (2004): *a* CUF2, Cauaxi, *b* TUF1, Tapajos, *c* TUF2, Tapajos, *d* CUF1, Cauaxi; *6* Yoneda et al. (1977); *7* Odum (1970); *8* Uhl and Kaufmann (1990), ≥7.6 cm; *9* Yoneda et al. (1990); *10* Harmon et al. (1995); *11* Delaney et al. (1998): Venezuela, ≥2.5 cm *a* moist forest, *b* dry–moist, *c* very dry; *12* Brown et al. (1995); *13* Summers (1998) cited in Chambers et al. (2000); *14* this study: *a* transect-based estimates, *b* plot-based estimates; *15* Kauffman et al. (1988): San Carlos, Venezuela, ≥7.6 cm *a* species-dominant terra firme forest, *b* species-rich terra firme forest, *c* caatinga forest, *d* bana forest; *16* Golley et al. (1975); *17* Martius and Bandeira (1998), ≥3 cm. Values reported in this study shown as *shaded bars*. Where available, *error bars* shown as ±1 SE

some of the highest reported values, in terra firme forests in eastern Amazonia (Fig. 1; Gerwing 2002; Rice et al. 2004). However, there have been no studies of CWD in lowland, western Amazonia, which covers a large region of approximately 1.3 million km^2 (based on national assessments of lowland Amazonian forest cover in Peru, Ecuador, Colombia, Bolivia and the Brazilian state of Acre; Food and Agriculture Organisation 2000). These forests are particularly interesting from a carbon-cycling perspective, as long-term plots indicate that these forests have much faster rates of tree turnover (Phillips et al. 2004), greater aboveground wood productivity (Malhi et al. 2004), lower stand-level wood density and lower aboveground biomass (Baker et al. 2004a) than forests in eastern and northern Amazonia. It remains unknown whether the higher tree turnover rates and different species composition influence CWD stocks in these highly dynamic systems.

Quantifying CWD stocks and fluxes is also a useful tool for understanding whether the forest has been substantially perturbed by a recent disturbance event (e.g. Yoneda et al. 1977; Rice et al. 2004). This issue has particular importance for assessing the causes of changes in the aboveground biomass in long-term forest plots and for understanding changes in the overall carbon balance of the stand (Körner 2003; Rice et al. 2004; Baker et al. 2004b). Over long timescales, depending on the magnitude of disturbance events and the CWD decomposition rate, changes in the CWD pool should be closely in balance with changes in the aboveground biomass. However, over shorter timescales, following significant disturbance events, the CWD pool generated by the disturbance event will decrease through decomposition, as the aboveground biomass of new and surviving trees increases as the forest recovers. Thus, carbon emissions from the CWD pool can temporarily offset carbon sequestration in the biomass of living trees (Wirth et al. 2002; Rice et al. 2004). Quantifying stocks and fluxes of CWD helps to inform us about the recent disturbance history of a site, and thus helps to assess whether repeated measurements of the aboveground biomass are likely to reflect changes in the total carbon stocks of the forest.

Using data from 11 long-term forest plots in southern Peru, we asked the following questions:

1. What are the CWD stocks in these southwestern Amazonian forests?
2. What is the rate of input of CWD from tree mortality and the turnover time of the CWD pool?
3. Are changes in the CWD pool likely to have offset observed increases in the living, aboveground biomass in these forests?

Materials and methods

Study sites

The study sites are located in old-growth, lowland rainforest (200–260 m.a.s.l.) near Puerto Maldonado in Madre de Dios in southern Peru (Fig. 2). This region has a sea-

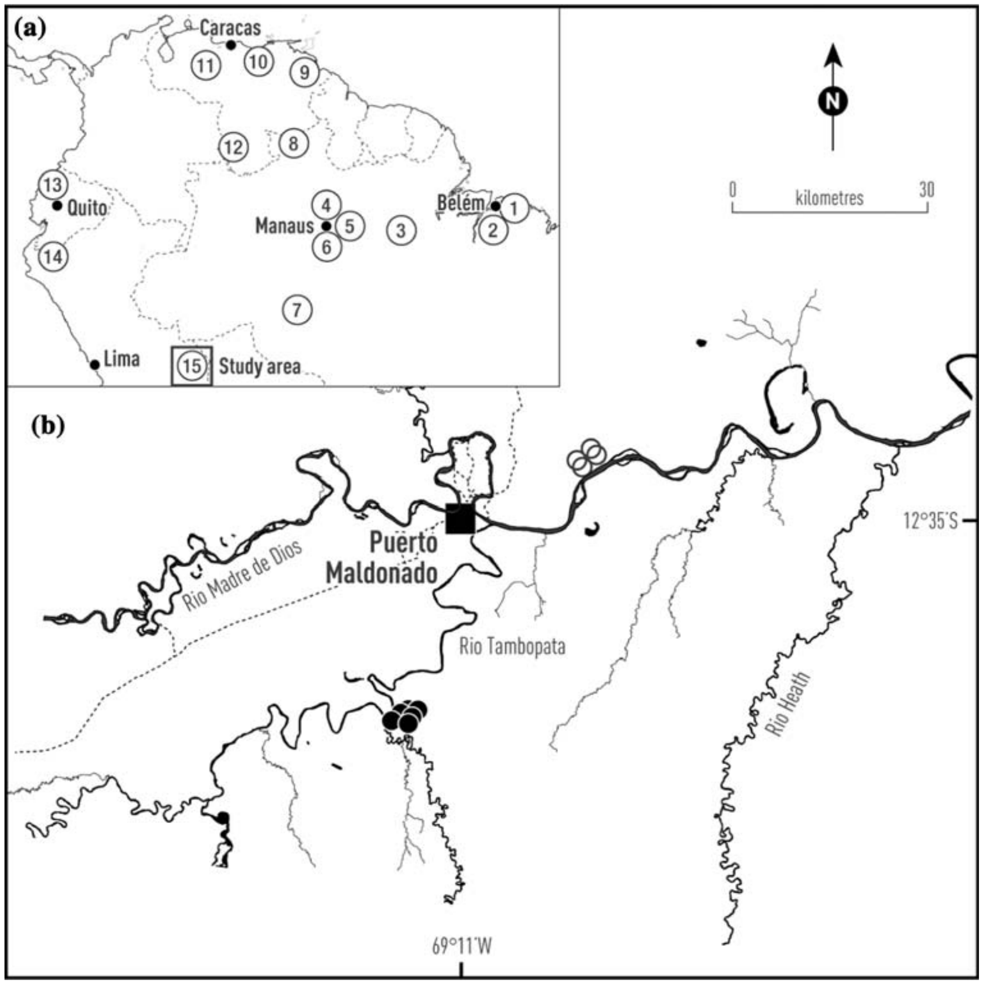

Fig. 2 **a** Locations of sites where coarse woody debris has been studied in South America. *1* Paragominas, Uhl and Kauffman (1990), *2* Cauaxi, Keller et al. (2004), *3* Tapajos, Rice et al. (2004), Keller et al. (2004), *4* BIONTE, Chambers et al. (2000), *5* Reserva Ducke, Martius and Bandeira (1998), *6* Marchantaria Island, Martius (1997), *7* Rondônia, Brown et al. (1995), *8* Maraca Island, Scott et al. (1992), *9* Rio Grande, Delaney et al. (1998), *10* Anzoátegui, Delaney et al. (1998), *11* Mérida, Delaney et al. (1998), *12* San Carlos de Rio Negro, Kauffman et al. (1988), *13* Hoja Blanca, Gale (2000), *14* Rio San Francisco, Wilcke et al. (2005), *15* This study, Madre de Dios, Peru. **b** Study sites in southwestern Peru. Seven plots at Explorer's Inn, Rio Tambopata (*filled circles*) and four 1-ha plots at Cusco Amazonico, Rio Madre de Dios (*open circles*)

sonal tropical climate (annual rainfall approximately 2,200 mm) with 3–4 months each year typically receiving less than 100 mm rainfall (Duellman and Koechlin 1991; Phillips et al. 2003). Mean annual temperature is approximately 25°C. The forest plots are found on ultisols on non-flooded Holocene or Pleistocene terraces (Phillips et al. 2003).

This study is based on 11 long-term plots on the Rio Tambopata (TAM 01–TAM 08) and Rio Madre de Dios (CUZ 01–CUZ 04; Fig. 2b; Table 1). These plots are either 100 × 100 m (Rio Tambopata, seven plots) or 20 × 500 m (Rio Madre de Dios, four plots) and have been monitored for up to 24 years (mean ± SE, 16.7 ± 3.5 years). The total area included in this study is 10.38 ha; part of one plot was excluded because it includes a swamp forest. At each census, stems ≥10 cm in diameter of all trees, including palms and lianas, have been measured. A complete inventory of CWD stocks was carried out within these plots during September and October 2003, and average CWD input rates per plot were calculated from tree mortality data for each 2–5 year census interval since plot establishment (1979–2001). In addition, during April–June 2006, CWD stocks were sampled using a line-intercept method around five of the plots at the Rio Tambopata site, to assess whether the CWD stocks in the plots were representative of the wider landscape, and to allow destructive sampling to calibrate the CWD decomposition classes at this site.

Plot-based CWD measurements

The 100% survey of CWD within the permanent plots included all portions of fallen and standing coarse woody debris ≥10 cm in diameter, within the plot boundaries. For all pieces of fallen CWD, the length and diameters at both ends were measured. For measurements at the bases of buttressed trunks, diameters were measured above the buttress. In cases where fallen pieces of dead wood were not approximately circular, the diameter was recorded at two perpendicular directions at the end of each piece, and the geometric mean used to calculate volume. Only one diameter was measured in the centre of fallen, dead palms, because palm stems maintain a similar shape and diameter along their length.

Table 1 Study plots at Rio Tambopata and Rio Madre de Dios, southern Peru

Code	Latitude (dec.)	Longitude (dec.)	Size (ha)	Initial census (dec.)	Final census (dec.)	CWD inputs (Mg ha^{-1} year^{-1})	
						Equation 1	Equation 2
CUZ-01	–12.50	–68.95	1.00	1989.39	2003.74	3.15 ± 0.31	2.54 ± 0.32
CUZ-02	–12.50	–68.95	1.00	1989.42	2003.75	3.34 ± 0.83	2.77 ± 0.95
CUZ-03	–12.49	–69.11	1.00	1989.40	2003.75	4.20 ± 0.43	3.19 ± 0.49
CUZ-04	–12.49	–69.11	1.00	1989.44	2003.76	5.21 ± 0.98	4.26 ± 1.19
TAM-01	–12.85	–69.28	1.00	1983.78	2003.68	4.55 ± 0.67	3.37 ± 0.85
TAM-02	–12.83	–69.28	1.00	1979.87	2003.68	3.57 ± 0.41	2.72 ± 0.50
TAM-04	–12.83	–69.28	0.42	1983.79	2003.71	3.52 ± 1.11	2.54 ± 1.52
TAM-05	–12.83	–69.28	1.00	1983.70	2003.70	4.01 ± 0.39	3.07 ± 0.46
TAM-06	–12.83	–69.30	0.96	1983.71	2003.68	2.75 ± 0.48	2.05 ± 0.62
TAM-07	–12.83	–69.27	1.00	1983.76	2003.72	4.44 ± 0.15	3.32 ± 0.23
TAM-08	–12.83	–69.27	1.00	2001.53	2003.72	3.03	2.27

Mean (±SE) CWD inputs per plot calculated using Eq. 1 from Chambers et al. (2000) and Baker et al. (2004a), and Eq. 2 from Chave et al. (2005), across all census periods

For standing dead trees the diameter at breast height or above any buttress was measured, the height estimated, and a taper function (Chambers et al. 2001) was used to estimate the upper diameter. The dimensions of persisting branches of these dead trees were also estimated.

In studies of CWD stocks, the state of decomposition is typically classified in the field into either three or five classes, based on simple characteristics of the dead wood. In this study, all pieces of CWD were initially classified in one of five decomposition classes:

Class 1: solid wood, recently fallen, with intact bark and fine branches still attached
Class 2: solid wood, but with no fine branches, and bark starting to fall off
Class 3: non-solid wood, in poorer condition, but where it was still difficult to push a nail into the wood by hand
Class 4: soft, rotten wood, where a nail could be pushed into the wood easily
Class 5: soft, rotten wood, which collapsed easily when stepped on

The volume of dead palm trees was calculated as a cylinder. For other pieces, CWD volume, V (m^3), was calculated using Smalian's formula as:

$$V = L\left[\frac{\pi(D_1/2)^2 + \pi(D_2/2)^2}{2}\right]$$

where L (m) is the length of the piece of CWD, and D is the diameter (m), at either end. Smalian's formula gives the correct volume if each piece of CWD is a frustum of a quadratic paraboloid or a cylinder. If the log tapers as a frustrum of a cone, then Smalian's formula will lead to an overestimate of volume, proportional to the length and degree of taper (Philip 1994). Thus, our volume results should be interpreted as maximum estimates.

Line-intercept-based CWD measurements

To complement the plot-based study, CWD was also sampled using the line-intercept technique (van Wagner 1968). From the corners of five of the permanent plots at the Rio Tambopata site, 100-m line transects were established, following the orientation of the plot boundary, but extending out into the surrounding forest. In total, 400 m of transect was sampled for each plot, and 2 km of line transect was established in total. For each plot, the line transects were orientated in two perpendicular directions, to avoid bias from non-random orientation of CWD. The diameter of all pieces of fallen CWD ≥10 cm in diameter that crossed the line were measured, and their decomposition class assessed using the categories above. As above, for non-circular pieces of CWD, diameter measurements were made at two perpendicular directions, and the geometric mean calculated.

Void space and calibration of decomposition classes

Void space and the density of the different decomposition classes was measured by taking cross-sectional pieces of a stratified random sample of 73 CWD pieces measured on the line transects. Void space, defined as a region enclosed by more than 180° of solid CWD, was measured by analysing digital photos of the cross-sections, following Keller et al. (2004). The proportion of the total area occupied by void space was calculated using ImageJ software (ImageJ 2006). Samples for density measurements were taken at 5-cm intervals from the centre of each chosen piece of CWD in one of four randomly chosen directions (top, bottom, left, right). The volume of these samples was calculated by direct measurement, or by sampling with a container of known volume in the case of very decomposed CWD. The samples were dried at 65°C, weighed, and density was calculated as dry mass divided by fresh volume. It was not possible to sample sufficient pieces of recently fallen CWD in decomposition class 1 to calibrate this decomposition class. Therefore, the mean living wood density of trees in these plots [Baker et al. (2004a)] was used as the density of pieces of CWD in decomposition class 1.

To estimate the mean mass of CWD, M (Mg ha^{-1}), in each decomposition class, n, external CWD volume (V, m^3) was multiplied by the mean proportion of solid wood space (S) and by the wood density values (ρ, g cm^{-3} ≡ Mg m^{-3}) of the different decomposition classes. Void space, wood density and volume measurements for each plot or transect were not correlated, so the standard error for M was calculated assuming independent random errors (Taylor 1997) as:

$$\mathrm{SE}(M)_n = (M)_n\left(\sqrt{\left(\frac{(\mathrm{SE}_V)_n}{V_n}\right)^2 + \left(\frac{(\mathrm{SE}_S)_n}{S_n}\right)^2 + \left(\frac{(\mathrm{SE}_\rho)_n}{\rho_n}\right)^2}\right)$$

The mean total mass of CWD was calculated by summing the mass of each decomposition class, and the standard error calculated conservatively as the sum of errors of the constituent classes (Taylor 1997).

Inputs of CWD from tree mortality

The study plots have been censused approximately every 2–5 years for the past 2–24 years, and we have comprehensive records of individual tree deaths. Inputs to the CWD pool for each census interval in each plot were calculated using allometric equations to estimate the aboveground biomass of trees that died during that interval, multiplied by 0.85 to account for the proportion of biomass in branches ≤10 cm in diameter (Higuchi unpublished data, cited in Chambers et al. 2000). Census intervals of less than 2 years were combined with subsequent intervals, to prevent short-term fluctuations in tree mortality rates unduly influencing the long-term trends (cf Phillips et al. 2004). To examine the sensitivity of the results to the allometric model used to estimate tree biomass, the aboveground biomass, AGB (Mg), of each tree that died during each census interval was estimated using two different equations:

$$\mathrm{AGB} = \left[\frac{\rho}{0.67}\exp\left(0.33[\ln D] + 0.933[\ln D]^2 - 0.122[\ln D]^3 - 0.37\right)\right]/1{,}000 \quad (1)$$

(Chambers et al. 2001; Baker et al. 2004a)

$$\mathrm{AGB} = 0.0509\left(\rho D^2 h\right)/1{,}000 \quad (2)$$

(Chave et al. 2005) where D (cm) is tree diameter, h (m) total tree height and ρ (g cm^{-3}) wood density. Equation (1) is based on a dataset of 315 trees harvested from six 20 × 20 m plots near Manaus, undertaken as part of the BIONTE project (Chambers et al. 2001) and corrected here for variation in wood density, following Baker et al. (2004a). Equation (2) is the general moist-forest equation including tree height derived from a pan-tropical compilation of tree biomass data (Chave et al. 2005). Wood density values were derived from a pan–Amazonian compilation (Baker et al. 2004a). Total height, h, was estimated from tree diameter using a log/linear relationship based on height measurements of a random sample of 400 trees from all 11 plots, stratified by tree diameter, made by TRB in September 2001:

$$h = 8.27(\ln D) - 8.85 : P < 0.005,\ r^2 = 0.66.$$

Turnover time of CWD

Assuming equilibrium conditions, the turnover time of the CWD pool in the plot-based study was calculated as the total mass of CWD, M, divided by the input rate, I. The standard error of the turnover time was estimated conservatively as the sum of the standard errors of M and I, respectively.

All errors terms are presented as ±1 SE.

Results

Volume and mass of CWD

In the plot-based study, the volume of all CWD across all plots, before correction for void space, was 44.1 ± 9.7 m^3 ha^{-1}, and the volume of fallen CWD was 33.5 ± 8.4 m^3 ha^{-1} (Table 2). The line-intercept study gave a higher value for fallen CWD, 62.3 ± 19.1 m^3 ha^{-1}, but this was not significantly different from the equivalent value from the plot-based study (t_{14} = 1.38, ns).

The proportion of cross-sectional area occupied by void space did not differ between decomposition classes, nor vary with piece diameter (proportion of void-space arcsine-

Table 2 Volume of CWD (m^3 ha^{-1}) measured in two different studies in southwest Amazonian forests

Decomposition class	Plot-based study (m^3 ha^{-1})						Line-intercept study (m^3 ha^{-1})	
	Total		Standing		Fallen		Fallen	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
1	3.33	1.12	0.59	0.21	2.74	1.08	1.50	1.35
2	5.96	1.24	1.18	0.69	4.78	0.99	5.10	2.91
3	11.58	2.48	2.76	0.78	8.82	2.01	32.75	7.17
4	10.77	1.43	3.20	0.84	7.57	1.34	15.39	4.70
5	12.42	3.39	2.85	1.03	9.57	2.99	7.52	3.01
Total	44.06	9.66	10.58	3.55	33.47	8.41	62.26	19.14

Values exclude correction for void space

transformed; decomposition class $F_{3,34} = 0.72$, ns, diameter $F_{1,34} = 0.87$, ns, decomposition class/diameter interaction $F_{3,34} = 0.98$, ns). Therefore, the mean proportion of solid area, 0.967 ± 0.015%, was used to adjust the values for external volume to total CWD volume, for all decomposition classes. Wood density varied significantly between decomposition classes 2–5, ($F_{3,65} = 4.3$, $P < 0.01$), principally due to higher wood density values for pieces of CWD in decomposition class 2 (Table 3). However, wood density did not vary with piece diameter ($F_{1,65} = 2.7$, ns).

As a result of these patterns, total CWD mass in the plot-based study was estimated as 17.7 ± 2.4 Mg ha^{-1}. The line-intercept study suggested a somewhat higher value for fallen CWD (24.4 ± 5.3 Mg ha^{-1}), but this was not significantly different from the value for fallen CWD from the plot-based study ($t_{14} = 1.91$, ns). Depending on the equation used to estimate biomass, the CWD estimate from the plot-based study represents 7.5% (Eq. 1) or 9.3% (Eq. 2) of the total biomass of all trees ≥10 cm in diameter in these plots.

Inputs to the CWD pool from tree mortality

Averaged across plots, inputs to the CWD pool from tree mortality were 3.80 ± 0.23 Mg ha^{-1} $year^{-1}$, using Eq. 1 or 2.92 ± 0.19 Mg ha^{-1} $year^{-1}$, using Eq. 2 (Table 1). Assuming that the CWD pool is at equilibrium, the turnover time is therefore 4.7 ± 2.6 or 6.1 ± 2.6 years, using inputs calculated using Eqs. 1 and 2, respectively.

Discussion

Compared to many other lowland tropical forests, CWD stocks are low in our sites (Fig. 1). In general, low CWD estimates may be the result of low rates of input or high rates of decomposition, or might simply reflect the methods that were used in a particular study. For example, one methodological difference between studies is whether they exclude or include standing dead trees; by definition, line-intersect sampling cannot be used to sample standing CWD, and in this site, standing dead trees comprised 24.3% of the total CWD in the plot-based study (Table 3). Also, plot size, or transect length, may influence whether the sampling adequately captures the full spatial variation in forest structure. Using the studies included in Fig. 1, but excluding those with nested sampling designs, both plot size ($n = 21$, $r^2 = 0.35$, $P < 0.01$) and transect length ($n = 14$, $r^2 = 0.43$, $P < 0.05$) are positively related to CWD stocks. This pattern suggests that small-scale studies may be preferentially located away from treefall gaps and show so-called majestic-forest bias (Condit 1997; Phillips and Sheil 1997), consistent with modelling studies suggesting that 10 ha is required to sample local variability in tree mortality adequately for measuring CWD stocks (Chambers et al. 2000). However, the total area (10.38 ha) or transect length (2 km), and the overall similarity in results between the two methods used in this study, suggests that the low total CWD in this study compared to other forests is not an effect of sample area.

Overall, the comparatively low stocks of CWD at these sites may be best explained by some aspect of carbon cycling in these forests—either low rates of CWD input, and/or high rates of CWD decomposition. Low rates of CWD input, for example, explain why CWD stocks are low in old-growth, lowland tropical forests growing on very nutrient-poor soils, or in very dry sites, where there are few trees ≥10 cm in diameter (Fig. 1, bana and caatinga vegetation, Kauffman et al. 1988; very dry forest, Delaney et al. 1998). However, low input rates do not appear to explain the low CWD stocks at these sites in southern Peru, as rates of CWD input are comparable with other sites where this term has been calculated. Averaged across plots, input rates are 3.80 ± 0.23 Mg ha^{-1} $year^{-1}$ (using Eq. 1) or 2.92 ± 0.19 Mg ha^{-1} $year^{-1}$ (using Eq. 2). In comparison, Rice et al. (2004) reported a CWD input rate of 4.8 Mg ha^{-1}

Table 3 Mass of CWD (Mg ha^{-1}) measured in two different studies in southwest Amazonian forests

Decomposition class	Density (g cm^{-3})		Plot-based study (Mg ha^{-1})						Line-intercept study (Mg ha^{-1})	
			Total		Standing		Fallen		Fallen	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
1	0.54	0.01	1.75	0.24	0.31	0.05	1.44	0.26	0.79	0.65
2	0.53	0.04	3.07	0.35	0.61	0.25	2.46	0.28	2.63	1.04
3	0.40	0.04	4.49	0.66	1.07	0.20	3.42	0.53	12.71	1.90
4	0.37	0.03	3.81	0.40	1.13	0.18	2.68	0.33	5.45	1.00
5	0.38	0.03	4.59	0.73	1.05	0.23	3.54	0.64	2.78	0.68
		Total	17.71	2.38	4.17	0.90	13.54	2.03	24.36	5.28

Values include correction factor for void space. Density for decomposition class 1 was estimated from mean plot-based values for living trees at this site (Baker et al. 2004a)

year^{-1} at Tapajós, Brazil, and Clark et al. (2002) measured a mean rate of 4.9 Mg ha^{-1} year^{-1} across three soil types at La Selva, Costa Rica. In addition, Chambers et al. (2000) reported a rate of 3.6 Mg ha^{-1} year^{-1} for forests near Manaus, Brazil. This limited variation in input rates contrasts with a fivefold variation in CWD stocks across these sites (Fig. 1).

If CWD input rates are comparable across sites, and CWD stocks are approximately at steady state, then variation in the quantity of CWD at different sites must be explained by variation in decomposition rates. Unfortunately, few studies have directly measured the decomposition rate of CWD in tropical forests, and existing studies vary widely in their approach, which complicates comparisons (Table 4). However, with the assumption that decomposition is exponential, these studies do give a possible range of decay constants for a variety of taxa, from decay-resistant (e.g. Odum 1970) to rather fast-decomposing species (e.g. Lang and Knight 1979). What range of decay constants are predicted by the observed variation in CWD stocks and inputs and are these reasonable in comparison with the published values?

The published decomposition rates, k (Table 4), give a range of plausible steady-state combinations of CWD stocks, M, and input rates, I, where $I = kM$ (Fig. 3). In general, measured CWD stocks tend to be higher than

Table 4 CWD decomposition rates measured in tropical forests

Country	Location	Forest type	Climate	Reference	Species (no.)	Study duration (years)	Decomposition rate, k		Method
							Mean	Range	
Panama	BCI	Lowland	Moist	Lang and Knight (1979)	9	10	0.46		Observation that trees ≥10 cm in diameter disappeared in 10 years
Brazil	Marchantaria Island	Lowland	Moist	Martius (1997)	11	1.7	0.34	0.049–1	Wood density decrease in boles
Malaysia	Pasoh	Lowland	Moist	Yoneda et al. (1977)	2	1.1	0.32	0.19, 0.44	Mass loss for 12-cm long, 1.5- to 6.5-cm branches and 4-cm thick, 7- to 10-cm discs
Mexico	NE Yucatan peninsula	Lowland	Dry	Harmon et al. (1995)	7	3–4	0.21	0.008–0.62	Wood density decrease in 1-m long, 15- to 30-cm diameter logs
Indonesia	Airsirah	Montane	Wet	Yoneda et al. (1990)	2	4.3	0.21	0.17, 0.25	Mass loss of 20-cm long, 4.4- to 11-cm diameter segments
Brazil	BDFFP	Lowland	Moist	Chambers et al. (2000)	All	>3	0.19	0.15–0.67	Mass loss for boles of known age
Puerto Rico	El Verde	Lowland	Moist	Odum (1970)	5	2	0.11	0.045–0.24	Mass loss of stump butts

Montane forests defined as >1,000 m.a.m.s.l, wet forests where rainfall ≥4,000 mm a^{-1}, moist forests, rainfall 1,200–4,000 mm a^{-1} and dry forests, rainfall <1,200 mm a^{-1}. Studies arranged in decreasing order of estimated mean decomposition rate

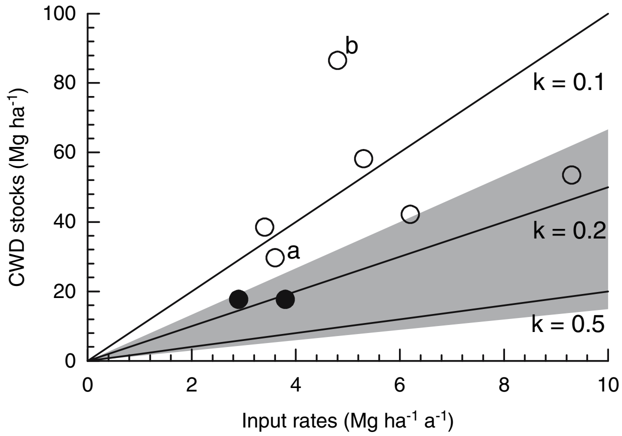

Fig. 3 Stocks (Mg ha^{-1}) and inputs (Mg ha^{-1} year^{-1}) of coarse woody debris ≥10 diameter (CWD) for a range of lowland, tropical forest sites. Values from this study (plot-based estimates of CWD stocks and CWD inputs estimated using two different allometric equations) shown as *filled circles*. Values from Manaus (*a* Chambers et al. 2000), and Tapajos (*b* Rice et al. 2004) also marked. Steady-state conditions resulting from three different decomposition rates, and assuming exponential decay, are indicated. *Shaded area* represents range of steady-state conditions for the range of decomposition rates reported by Chambers et al. (2000)

estimates calculated under steady-state conditions using the published measurements of decomposition rates. This pattern may be a result of using average values of *k* to predict community-level patterns; in contrast, an individual-based forest dynamics model, incorporating the measured range of decomposition rates for forests near Manaus, estimated CWD stocks that were approximately 50% higher than predictions based on the average community-level value for *k* (Chambers et al. 2000). Nevertheless, Fig. 3 provides a guide for interpreting observed variation in CWD stocks and inputs. For example, field measurements of CWD stocks and inputs for both Manaus and southern Peru are broadly consistent with steady-state conditions, if decomposition rates are higher in the western Amazon site—the estimated steady-state turnover time of the CWD pool is 8.2 years in Manaus, compared to 4.7–6.1 years in the plots in southern Peru. This difference in decomposition rates is plausible: wood density, which correlates negatively with decomposition rates and explains an important part of the species-level variation in decomposition rates found in tropical forests (Harmon et al. 1995; Martius 1997; Chambers et al. 2000; Mackensen et al. 2003), is 15% lower in western than eastern Amazon forests (Baker et al. 2004a). Also, the more fertile soils found in western Amazonia (Sombroek 2000) may lead to higher concentrations of nutrients in wood, which may increase rates of decomposition (Merrill and Cowling 1966; but see also Martius 1997), and, in particular, benefit saprotrophic fungi, which contribute most to the loss of carbon from CWD through respiration (Mackensen et al. 2003) and are known to be able to take up and translocate soil mineral nutrients to regions of active decomposition (e.g. Wells et al. 1990).

Variation in decomposition rates cannot, however, explain all the variation in CWD stocks and inputs in these studies. For example, the Tapajos site falls well outside steady-state conditions given known variation in CWD decomposition rates (Fig. 3). This pattern is consistent with the suggestion that this site is recovering from a recent period of high mortality, prior to plot establishment (Rice et al. 2004). Identifying that the CWD pool at this site is not at equilibrium has important implications for interpreting changes in the living, aboveground biomass: Rice et al. (2004) found that losses of carbon from the decomposition of the large CWD pool (Table 1) counteracted increases in the aboveground biomass of living trees. By contrast, the low total stocks of CWD we find in southern Peru show that these plots have not suffered any recent catastrophic disturbance. This suggests that the carbon sequestration caused by net gains in the aboveground biomass of living trees over decadal timescales in these plots (Phillips et al. 1998; Baker et al. 2004b) has not been offset by net losses of carbon to the atmosphere from CWD.

In conclusion, the CWD dynamics described in this study, taken together with the greater rates of tree turnover (Phillips et al. 2004), wood productivity (Malhi et al. 2004), and lower aboveground biomass (Baker et al. 2004a) emphasise the distinctive, rapid nature of carbon cycling at these sites in southern Peru. However, important uncertainties remain. Notably, this is the first such study from western Amazonia, so clearly more research into CWD dynamics across the region is required. In particular, studies of CWD stocks and inputs are needed at more long-term sites to obtain a better understanding of the impacts of disturbances on the carbon balance of Amazonian forests. Direct measurements of decomposition rates and experimental studies of the controls of decomposition and the fate of its products would further improve our understanding of carbon cycling within these forests. These studies could focus on forests growing on different soil types in climatically similar regions, to test whether edaphic conditions are a key driver of the observed patterns.

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