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Stocks and flows of coarse woody debris across a tropical rain forest nutrient and topography gradient

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Abstract

Large pieces of standing or fallen dead wood, known as coarse woody debris (CWD), play important roles in temperate forest carbon and nutrient cycles, and affect the abundance and distribution of many classes of organisms. CWD biomass and inputs are poorly documented in tropical rain forests (TRF), and the causes for their variation at landscape-scales in this biome have not been studied. We quantified standing and fallen CWD stocks and inputs in upland (non-swamp) old-growth TRF at the La Selva Biological Station, Costa Rica. We used a network of 18 0.5 ha plots sited in three edaphic conditions to analyze soil nutrient effects on CWD stocks and inputs controlling for topography, and to examine topographic effects controlling for soil nutrients. The edaphic conditions were flat inceptisols, flat ultisols, and steep ultisols. Chemical analyses confirmed the existence of an almost three-fold gradient in total P and K in the upper 1 m of soil. We also annually censused all live woody stems $\geq$10 cm diameter above buttresses in each plot in September/October from 1997 to 2000 to obtain data on stand structure and dynamics.

Fallen CWD stocks averaged 46.3 Mg ha^{-1} (22.3 Mg C ha^{-1}), while standing CWD averaged 6.5 Mg ha^{-1} (3.1 Mg C ha^{-1}). There were no significant differences in volume or mass of standing or fallen CWD among edaphic conditions. Annual inputs of CWD averaged 4.9 Mg ha^{-1} (2.4 Mg C ha^{-1}). Turnover time of fallen CWD was ca. 9 year. Neither stocks nor inputs were correlated with stand structure (number of trees per plot, plot basal area, or plot estimated above-ground biomass). Potential differences in CWD stocks and inputs among sites with different edaphic conditions may have been obscured by a 10-fold variation in tree mortality among plots and a two-fold variation in mean CWD input among years. Analysis of sample variance showed that stocks of CWD were adequately sampled with the 18 0.5 ha plot design, but that inputs were measured with low precision.

At La Selva fallen and standing CWD stocks together equaled ca. 33% of estimated above-ground live woody biomass. Tropical rain forest CWD and its associated carbon are intermediate in pool size and turnover rate between fine litter and live trees. Our results show that scaling up TRF CWD estimates to larger spatial scales may be more constrained by the quality of data obtained over single landscapes than by variation due to zonal soil nutrient and topographic conditions. Both the

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magnitude and vagility of TRF CWD pools are likely to change with global climate change, but the overall direction of change is uncertain.

Keywords: Coarse woody debris; Tropical rain forests; La Selva; Costa Rica; CWD turnover; Carbon stocks; Carbon fluxes

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1. Introduction

Large pieces of standing or fallen dead wood, termed coarse woody debris (CWD), play important ecological roles in forest systems. Depending on the forest type, stage of succession, land-use history and management practices, the pool of CWD may contain significant portions of a given forest's carbon and nutrient stocks. McGee et al. (1999) and Spetich et al. (1999) reviewed several dozen studies showing the importance of CWD in temperate forests for a range of plant and animal groups, including amphibians, reptiles, birds, mammals, arthropods, vascular plants, bryophytes, lichens and fungi. In addition, CWD has strong physical and biological effects on freshwater ecosystems (Harmon et al., 1985). The biomass, rates of production, and ecological roles of large pieces of dead wood have been extensively studied in temperate forests. More than a decade ago, Harmon et al. (1985) reviewed more than 500 papers on CWD ecology in temperate forests, and hundreds of articles have been published subsequently. In contrast, data on CWD stocks and inputs in lowland tropical rain forests (TRF) are limited (Yoneda et al., 1977, 1990; Raich, 1983; Kauffman et al., 1988; Uhl et al., 1988; Uhl and Kauffman, 1990; Foster Brown et al., 1995; Delaney et al., 1998; Chambers et al., 2000, 2001; Gale, 2000), and studies on the biological effects of tropical CWD are rare (cf. Gibbs et al., 1993).

Tropical landscapes play a key role in the global carbon cycle due to the large amounts of carbon currently stored there (Dixon et al., 1994) and to high rates of land-use change. CWD is potentially a significant component of the stocks and fluxes of tropical forest carbon cycles in terms of magnitude and vagility. However, there are currently insufficient data from tropical forests to evaluate the factors that control CWD total stocks, annual inputs and rates of turnover. Another issue that has not been addressed is how to scale up estimates from small plots to larger landscapes.

In this research, our goal was to assess the magnitude of CWD stocks and inputs across an upland old-growth TRF landscape. We asked if within-landscape variation in soil nutrients, topography and various metrics of stand structure and function influenced the magnitude of CWD stocks and inputs. This study was conducted within a larger project analyzing the factors that control carbon stocks and fluxes in old-growth lowland TRF (the Carbono Project). The experimental design was conceived specifically to enable comparisons between areas of similar topography, but widely differing soil nutrients, and between areas with similar soil nutrients, but contrasting topography. We thus had a priori planned comparisons for soil nutrient effects controlling for topography, and for topographic effects controlling for soil nutrients.

Our questions were:

1. What are the stocks of CWD under different soil nutrient and topographic conditions in this old-growth tropical wet forest?
2. What are the rates of CWD input, and what factors control these rates?
3. Are CWD stocks and inputs related to stand structure and dynamics?
4. How precise were the estimates we obtained for stocks and rates of input of CWD, and what does this tell us about sampling strategies and scaling up?
5. What is the current role of CWD in TRF carbon and nutrient cycling, and how might this change with on-going global climate change?

2. Methods

2.1. Study site

The study site was the La Selva Biological Station in Costa Rica. La Selva is classified as tropical wet forest in the Holdridge system (Hartshorn and Peralta, 1988), and averages ca. 4000 mm annual rainfall and

26 °C (Sanford et al., 1994). Our study area is all upland (non-swamp) old-growth. We used a network of 18 0.5 ha plots (the Carbono Project) that were sited to sample three edaphic conditions in an unbiased fashion: flat inceptisol (old alluvial) terraces, flat ultisol ridgetops, and steep ultisol slopes. Details of plot siting, stand structure and a map are given in Clark and Clark (2000).

2.2. *Documentation of soil and slope conditions among different edaphic conditions*

To document nutrient conditions among edaphic site types we sampled soil nutrients to 1 m depth in all plots. Soil analyses were based on six composited samples per plot for the inceptisol and ultisol plateaus, and on 18 composited samples from the ultisol slope plots (six each from upslope, midslope, and downslope positions). Sample depths were 0–10, 10–30, 30–50, and 50–100 cm. The pH was determined by a glass electrode. Exchangeable cations were extracted by slowly leaching 2.5 g of air-dried soil with 100 ml of 1 M NH_4Cl (Meiwes et al., 1984). Concentrations of Na, K, Ca, Mg, Mn and Al (determinations of exchangeable cations) were measured by atomic absorption spectroscopy. Concentrations of N and C (soil organic C) were determined by a C/N analyzer (Heraeus vario EL). Bulk density of the soil was determined with the core method (Blake and Hartge, 1986), using 3×10^{-4} m^3 stainless steel cores to 0.07 m depth. Nutrient contents were converted to area basis using bulk density data and thickness of layer.

To document slope conditions, we measured slope angle (±0.5°) at 55 standard locations in each plot using a clinometer and sighting between two vertical 1.5 m tall staffs.

2.3. *Estimation of CWD stocks*

2.3.1. *Standing CWD*

We annually measured stem diameter (±1 mm) at breast height or above buttresses, and assessed mortality for all trees, palms, and lianas $\geq$10 cm diameter in all 18 plots. Data from the September/October 1997–2000 censuses were used here (the Carbono Project is on-going). We also measured annually the diameter of all standing dead stems, and in 1999 and 2000 their height, using a 15 m telescoping rod or a laser rangefinder (Laser Technology), measuring to the highest point. Volume of standing CWD (dead stems >130 cm tall and $\geq$10 cm diameter) was calculated as the frustum of a cone, using the measured diameter as the basal diameter and the upper diameter calculated from the formula (Chambers et al., 2000):

$$d_h = 1.59 \times D \times (h^{-0.091})$$

where d_h is the calculated diameter at measured height h. Biomass was calculated from volume using the factor 0.453 Mg m^{-3}, and converted to C at 48.3% and N at 0.30% (see Section 3 and Tables 2 and 3).

2.3.2. *Fallen CWD*

In a pilot study to determine how much fallen CWD could be sampled given available resources, we mapped every piece of CWD with a minimum diameter of 10 cm in one 0.5 ha plot (A2). We measured the length plus three diameters of each piece of CWD, then sketched it in pencil on waterproof paper maps. A large tree calipers was used for diameter measurements (±1 cm). For pieces that crossed the plot boundaries, only the section within the plot was measured. For sections that decreased in diameter to <10 cm, only the section $\geq$10 cm diameter was measured. The volume of each piece was calculated using Newton's formula (Harmon and Sexton, 1996), minus the volume of externally visible hollow sections, calculated as cones using $V = \pi r^2(h/3)$, where V is the cone volume, h the height of cone and r the radius of the base. There were 174 pieces of CWD in the plot. Pieces with a maximum diameter $\geq$30 cm ($N = 32$) accounted for 78.2% of the total volume. Based on that value and available resources, we decided to map all pieces of fallen CWD of this size in all 18 plots.

To determine how many of the pieces of fallen CWD between 10 and 30 cm diameter could be measured, we calculated the total volume of CWD of this size for each of the 10 0.05 ha subplots in the pilot 0.5 ha plot. We calculated (Zar, 1996, 3rd Edition, p. 108) the number of 0.05 ha subplots necessary to measure the average mass of the 10–30 cm diameter component of CWD to within differing precisions with 95% confidence. For estimates within ±50% of the mean, 11 subplots would have been required (note that there are only 10 such subplots per 0.5 ha plot).

Given that the 10–30 cm diameter CWD was found to be only ca. 20% of the volume, we decided to map this size class in three 0.05 ha subplots in each CARBONO plot. The three 0.05 ha plots were selected to span the 0.5 ha plot (the same 0.05 ha plots were used in all 0.5 ha plots).

All pieces were classified in one of three decomposition categories.

2.3.2.1. Sound. More than 75% of the volume intact and/or hard. This could be a recently fallen bole or branch, or could be a piece that had weathered until only the hard heart was left (a common situation with the dominant tree species *Pentaclethra macroloba* (Mimosaceae)).

2.3.2.2. Fully decomposed. More than 75% of the wood soft and rotten, a machete blade entered easily, collapsed when stepped on.

2.3.2.3. Partially decomposed. Intermediate between sound and fully decomposed.

To sample for density, a further subsampling of the mapped pieces was necessary for strictly logistic reasons. We assumed that within-log density variance would increase with log length. Given the available resources, we decided to sample logs at the rate of one sample per 4 m length. Thus, for logs $\leq$4 m long we extracted one sample, >4–8 m two samples, >8–12 m three samples, etc. The location of each sample was determined by eye to divide the log into equal-length sections. We sampled for density in this way all CWD pieces >50 cm diameter, 50% of all pieces 30–50 cm diameter, and 33.3% of pieces 10–30 cm diameter. For the 30–50 cm pieces, we selected every other piece as they appeared in order on the datasheet; for the 10–30 cm pieces, we took every third piece. Samples were cut with a chain-saw into wedge-shaped sections from the exterior to the center of each piece. In the field, some logs were measured as two or more sections. These are written down as consecutive lines in the datasheets; each of these sections was considered a separate piece of CWD. The decomposition category of each piece was not considered in this selection.

Density of each piece was determined using volumetric displacement of water by the fresh wood sample and its oven-dry mass. To measure volumetric displacement of water, we used 8 l pails with a right-angle 1.5 in. PVC tube as the water exit. A bucket was considered "stable" when it dripped one drop every $\geq$5 s. The time elapsed between cutting the piece in the field and determining its volume averaged around 2–3 months (with a maximum of ca. 5 months). During the period between cutting and volume measurement, each wood piece was kept under shade-cloth and sprinkled with a hose daily to minimize drying and shrinkage.

After volume determination the pieces were oven dried at 80 °C. Because of oven space constraints, pieces were frequently air-dried under a clear plastic roof for several weeks before oven space was available. Oven-dried pieces were weighed ($\pm$0.1 g) until they varied $\pm(\leq 0.2\%)$ between weighings. This typically took 7 to 20 days total oven time.

Seven samples from each of the three decomposition classes were haphazardly selected for analysis of C and N. Samples were finely ground and a subsample was taken for C and N analyses. Concentrations of N and C were determined by a C/N analyzer (Heraeus vario EL).

To determine annual input of CWD, from 1998 to 2000, we mapped and measured all pieces of fallen CWD $\geq$30 cm diameter that appeared on the ground in that year, using the techniques described above. We measured all new CWD 10–30 cm diameter in one 0.05 ha subplot in each 0.5 ha plot, thus sampling (+1 S.E.) 10% of the area for this size class.

3. Results

3.1. Variation in soil nutrient stocks and slope conditions

Soil analyses confirmed the existence of strong soil nutrient differences among sites on the three contrasting edaphic types; P and K stocks varied almost three-fold among plots. Compared to the flat ultisol plots, the inceptisol plots had significantly larger stores of P and K in the first meter of soil, as well as lower C/N ratios (Table 1). Between plots on ultisol slopes and ultisol flats, the flat plots had significantly higher stocks of C and N, but the C/N ratio did not differ, nor did stocks of P, K, Ca, and Mg.

Mean slope angles (55 measurements per plot) among edaphic types were: 0.8°, flat inceptisol plots

Table 1

Mean carbon and nutrient stocks (+1 S.E.) to 1 m depth in 18 0.5 ha plots at the La Selva Biological Station, Costa Rica[a]

Edaphic condition	C (Mg ha^{-1})	N (Mg ha^{-1})	C/N	P (Mg ha^{-1})	K (kg ha^{-1})	Ca (kg ha^{-1})	Mg (kg ha^{-1})	Fe (kg ha^{-1})	Mn (kg ha^{-1})	Al (kg ha^{-1})
Inceptisol flats	191.1 +/− 11.6 a	17.8 +/− 0.7	10.7 +/− 0.3 a	9.0 +/− 0.9 a	375.3 +/− 49.1 a	408.4 +/− 74.9	116.1 +/− 13.2	43.2 +/− 17.7	362.8 +/− 136.8	3600.7 +/− 363.2
Ultisol flats	224.2 +/− 4.7 b,x	18.8 +/− 0.4 x	12.0 +/− 0.1 b	5.0 +/− 0.4 b	226.3 +/− 14.4 b	296.1 +/− 19.2	156.6 +/− 11.0	83.1 +/− 13.0	81.0 +/− 16.3	3405.8 +/− 101.1 x
Ultisol slopes	184.6 +/− 13.6 y	15.8 +/− 1.0 y	11.6 +/− 0.2	6.7 +/− 0.8	222.9 +/− 12.8	291.4 +/− 19.3	158.7 +/− 14.1	59.5 +/− 13.1	144.1 +/− 44.8	2904.6 +/− 98.9 y

[a] Stocks were compared between plots on the same topography, but different soil types (flat inceptisol versus flat ultisol), and within soil type between topographic classes (ultisol flats versus ultisol slopes). Means with different letters (a, b, x, y) differ at $P < 0.05$; a and b represent comparisons between soil types, x and y comparisons between topographic classes within one soil type. $N = 6$ 0.5 ha plots per edaphic condition (see Section 2).

Table 2
Mean densities (+1 S.E.) of CWD pieces in three decomposition categories (see Section 2)[a]

Decomposition category	Density (g cm^{-3})			
	Mean	Median	Range	N
Sound	0.453 +/− 0.003 a	0.454	0.080–1.374	1366
Partially decomposed	0.349 +/− 0.007 b	0.353	0.096–0.655	291
Fully decomposed	0.245 +/− 0.011 c	0.222	0.044–0.646	116
Total sample	0.422 +/− 0.003	0.439	0.044–1.374	1773

[a] Different letters (a, b, c) indicate groups with significantly different medians in an a posteriori test (overall Kruskal–Wallis ANOVA $P < 0.001$).

(range 0.0–2.3°); 2.2°, ultisol ridgetops (0.2–5.7°); and 20.9°, ultisol slopes (17.8–26.2°).

These results validate the basic experimental design. Comparisons of flat ultisols with flat inceptisols contrast areas with soils of differing fertility, but similar topography, while comparisons of flat ultisols to ultisol slopes contrast areas with similar nutrient stocks, but different topography.

3.2. Fallen CWD density and decomposition classes

Density of fallen CWD pieces varied significantly among decomposition classes (Table 2). Pieces classified as sound averaged 85% denser than fully decomposed pieces; partially decomposed pieces were intermediate. Between soil types, CWD density was slightly higher on the more fertile sites (0.423 versus 0.400 g cm^{-3}); between the ultisol flats and slopes, densities were higher on the slopes (0.436 versus 0.400 g cm^{-3}; Mann–Whitney $P_{2\text{-tailed}} < 0.01$ in both cases). The distribution of decomposition classes also varied significantly between slopes and flats in the ultisols (Chi-square $P < 0.04$), due to less partially decomposed samples than expected on the slopes and more on the flats. There was no difference in frequency of decomposition classes between the flat sites on the two soil types.

Mean CWD carbon concentrations decreased and nitrogen concentrations increased along the decomposition sequence (Table 3). As a consequence, mean C/N ratios declined from 170.5 in sound CWD samples to 119.3 in fully decomposed pieces. However, sample sizes were small and the variation considerable, and only the decrease in carbon concentration was statistically significant (Kruskal–Wallis ANOVA $P < 0.004$).

3.3. CWD stocks

Fallen CWD averaged 46 Mg ha^{-1}, distributed in 469 pieces with a total volume of 109 m^3 (Table 4). The area covered on the ground, estimated as the square of the cube root of CWD volume, was 22.8 m^2 ha^{-1}, comparable to the basal area of living trees (23.6 m^2 ha^{-1}, Clark and Clark, 2000). Fallen CWD biomass, volume and number of pieces did not differ significantly between flat ultisols and inceptisols, or between ultisol flats and slopes. However, all three variables were considerably higher on the ultisol slope plots than on the flat ultisols and inceptisols, suggesting that differences might be detectable with larger sample size.

Table 3
Mean chemical composition (+1 S.E.) of coarse woody debris in different decomposition classes from old-growth tropical wet forest, La Selva Biological Station, Costa Rica[a]

Decomposition class	Density (g cm^{-3})	% C	% N	C/N ratio
Sound	0.501 +/− 0.026	48.3 +/− 0.3	0.299 +/− 0.029	170.5 +/− 15.6
Partially decomposed	0.238 +/− 0.050	47.2 +/− 0.3	0.318 +/− 0.033	155.7 +/− 12.6
Fully decomposed	0.198 +/− 0.035	46.4 +/− 0.4	0.462 +/− 0.071	119.3 +/− 21.6

[a] $N = 7$ samples per decomposition class.

Table 4
Mean stocks (+1 S.E.) of fallen coarse woody debris (CWD) in old-growth tropical rain forest at the La Selva Biological Station, Costa Rica[a]

Edaphic condition	Biomass (Mg ha^{-1})	Volume (m^3 ha^{-1})	N pieces CWD ha^{-1}
Flat inceptisol	38.5 +/− 3.4	91.1 +/− 8.6	438 +/− 15
Flat ultisol	42.2 +/− 4.9	99.3 +/− 11.3	459 +/− 25
Steep ultisol	58.2 +/− 5.6	135.6 +/− 12.6	508 +/− 65
All 18 plots	46.3 +/− 3.3	108.6 +/− 7.6	469 +/− 23

[a] Data for each edaphic condition are from six 0.5 ha plots (see Section 2), and are extrapolated to a per-hectare basis.

C and N contents for each section of fallen CWD were calculated using the mean concentrations of these elements for each decomposition class (Table 3). The decomposition-class-weighted mass percentages of CWD stocks for C and N were 48.16 and 0.304%, leading to stock estimates of 22.3 Mg C ha^{-1} and 141 Kg N ha^{-1}.

Standing CWD averaged about 22 stems per ha with a total volume of 14.5 m^3 and total mass of 6.5 Mg (Table 5). This represents 3.1 Mg C ha^{-1} and 20 kg N ha^{-1}. There were no significant differences in number of standing dead stems, their total volume, or their total basal area among sites on different edaphic types (Kruskal–Wallis ANOVA $P > 0.05$ in all cases).

3.4. CWD inputs and turnover

Annual inputs of fallen CWD were highly variable among plots as well as between soil types and years (Table 6). The number of pieces of CWD and their total volume and mass were higher in 1998 than in 1999 and 2000 (Kruskal–Wallis $P = 0.006, 0.08, 0.08$, respectively). There was no significant difference in average annual input of fallen CWD from 1998 to 2000 between topographic classes with the ultisols or between flat ultisol and inceptisol sites. However, the CWD input volume and mass comparisons between the flat sites were $P < 0.07$, suggesting that significant differences may emerge with longer-term data. The C and N percentages by decomposition classes (Table 3) were used to calculate the decomposition-class-adjusted C and N annual inputs in CWD. CWD inputs averaged 48.2% carbon and 0.300% N, leading to annual inputs of 2.4 Mg C ha^{-1} per year and 14.8 kg N ha^{-1} per year. Inputs had about half the percentage of mass in partially and fully decomposed wood as the CWD stocks (5.6 versus 10.8%).

The ratio of mean fallen CWD stocks to mean annual inputs over this 3-year period (46.3 Mg ha^{-1}/4.9 Mg ha^{-1} per year) implies a turnover time of approximately 9 year for the fallen CWD pool, assuming long-term equilibrium of stocks and inputs. We estimated turnover of the standing CWD pool using the ratio of the total basal area of standing CWD in a year compared to the amount of this total that fell in the subsequent year. The average turnover time for standing CWD, based on the three inventories from 1997 to 2000, was 8.0 ± 1.1 S.E. year.

Table 5
Mean characteristics (±1 S.E.) of standing dead coarse woody debris in old-growth forest on different edaphic conditions at the La Selva Biological Station, Costa Rica[a]

Edaphic condition	Number ha^{-1}	Basal area (m^2 ha^{-1})	Volume (m^3 ha^{-1})	Mass (Mg ha^{-1})
Flat inceptisols	17.7 +/− 2.4	1.2 +/− 0.3	13.3 +/− 4.8	6.0 +/− 2.2
Flat ultisols	24.2 +/− 3.4	1.7 +/− 0.3	14.6 +/− 2.7	6.6 +/− 1.2
Steep ultisols	24.8 +/− 3.1	1.7 +/− 0.2	15.6 +/− 3.3	7.0 +/− 1.5
Mean	22.2 +/− 1.8	1.5 +/− 0.2	14.5 +/− 2.0	6.5 +/− 0.9

[a] Data are averages of the 1999 and 2000 inventories for six 0.5 ha plots per edaphic condition, extrapolated to a per-hectare basis. Standing CWD was considered all dead woody stems ≥ 10 cm diameter and >130 cm tall; stumps (≤ 130 cm tall) were considered as fallen CWD.

Table 6
Annual input of CWD in old-growth tropical rain forest at the La Selva Biological Station, Costa Rica[a]

Edaphic condition	N CWD pieces (# ha^{-1} per year)	Mean volume (m^3 ha^{-1} per year)	Mean dry mass (Mg ha^{-1} per year)
Flat inceptisols	70 +/− 20	7.5 +/− 2.3	3.4 +/− 1.1
Flat ultisols	71 +/− 7	13.9 +/− 1.2	6.2 +/− 0.5
Steep ultisols	58 +/− 9	11.8 +/− 3.8	5.3 +/− 1.7
Mean	66 +/− 7	11.1 +/− 1.6	4.9 +/− 0.7

[a] Areas sampled per plot were 0.05 ha for CWD 10 to ≤30 cm maximum diameter and 0.5 ha for CWD ≥30 cm diameter. $N = 6$ plots for each edaphic condition. Data are expressed as the mean (±1 S.E.) of measurements in 1998, 1999 and 2000, extrapolated to a per-hectare basis.

We calculated an independent estimate of CWD input using the estimated biomasses of trees dying and falling to the ground, as well as an estimate of the input from standing dead trees falling during this interval. Biomass of trees that died and fell was estimated from their last live diameter using Brown's (1997) tropical wet forest allometric equation. This method overestimates potential CWD biomass because it predicts whole tree biomass, including leaves as well as trunks and branches <10 cm diameter, which are not CWD as defined here. Average estimated annual CWD input from live trees that died and fell to the ground over the 3-year period was 3.1 Mg ha^{-1} per year ±0.9 (1 S.E.). Average input from standing CWD was calculated as the mean estimated biomass of standing CWD in 1999 and 2000 divided by the mean basal area turnover time from 1997 to 2000 (6.54 Mg ha^{-1}/8.02 year $= 0.82$ Mg ha^{-1} per year). The resulting estimate of CWD input ($3.1 + 0.8 = 3.9$ Mg ha^{-1}per year) not statistically distinguishable from the measured input of 4.9 ± 0.7 (1 S.E.) Mg ha^{-1} per year.

3.5. Relation of CWD stocks and inputs to forest structure and stand dynamics

Mean mass of CWD inputs over the period 1997–2000 was significantly correlated with stand dynamics in each plot, expressed as the summed basal area of trees falling during that period ($r_s = 0.54$, d.f. $= 17$, $P < 0.03$). In contrast, there was no relation between stocks or inputs of CWD in plots and measures of plot stand structure. Among the 18 plots, neither fallen CWD volume, mass, number of pieces, nor mean rates of annual CWD input were significantly correlated with number of trees per stand, their basal area, or their estimated above-ground biomass in 1997 (Spearman's r_s, $P > 0.05$ in all cases).

4. Discussion

4.1. Landscape-scale factors affecting CWD stocks and inputs

CWD stocks and inputs were largely independent of the substantial differences in soil nutrients and topographic conditions sampled across this upland TRF landscape. This contrasts with the results of Gale (2000), who found significant differences in CWD stocks in relation to topographic position in Bornean and Ecuadorian forests. We had a priori expected more differences in CWD among edaphic conditions in this study, given the wide range of site conditions sampled. For example, total soil phosphorus in the upper 1 m varied 268% among plots, total K varied 297%, and mean slope angle varied from 0 to 26°. Stand structure varied considerably as well, with significantly more and smaller stems on the ultisols than on the inceptisols (Clark and Clark, 2000). Stem number, basal area, and estimated above-ground biomass varied by factors of 173, 168, and 185%, respectively among plots in 1997.

There are at least three potential explanations for the general lack of relation of CWD stocks and input to edaphic conditions and to stand structure. It is possible that no landscape-scale differences in CWD stocks and inputs actually exist. Although stem number and mean tree size varied significantly among the three edaphic conditions, mean estimated above-ground biomass did not (Clark and Clark, 2000). However, even given the very substantial sampling effort in this study, the uncertainly in our estimates of CWD stocks and inputs was still high. Our sample was sufficient to reliably detect differences of ±20% in fallen CWD stocks among edaphic conditions (see below). For CWD inputs, however, the variability was much higher, and we could easily have failed to detect real differences of ±20% among edaphic conditions.

Another reason for the general lack of explanatory power of the edaphic and stand structure variables is that the highly variable nature of tree mortality had much greater and immediate effects on CWD distribution. Tree mortality varied 10-fold among plots during the study period and CWD inputs varied considerably more, thus emphasizing the need for long-term studies. There was also significant interannual variability in CWD input, presumably related to climatic factors, that may have contributed to masking any edaphic influences. Annual rainfall was not outside of normal bounds in 1997/1998 (El Niño), 1998/1999 (La Niña), or 1999/2000 measurement year (OTS unpublished records). However, the mean minimum 1997/1998 temperature was the warmest in the 18-year record. Overall, 1997/1998 CWD mass input was over twice as high as in 1998–2000, tree mortality was 31% higher and mean estimated above-ground biomass increase was lower in all 18 plots in 1997/1998 than in either 1998/1999 or 1999/2000. These levels of variation could swamp even substantial differences among edaphic types over the spatial and temporal scales of this study.

4.2. Evaluating CWD at landscape-scales and prospects for scaling up

Table 7 shows the sample sizes necessary to estimate fallen CWD characteristics based on the landscape-scale degree of variation encountered at La Selva. The standard error of the mean of the estimated stocks was relatively low (Table 4), and the Carbono plot system had sufficient replicates to have a probability of >95% of measuring the landscape mean fallen CWD biomass within ±20%. Annual CWD input was considerably more variable, however, and even 18 0.5 ha annual samples averaged over a 3-year period were not sufficient for a very precise estimate. This was undoubtedly due to the spatially patchy nature of tree mortality over this 3-year interval; mortality of stems $\geq$10 cm diameter ranged from 0.8 to 8.2% per year among the 18 plots. Our data suggest that, for studies lasting one to several years, a very large sampling effort would be needed to precisely estimate CWD inputs over upland landscapes of old-growth tropical forest.

An alternative approach to measuring CWD inputs is to calculate them based on estimated above-ground biomass (EAGB) of trees falling during a given interval (cf. Chambers et al., 2000). The biomass of trees initially present as standing deads and falling during the interval must also be included. This is an indirect approach, as it relies on allometric equations for living and standing dead trees to estimate biomass, and there is no direct validation of the EAGB. Here we found that the annual input estimate derived from EAGB of falling live and standing dead trees (3.9 Mg ha^{-1} per year) was within the 95% confidence interval of the estimate derived by ground measurements of CWD inputs (4.9 ± 0.7 Mg ha^{-1} per year). Our CWD input data were developed using a total of 9 ha sampled annually for 3 year, requiring approximately 120 total person-days of field work. This level of effort was not sufficient to produce very precise estimates, but it was sufficient to show the general magnitude of CWD input, and to show that it was similar to the estimates based on falling (live + previously standing dead) trees. For long-term studies, and to be able to compare many sites, it will usually be necessary to calculate CWD inputs from tree death. Our results suggest that the effect of not accounting for standing dead trees may be significant for short-term studies, but negligible for decadal and longer studies in TRF. If precise estimates of annual CWD input are required, our results indicate that a major sampling effort will be necessary.

In contrast to CWD stocks and inputs, the mean density of fallen CWD could be estimated with relatively few samples. With as few as 35 samples taken randomly from all CWD pieces over the landscape, there was a 95% probability of estimating the true mean density within ±10% (Table 7). If, however, wood density estimates within each decomposition class are required, more samples are necessary, because the more advanced decomposition classes have more variable densities.

Our results suggest that, for upland TRF landscapes, scaling up CWD estimates to larger spatial scales is

Table 7
Sample sizes needed to estimate stocks and fluxes of CWD within 10 and 20% with a 95% probability in old-growth tropical wet forest at the La Selva Biological Station, Costa Rica[a]

Variable and units	Sample description	Mean	s^2	*N* samples for ±10%	*N* samples for ±20%
Fallen CWD (Mg ha^{-1})	18 0.5 ha plots, complete sampling for CWD >30 cm maximum diameter, subsampling for CWD <30 cm diameter (see Section 2)	46.3	196.1	38	12
Falling CWD input (Mg ha^{-1} per year)	18 0.5 ha plots, complete sampling for CWD >30 cm maximum diameter, subsampling for CWD <30 cm diameter (see Section 2); annual measurements averaged over 3 years	4.9	9.2	148	39
Fallen CWD density, sound samples (g cm^{-3})	Randomly sampled for all CWD over 18 0.5 ha plots, $N = 1366$	0.453	1.04E−02	23	8
Fallen CWD density, partially decomposed samples (g cm^{-3})	Randomly sampled for all CWD over 18 0.5 ha plots, $N = 291$	0.349	1.43E−02	48	14
Fallen CWD density, fully decomposed samples (g cm^{-3})	Randomly sampled for all CWD over 18 0.5 ha plots, $N = 116$	0.245	1.48E−02	98	26
Fallen CWD density samples, all decomposition class mixed (g cm^{-3})	Randomly sampled for all CWD over 18 0.5 ha plots, $N = 1773$	0.422	1.50E−02	35	11

[a] Calculations follow Zar (1996, p. 108). The 18 0.5 ha plots are blocked in a stratified random design to provide an unbiased estimate of the upland landscape at La Selva (see Section 2).

more likely to be limited by within-site measurement variation than by major effects of nutrients and topography on CWD stocks. We emphasize that we did not study azonal soils such as white sands, and that our slopes were both relatively mild and short (ca. 21° over ca. 50 m). However, this degree of variation in soil nutrients and slope is typical of large areas of the tropics (cf. Duivenvoorden, 1995; Laurance et al., 1999).

4.3. The role of CWD in tropical rain forest carbon cycles

Our results from La Selva are in broad agreement with those from similar studies in other tropical rain forests in showing that CWD forms a significant fraction of above-ground biomass (cf. Yoneda et al., 1977, 1990; Vogt et al., 1986; Kauffman et al., 1988, 1995; Delaney et al., 1998; Chambers et al., 2000, 2001; Clark and Clark, 2000; Gale, 2000). Fallen and standing CWD at La Selva represented ca. 33% of the above-ground biomass of live trees $\geq$10 cm diameter (present study; Clark and Clark, 2000). This is a substantial amount of biomass that is often unmeasured in forest carbon inventory studies. Our results are also consistent with findings from previous studies (Yoneda et al., 1990; Delaney et al., 1998; Chambers et al., 2000) in showing that the CWD pool is more labile than the live wood pool. At La Selva, the mean turnover rate of estimated above-ground live tree biomass from 1997 to 2000 was 28.5 year (an average of 155.8 Mg ha^{-1} in live trees, of which a mean of 5.5 Mg ha^{-1} per year died), compared to the fallen CWD turnover rate of ca. 9 years.

The relation of CWD to above-ground carbon fluxes and pool sizes in old-growth TRF can be summarized as follows:

Carbon stock: Live tree biomass $>$ fallen CWD $>$ standing CWD $>$ fine litter.

Annual inputs to forest floor: Fine litter $>$ CWD $\cong$ (live trees dying and falling $+$ standing dead falling).

Turnover time: Fine litter $<$ standing CWD $\approx$ fallen CWD $<$ live tree biomass.

The magnitude of the CWD pool will vary as a function of the relationship between inputs and outputs. CWD input rates (rates of crown and major branch fall and tree mortality rates) at landscape-scales may be increasing in tropical forests, due to the effects of forest fragmentation (Ferreira and Laurance, 1997; Laurance et al., 1997), rising global temperatures, and increasing fire frequency (Cochrane et al., 1999; Nepstad et al., 1999). Output rates (CWD decomposition) are controlled by temperature, humidity and substrate quality (Harmon et al., 1985) and fire frequency. Global climate change is already affecting temperature and possibly precipitation patterns in many areas. In addition, understory temperature and humidity in TRF have changed over large areas due to forest fragmentation and increased fire frequency (Kapos, 1989). The net result of these changes in CWD inputs and decomposition rates is not possible to predict. However, it seems likely that CWD pools are likely to change in magnitude and vagility under many plausible climate and land-use change scenarios.

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