Soil-induced impacts on forest structure drive coarse woody debris stocks across central Amazonia

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Abstract

Background: Coarse woody debris (CWD) is an essential component in tropical forest ecosystems and its quantity varies widely with forest types.

Aims: Relationships among CWD, soil, forest structure, and other environmental factors were analysed to understand the drivers of variation in CWD in forests on different soil types across central Amazonia.

Methods: To estimate CWD stocks and density of dead wood debris, 75 permanent forest plots of 0.5 ha in size were assessed along a transect that spanned ca. 700 km in undisturbed forests from north of the Rio Negro to south of the Rio Amazonas. Soil physical properties were evaluated by digging 2-m-deep pits and by taking auger samples.

Results: Soil physical properties were the best predictors of CWD stocks; 37% of its variation was explained by effective soil depth. CWD stocks had a two-fold variation across a gradient of physical soil constraints (i.e. effective soil depth, anoxia and soil structure). Average biomass per tree was related to physical soil constraints, which, in turn, had a strong relationship with local CWD stocks.

Conclusions: Soil physical properties appear to control average biomass per tree (and through this affect forest structure and dynamics), which, in turn,-is correlated with CWD production and stocks.

Key words: Anoxia, effective soil depth, carbon, forest dynamics, line intercept sampling, soil physical properties, topographic index, tropical forest, vegetation structure, necromass.

Introduction

The interaction between different carbon stocks and flows constitute the carbon cycle. Of the different stocks, above-ground biomass is most often assessed in tropical forests, however coarse woody debris (CWD) is also an essential component because of its role in biogeochemical cycles (Chambers et al. 2000; Clark et al. 2002; Wilcke et al. 2005; Palace et al. 2008). Within tropical forests, CWD accounts for 6 to 25% of total above-ground carbon stocks (Nascimento and Laurance 2002; Rice et al. 2004; Baker et al. 2007; Palace et al. 2012), implying a total pan-Amazon CWD carbon stock of ca. 10 Pg (Chao et al. 2009a). The variation in CWD stocks across the Amazon Basin is thought to be modulated by environmental factors, such as hydrology and soils, and by forest biomass itself (Rice et al. 2004; Baker et al. 2007; Chao et al. 2009).

Amazonia holds a great diversity of tree species (ter Steege et al. 2000), and its forests vary substantially in both vegetation dynamics (Phillips et al. 2004; Quesada et al. 2012), and structure (Baker et al. 2004; Malhi et al. 2006; Nogueira et al. 2008; Feldpausch et al. 2011). Our current understanding suggests that CWD stocks generally decrease from north-eastern to south-western Amazonia (Baker et al. 2007; Chao et al. 2009a). Spatial variation in CWD stocks across the landscape may respond both to short-term climatic disturbances (e.g. Phillips et al. 2009; Negrón-Juárez et al. 2010) and to long-term differences in forest dynamics in response to environmental characteristics (Keller et al. 2004; Malhi et al. 2006; Chao et al. 2009a). Soils represent an important environmental gradient in Amazonia, with a wide variety of soil types across the Basin and with diverse chemical and physical conditions (Quesada et al. 2010; 2011). Variations in soil physical properties across the Basin have been related to a large proportion of the variation in tree turnover rates and mean forest wood density, with disturbance levels and vegetation structure of Amazonian forests being related to different soil types (Quesada et al. 2012).

Very few studies have tried to understand landscape-scale drivers of CWD stocks. Kissing and Powers (2010), working in secondary forests in Costa Rica, showed strong positive correlations between stand age and the amount of CWD. Chao et al. (2009a) working in mature forests in Amazonia showed that there was a relationship between forest structure and CWD, in particular with regard to biomass, wood density of living trees and mass of individual dead stems. Although these studies successfully associated CWD stocks with forest structure and dynamics, to our knowledge there has been no analysis of a potential effect of edaphic properties on CWD stocks. Since edaphic factors, such as effective soil depth and structure are important factors controling forest structure and dynamics (Quesada et al. 2012; Jirka et al. 2007), they are likely to be related to both the production and the stocks of CWD. We hypothesise that because poor soil physical conditions impose constraints on tree growth and survival, they result in increased stem turnover rates, and, in turn, limit the maximum size that trees can attain. This way smaller trees yield smaller CWD stocks. Therefore, we may expect landscape-scale variation in soils to be linked to variation in CWD stocks. The forests south of the Rio Amazonas represent a vast, but poorly studied region in central Amazonia, both in terms of vegetation and soil. Broadly, this region (Figure 1) is characterised by hydromophic soils (RADAMBRASIL 1978; Sombroek 2000) of poor physical structure (Quesada et al. 2011), in contrast to soils north of Manaus which are dominated by well-drained deep soils. This region is also expected to have large variation in above-ground biomass (AGB) (IBGE 1997). Central Amazonia, therefore, represents an ideal testing ground for exploring edaphic and vegetation linkages with CWD stocks.

We examined stocks of CWD in function of variables related to biomass and stem density, and soil properties across central Amazonia in order to understand the factors that modulate the variation of these stocks. Specifically, we tested the hypothesis that CWD stocks were larger in soils with no physical constraints and smaller in soils with increased physical constraints.

Materials and methods

Study sites

Fieldwork was conducted across a ca. 700-km-long transect (Figure 1) in central Amazonia over a 1-year period (2010–2011). Data were collected in permanent plots of 0.5 ha, located north and south of the Rio Amazonas in the State of Amazonas, Brazil. There were two sites north of the Amazonas river, the Adolfo Ducke Forest Reserve (hereafter Ducke Reserve – 18 plots), and the Biological Dynamics of Forest Fragments Project site (BDFFP – 12 plots). The southern sites were located in the Purus – Madeira interfluvial zone on a ca. 600 km transect established along the Manaus – Porto Velho road (BR-319 – 45 plots).

The Ducke Reserve has 10,000 ha of mature *terra firme* tropical moist forest and is situated at the periphery of the city of Manaus (02° 95’ S, 59° 95’ W). The topography is undulating with alternating plateaux and rivulet valleys. The vegetation has a 30 to 37 m tall closed canopy, with emergent trees reaching 45 m (Ribeiro et al. 1999). Mean annual precipitation is 2524 mm (Coordenação de Pesquisas em Clima e Recursos Hídricos, INPA, unpublished data). In general, soils are deep, well-drained, and have low bulk density. Ferralsols and Acrisols are found along the slopes and plateaux, which are highly weathered and have favourable physical conditions (i.e. stable aggregate structure, associated with good drainage) (Chauvel et al. 1987; Quesada et al. 2010). Near streams and valley bottoms, wet and sandy soils (Podzols) occur, but these were not included in this study. A total of 18 plots were sampled on Acrisols and Ferralsols for CWD and soils. Plots were at least 1 km apart and were 250 m long and 20 m wide (0.5 ha), following the topographic contour (Magnusson et al. 2005).

The BDFFP study site is located 80 km north of Manaus (2º 30´ S, 60º 00’ W). Data were collected in mature *terra firme* tropical moist forest, at least 1000 m away from fragment edges in forest fragments > 500 ha (Laurance et al. 1998). The forest canopy was 30 to 37 m tall, with emergent trees reaching up to 55 m. Annual mean precipitation ranged from 1900 to 3500 mm (Nascimento and Laurance 2002). CWD and soil were sampled in twelve 0.5 ha plots (positioned independently of topographic features, Laurance et al. 1998) over Ferralsols and Acrisols.

The plots located south of the Rio Amazonas were spaced along the BR-319 road on the interfluvial area between the Purus and Madeira rivers. Plots located closer to Manaus had closed lowland evergreen forest vegetation (IBGE 1997), while plots located closer to Porto Velho had a more open type lowland evergreen forest. This entire region is characterised by a flat topography with elevations varying between 30 and 50 m (a.s.l.) over large distances. Mean annual precipitation in this area varies from 2155 to 2624 mm (WorldClim; Hijmans et al. 2005). The soils are predominantly Plinthosols and Gleysols (Sombroek 2000), generally having varying degrees of soil water saturation and anoxic conditions. Soil physical structure is generally restrictive to root growth, with very high bulk density in the subsoil, and thus these soils have varying degrees of hardness and effective soil depth. Subsoil layers that limit root penetration are frequent and vary from 30 to 100 cm in depth (RADAMBRASIL 1978; Sombroek 2000). In all sites, we sampled a total of 45 plots deployed in nine site clusters, the clusters being at distances between 40 and 60 km apart (Figure 1). Each site cluster was composed of a 5-km-long transect with five plots of 250 m x 20 m in size, at intervals of 1 km; following the topographic contour.

Coarse woody debris (CWD) stocks

Field sampling of dead wood was made by (1) line intersect (van Wagner 1968) for fallen dead wood and (2) belt transects for standing dead trees (Palace et al. 2007; Chao et al. 2008). For line intersect sampling, every piece of fallen dead woody material (trees, palms, lianas) with a diameter ≥10 cm that crossed the transect line was measured and classified into one of three decay classes, following Chao et al. (2008): (1) recently fallen, solid wood, sometimes presenting minor degradation; (2) sound wood but already showing some sign of decay, such as the absence of bark; (3) heavily decayed wood. In partly buried material, two perpendicular measures were taken and their mean was recorded as diameter. In plots that followed the topographic contour, the central line of the 250-m long plot was used as the intersect line. In square plots, the intersect line was also 250 m length but followed the plot perimeter. Each 250-m transect was considered as an independent individual sample of CWD. To reduce biased estimation arising from multiple crossing of CWD pieces and endpoint partial intersection (Affleck et al. 2005), we counted only once each piece of CWD (e.g. Gregoire and Valentine 2003). Pieces at the endpoint of an intersect line were included only if at least 50% of them was touched by the transect line. As these plots along the contour did not run in a straight line and sometimes doubled up and ran at an acute angle, we took provisions to avoid multiple crossing sampling bias. We discounted areas where the same piece of dead wood crossed the same transect line more than once. To compensate for lost plot area caused by multiple crossing, an identical area was added to the plot to keep the total sampling area at 0.5 ha. As we assumed that the orientation of pieces of dead wood on the forest floor was random we did not see advantage in using one line intersect design over another (see Bell et al. 1996).

The belt transects for estimating standing dead trees and broken snags were 20 m wide along the 250 m transect line. Standing dead stems with a diameter > 10 cm were measured at along the 250 m transect line. Standing dead stems with a diameter ≥ 10 cm were measured at 1.3 m height or at the lowest part of the snag trying to avoid buttress roots when possible. If the snag was shorter than 1.3 m, the measurement was taken at the highest point possible. The height of snags taller than 2 m was measured with a digital hypsometer (Vertex Laser VL400 Ultrasonic-Laser Hypsometer III, Haglöf Sweden) to the point where the diameter was 10 cm. The length and diameter (≥ 10 cm) of attached branches in standing dead trees were visually estimated. To account for wood density variation following decay, standing dead trees and their occasional branches were also classified in the same way as wood for the line intersects.

CWD wood density

Samples of dead wood (n=726) that crossed the line intersect in the plots were collected for measuring the density of CWD (dry weight per unit volume). A chain-saw was used to cut a disk sample from hard pieces. Softer wood pieces were sampled by using a bush knife. The disks were sub-sampled randomly. Void spaces were taken into account for volume estimation by visually estimating their proportion (Keller et al. 2004), but were not used for density correction which may have caused an overestimation of up to 10% in some decay classes (Keller et al. 2004; Chao et al. 2008).

CWD density was determined as the ratio of oven dry mass and fresh wood volume. The water-displacement method was used to determine fresh volume (Chave 2005). Before measuring, the volume segments of samples in classes 1 and 2 were pre-wetted for about 2 h to fill pores with water, because dry wood absorbs more water and leads to overestimating density values. As material in decay class 3 was very friable, samples in this class were saturated with water for several minutes. After volume measurement the segment samples were oven dried at 60 ºC until constant mass (Keller et al. 2004). The density of each sample segment was then calculated and used to average the density of each decay class at each site.

Vegetation

Vegetation parameters (basal area, density of trees and palms, above-ground biomass and wood density of live individuals) were acquired from a database of the permanent vegetation plots. As tree height data were unavailable for the permanent sample plots, an allometric model presented in Feldpausch et al. (2012) to estimate tree height (H) was applied to reduce bias in biomass estimates.

where D is the tree diameter at breast height.

To estimate plot-level dry above-ground biomass (AGB) we used the allometric model developed by Feldpausch et al. (2012). The variables included in this model were tree diameter at breast height (D), wood density (ρ_T) and height (H) for tree T.

To account only for stocks of biomass that related to branches ≥ 10 cm diameter we reduced the estimated AGB values of each tree by 15% (N. Higuchi unpublished data cited in Chambers et al. 2000.).

Wood density of living trees was obtained from a database (Chave et al. 2009; Zanne et al. 2009). The individuals in each plot were matched to wood density at species level. In cases where this information was unavailable, matches were made by genus average or family (as in Baker et al. 2004). When species information for a tree was missing, the mean density of known trees, weighted by basal area of the plot was used. Species level identifications were made for 53.7% of stems, with an additional 37.9% identified to genus, 6.2% to family and 2.2% unidentified. At the BR-319 transect plots (south from the Rio Amazonas), there were no floristic data available. For those plots an average living wood density was estimated for each plot by sampling wood cores in at least 20 trees per plot, (trees ≥30 cm diameter only, with a total of 1,005 trees sampled in the region by J. Schietti, unpublished data).

Soil data

Soil sampling followed a standard protocol (http://www.geog.leeds.ac.uk/projects/rainfor/pages/manualstodownload.html); for a full description see Quesada et al. (2010). We used the World Reference Bases for soil resources to classify soil types (IUSS Working group, WRB 2006). Three soil pits were dug at the Ducke Reserve, and three at the BDFFP site; one soil pit was dug in six out of nine site clusters along the BR-319. To increase spatial coverage of soil properties, auger sampling was carried out in plots without soil pits at all sites. All pits were 2 m in depth, even if the effective soil depth was shallower. Effective soil depth is defined here as the depth where clear impeding layers to root growth occur. Soil was sampled from the pit walls to estimate bulk density, using specially designed container-rings of known volume in the following depths: 0-10, 10-20, 20-30, 30-50, 50-100, 100-150, 150-200 cm.

Topography and soil properties that could limit root growth were assessed semi-quantitatively (Table 1; Quesada et al. 2010). The score for each category was then summed to form a general index of soil physical quality (Π): Π_1 was formed by the sum of scores for effective soil depth, soil structure quality, topography and indicators of anoxia. Π_2 equalled Π_1 less anoxia. These semi-quantitative scores were used in statistical analyses. Soil fertility was similar across the entire study area (RADAMBRASIL 1978).

Additional environmental data

Mean annual precipitation and precipitation in the driest quarter were obtained from the WorldClim global database at 30 arc-seconds (ca. 1 km) resolution (Hijmans et al. 2005).

The topography data were obtained using a Digital Elevation Model (DEM) at 90-m spatial resolution from Shuttle Radar Topography Mission (SRTM). A topographic index (TI) that estimates drainage of each SRTM pixel (Moore et al. 1991) was calculated using ArcMap:

where α is the contributing upslope drainage area and β is the slope.

Sites with higher TI values have greater drainage constrains (e.g. water saturated). This topographic feature may be important as there is a relationship between TI and tree species distribution (Feldpausch et al. 2006) that could be related to CWD distribution across the landscape.

Calculations

Volume of line intersect sampling (V_{LIS}) (m^3 ha^{-1}) and fallen volume in each decay class was estimated using the following equation (van Wagner 1968):

d_{i} is the diameter (cm) of each CWD segment $_i$ and L (m) is the length of the transect line.

For the estimation of standing dead volume (V_{Belt}, m^3 ha^{-1}), Smalian's formula was used:

where H (m) is the height of the tree, D_1 and D_2 are the diameters (cm) at 1.3 m above the ground and at the top of the snag, respectively. To estimate D_2 a taper function was used (Chambers et al. 2000):

where D_2 is the diameter at height H for a trunk of given D_1. This is an equation defined for central Amazonian trees and often used in other studies (Clark et al. 2002; Palace et al. 2007). CWD (Mg ha^{-1}) in each of the three decay classes was calculated as follows:

where V (m^3 ha^{-1}) and ρ (Mg m^{-3}) correspond respectively to volume and density in decay class *i*.

To calculate error for each CWD_i (E_{CWD}) the following equation was used:

$$\mathrm{E_{CWD}} = \mathrm{V\,E\rho + \rho\,E_V} \qquad (8)$$

where E_ρ and E_V are the errors in density and volume, respectively. Equation (8) is valid when *V* and density of the material in the respective class are not correlated (Keller et al. 2004). In this study covariance between *V* and density although significant (P=0.0175) was very small (r^2_{adj}=0.01965). To estimate total error in mass in each decay class we used a conservative approach by summing the errors of each component.

Statistical analysis

For the statistical analysis, plots were divided into three groups: (1) no physical restriction (NR, index Π_1 value $\leq$2); (2) low levels of soil physical restriction (LRL, index Π_1 value between 2 and 6 and Anoxia value $\leq$1); and (3) high restriction levels (HRL, index Π_1 value $\geq$6 and Anoxia value >1. Physically restricted soils (LRL and HRL) occurred in the interfluvial region, but not north of Manaus.

Each plot was considered as a sample unit in linear regressions (*n*=75). Correlations were used to choose which non-collinear variables could be combined in the same regression model. In an attempt to better understand landscape-scale CWD patterns, CWD relationships with environmental, climatic and edaphic variables were explored by using mixed models (nlme package in R) with a random intercept, as the study had a hierarchical design. Therefore, the BDFFP, the Ducke Reserve, and each of the nine site clusters along the BR-319 were all considered as groups, within which the individual plots were nested. CWD values were transformed, using natural logarithm (ln) to improve normality. To understand the variance explained by the models, we used a method suggested by Nakagawa and Shielzeth (2013) for obtaining a marginal R^2 ($R^2_{(m)}$) which describes the proportion of variance explained by the fixed factor and conditional R^2 ($R^2_{(c)}$) that describes the proportion of variance explained by both the fixed and random factors. To compare mean wood density of decay classes in each forest type we also used mixed models. All analyses were carried out in R version 3.0.0 (R Development Core Team 2013)

Results

Variations in edaphic properties

Sites located north of the Amazonas river had no physical soil restriction (Figure 3a). All of these soils were deep, had low subsoil bulk density (Table 2), had good particle aggregation (good structure, friable) and were well drained (Table 2). Conversely, soils in the southern plots (BR-319) were generally shallow (maximum effective soil depth varying from 20 to 100 cm), with high subsoil bulk density (Table 2), little or no aggregation (deficient structure, very hard and compact), thus being generally root-restrictive, and had varying levels of anoxic conditions (from seasonally flooded with patches of stagnating water to soils showing redox features, such as mottling) (Table 2). Some site clusters were severely constrained (Π_1 values ranging from 6 to 11) while other plots/site clusters had lower Π_1 values, ranging from 2 to 6. All soils along the BR-319 had poorer physical conditions when compared to the predominantly Ferralsols/Acrisols at plots north of the Amazonas river.

Stocks of CWD

The volume of CWD varied significantly among soil groups (i.e. NR, LRL and HRL) and decay classes (Table 3). The volume of total CWD in forests growing on NR soils (69.5±11.1 $m^3\ ha^{-1}$) was similar to that on LRL soil (69.5±11.6 $m^3\ ha^{-1}$). In contrast, forests on HRL had significantly less CWD (33.8 ±2.0 $m^3\ ha^{-1}$) than forests on the other two soil groups.

Densities of CWD samples were significantly different among decay classes, decreasing considerably with degree of decomposition (Table 3). Nevertheless, there was no significant difference among soil groups that grew on soils with different levels of soil physical constraints (decay class, P<0.001; soil groups, P=0.76)

CWD stocks varied in a predictable way across our study area (Figure 1), and also varied considerably at the site cluster level, with the northern sites showing the largest variation. For instance, CWD ranged from 6.7 to 72.9 Mg ha^{-1} among the plots of the Ducke Reserve. In comparison, CWD stocks varied little and were consistently lower at site clusters 1 to 5 along the BR-319 road (just south of Manaus), and also at site cluster 11, located at the far south end of the BR-319 road. Along the middle (site clusters 6 to 10), CWD was locally highly variable.

Total CWD stocks followed the same pattern as total CWD volume, which is expected as CWD stock estimate is a function of site-specific CWD density values and the density of decay classes did not vary significantly among soil groups (Table 3). Forests in NR soil had a mean CWD stock of 33.1±7.1 Mg ha^{-1} (Table 5) and these values did not differ significantly from LRL soils. However, CWD stocks for HRL soils were significantly and substantially lower than in both other soil types (soil groups, $P<0.001$; decay class, $P<0.001$).

Standing and fallen fractions of CWD

Significant differences in fallen CWD were found among all soil groups ($P<0.001$) (Table 4). Mean stocks of standing CWD represented 20 to30% of the total CWD in the study area and this fraction did not differ significantly among soil groups ($P=0.08$) with NR showing higher stocks than HRL. Fallen dead wood CWD stocks were significantly highest in LRL, intermediate in NR forests and lowest in HRL (Table 4). The proportion of fallen stocks to total CWD did not differ among soil groups. Also, the ratio of standing to fallen dead wood was not different among soil groups. The CWD to AGB ratio on the NR soils (0.13±0.01) and LRL (0.17±0.01) was significantly greater than on HRL soil (0.08±0.01) ($P<0.001$).

Vegetation

Each of the three soil groups was associated with a distinct forest structure (Table 5). Above-ground biomass was highest at the NR forests and lowest at HRL, and with the AGB at LRL sites not being significantly different from HRL. Stem density was significantly higher in HRL than in either NR or LRL (Variables associated with individual tree size were usually significantly different among soil groups. For instance, the average biomass per tree, was significantly different among soil groups (NR>LRL>HRL; Table 5). Mean tree height (estimated from DBH) was also significantly different among the three soil groups (Table 5); mean DBH was significantly lower in HRL soil than in NR and LRL (Table 5).

Determinants of CWD across landscape

CWD was significantly related to average biomass per tree, the only significant forest structure parameter directly related to CWD ($r^2_m=0.09$, $r^2_m=0.31$, Figure 3j). This shows that trees in HRL soil are generally smaller and store individually less biomass than in LRL and NR soils, with LRL showing an intermediary behaviour. Considering further the relationship between CWD stocks and parameters related to average maximum tree size (mean tree diameter, estimated height and AGB per tree, Figure 3), we observed a clear separation among the different soil groups, with forests consistently showing lower CWD on HRL where trees were smaller, and high CWD in NR where trees were larger. Forests on LRL consistently appeared as an intermediary group, with some superposition on NR, but with a clear separation from HRL, despite these two groups occurring in the same geographical area (HRL and LRL only occur along the BR-319 interfluvial area). Since plot level variation in vegetation biomass stocks could potentially influence CWD whereby larger AGB stocks may produce larger CWD stocks, we repeated our analyses after normalising data, using a CWD to above-ground biomass ratio (CWD:AGB, Table 6). This resulted in stem density and wood specific gravity becoming significantly related to CWD.

The presence and magnitude of soil physical constraints varied greatly across the study area and were generally negatively related to CWD (Figures 3a- 3e; Table 6). Individual soil parameters were significantly related to CWD, with effective soil depth and anoxia being the best correlated variable (Table 6). Topography, including the continuous topographic index (TI, a proxy for hydrological gradients) had no significant relationship with CWD due to the characteristics of the study sites discussed above.

Π_1, which represents the combination of all physical parameters, was strongly related to CWD (Table 6). This varied from score 0 (very good physical conditions) to 11 (high level of root growth restriction, Figure 3a) with the soils having high levels of physical constraints (Π_1>6) showing much lower values of CWD. The index Π_2 showed a similar trend to Π_1 (Figure 3b, Table 6). The only difference between Π_1 and Π_2 was the absence of anoxia in Π_2.

Edaphic drivers of CWD stocks could be obscured by varying vegetation biomass stocks, whereby larger AGB stocks produce larger CWD stocks. We therefore, carried out similar analyses by normalising data using a CWD:above ground biomass ratio (CWD:AGB, Table 6). Soil physical constraints were highly significant with the CWD:AGB ratio. The relationship between CWD:AGB and stem density and wood specific gravity was also statistically significant. We found no significant relationship between CWD and climatic variables (mean annual precipitation and precipitation in the driest quarter of the year, Table 6).

Discussion

Large-scale patterns in central Amazonia

CWD is a substantial fraction of forest carbon stocks. We found that by adding CWD stocks to above-ground biomass pool total above-ground wood mass stocks in forests in NR, LRL and HRL soils increased by ca. 13%, 17% and 8%, respectively. We also found large variability in CWD stocks, often with considerable variability at local level (Figure 1). However, there was low variation in CWD in the first 300 km from Manaus of BR-319 road, as well as at 600 km. All those sites (site clusters 1 to 5, and site cluster 11) had the lowest CWD stocks. They all had in common very high levels of soil physical constraints, such as deficient soil structure, shallow soil depth and anoxia, suggesting that the investigated soil properties could indeed be the driving mechanism of low CWD in waterlogged forests. The largest variability in CWD was observed at sites where soil physical properties were not restrictive. It is likely that at such sites sporadic and largely stochastic mortality events are the main determinants of CWD stocks at any one point in time. This may be particularly important in small plots (0.5 ha).

Despite large differences in soil physical conditions, no differences in the proportions of standing:fallen CWD stocks were observed across our study area. Standing:fallen ratios in our plots (0.29-0.59) were higher than those found by Palace et al. (2007) in the Brazilian states of Mato Grosso and Para (0.14-0.17), but much lower than values presented by Delaney et al. (1998) in Venezuela (0.80). These differences among regions suggest that the ratio of fallen to standing CWD varies across Amazonia as varies the mode of death (standing vs. fallen) (Chao et al. 2009b).

In addition to the observed relationships among CWD, soils and vegetation structure, it seems likely that variations in wood decomposition rates may be a source of variability for CWD stocks at landscape level. For instance, we noted that low stocks in HRL forests were similar to the ones reported by Martius (1997) in fertile floodplain forests (*várzea*) in central Amazonia and by Chao et al. (2008) from a floodplain forest in Peru. These studies argued that the lower CWD stocks in these areas should be a result of higher wood decomposition rates under the cycle of wetting and drying. Here we argue that differences in forest structure, such as average tree diameter (DBH per tree) may also be a source of variation in wood decomposition rates (van Geffen et al. 2010). Stem thickness and surface area may exert controls on decomposition, with thinner trees associated with greater decomposition rates. As wood density, which is commonly recognised as a primary wood trait that affects decomposition rates (Chambers et al. 2000; Chao et al. 2009a; Chave et al. 2009), did not vary significantly across our study area, therefore differences in tree diameter may be the primary driver of decomposition.

Another source of CWD variation in floodplain soils has been suggested by Martius (1997) who argued that flooding may redistribute CWD from higher lying areas to lower forests. This cannot be applied in our study area since plots are not located adjacent to large rivers. Out of the 45 of our interfluvial plots, only nine were located in flooding-affected areas, but none of them were close to high energy - high volume rivers that could carry wood areas, but none of them were close to high energy - high volume rivers that could carry wood away. None of the other plots that had high values of anoxia (Anoxia value ≥2) had indicators of large-scale flooding. Therefore, we infer a mechanistic role for soil physical properties, whereby stagnate soil water creates an anaerobic environment that inhibits deep root growth (Gale and Barfod 1999). This may result in small size of trees and increased tree mortality, which may decrease CWD stocks.

Underlying causes of variation

Soil and CWD. Sites north of the Amazonas river had no soil physical restriction. In such edaphic conditions CWD production may be driven by stochastic patterns of tree mortality, mostly related to senescence and storms (Gale and Barfod 1999; Toledo et al. 2012). As with the southern sites, restrictive soil physical conditions appeared to be important predictors of CWD, most likely resulting from edaphic influences on forest dynamics at the waterlogged sites. Topography in these areas was flatter than in the north, but other soil parameters were good predictors of CWD. Physical properties, such as shallow soils with high bulk density, poor aggregation and severe anoxic conditions can restrict deep root growth. In addition, such soil conditions limit tree establishment and tend to increase tree mortality rates (Gale and Barfod 1999; Gale and Hall 2001; Quesada et al. 2012). From all edaphic properties studied, effective depth and anoxia seem to be the most related to CWD in our study area (Table 6). However, we observed that instead of increasing the volume of CWD and CWD stocks, severe soil physical conditions led to a decreasing in CWD stocks. In our study area, soil physical restrictions are likely to affect CWD by changing the overall forest structure – reducing average tree size and thereby also increasing decomposability – rather than by selecting low wood density species common to more dynamic forests, such as occurs in western Amazonia (Chao et al 2009a). This was supported by the fact that average plot wood density did not vary with soil physical limitations in our study area. As soil water saturation exerts controls on soil weathering and development, it may imply that soil depth and structure are correlated with soil anoxia levels (Quesada et al. 2010; 2011). In this case, relationships between these soil variables and CWD could be interpreted as reflecting combined soil-vegetation effects (Figure 2).

Vegetation and CWD. The lack of a relationship between CWD and biomass found here can be compared to those presented by Chao et al. (2009a), who found weak relationships between CWD stocks and above ground-biomass across a broader area in Amazonia. Above-ground biomass per tree was a better predictor of CWD, however, the relationship was relatively weak.

Different levels of soil physical restrictions appeared to significantly correlated with forest structure (Table 5), implying an important influence on how, and for how long, living biomass is stored in forest ecosystems (Quesada et al. 2012). Soil restrictions may decrease average residence time of trees (Quesada et al. 2012), resulting in a population of thinner and shorter trees that individually store less biomass (also with more individuals per hectare). On the other hand, we hypothesise, forests on soils without physical limitations tend to be populated by larger trees, simply because they can live longer. The death of individuals with a high biomass results in a high mass of individual dead stems dead wood mass; small trees, such as those observed in HRL soil, would contribute smaller amounts of dead wood, even if at slightly higher mortality rates than in the other soil groups. For instance, NR and LRL had 1.6 and 1.3 higher AGB per tree than HRL. Therefore, inputs of dead wood from mortality in both of these soil groups should be greater than in HRL sites, as we found, a two-fold difference of CWD stocks between NR or LRL and HRL sites. Hence, our study reinforces an important relationship, already pointed by Chao et al. (2009a), between mortality of mass input and CWD: the size of stems that die may be more important for CWD stocks than the number of stems that die. Furthermore, trees with higher biomass also have larger diameter and, therefore, lower potential decomposition rates (van Geffen et al. 2010). The balance of these factors should result in higher CWD stocks in NR and LRL soil and lower in HRL.

Moreover, as LRL sites had an intermediate level of edaphic restrictions, we also speculate that CWD stocks there were similar to those found in NR probably because of subtle differences in tree mortality rates and tree size between NR and LRL. While forests on LRL soil had certain edaphic restrictions (e.g. soils shallower than NR soils) they had similar AGB to forests on NR soil, but with differences in stem density. Lower biomass per tree in

LRL should have yielded lower CWD stocks than in NR, but it was not the case. It may have been due to that fact that in the presence of some edaphic restrictions tree mortality in LRL increased slightly, such as in Quesada et al. (2012) (but not determined in this study), and this resulted in equal or higher CWD stocks than those found on NR.

CWD:AGB ratio was not constant across the studied forests. CWD contributed proportionally less in HRL forests (Table 5) than in NR and LRL. Proportions of CWD:AGB at NR and LRL sites were larger than proportions in north-western Amazonia (0.103±0.011), but similar to those in eastern Amazonia (0.132±0.013, Chao et al. 2009a). Furthermore, the CWD:AGB ratios in this study were lower than those presented by Palace et al. (2007) in Mato Grosso and Pará (0.19–0.20). This points to the importance of including CWD measurement in local carbon balance studies since it is not an invariant proportion of AGB across Amazonia.

CWD stocks have usually been expressed as the CWD:AGB ratio following the rationale that variation in CWD stocks should reflect the variation of AGB. We suggest that the use of CWD:AGB ratio may not always be informative, as AGB is a function of varying combinations of tree size and number of individuals (for example, similar AGB can be attained by a few large trees or by many small trees), and such variations in how the wood component is stored in AGB stocks may disconnect CWD stocks from AGB. Therefore, we suggest that CWD:AGB ratio over large spatial scales should be used cautiously for the following reasons: (1) CWD stocks are a function of dead wood input from mortality and decomposition rates (fluxes), which are more influenced by tree size at the moment of death than by whole stand AGB; (2) CWD:AGB is not a constant proportion, varying widely at large scales. (3) AGB is not related to CWD in the scale of this study, and is only weakly related to CWD stocks in a wider scale (Chao et al. 2009a), because stand AGB values are weakly related to individual tree size.

Conclusions

The findings of this study fill a gap in understanding the causes of CWD variation across central Amazonia. We found that differences in CWD stocks across the study area were related to a gradient of soil physical conditions, which affected forest structure and dynamics, and, in turn, influenced CWD stocks. CWD was found to be positively related to biomass per tree and negatively related with soil physical restriction. We suggest that edaphic constraint may act on vegetation structure by decreasing individual tree biomass at time of death (earlier death), by reducing tree height, diameter, and individual biomass. Such changes on vegetation structure may result in a reduction in the mass of individual dead stems, along with increased rates of stem mortality and decomposition. This study thus highlights the importance of soil properties and its modulating power over forest structure, and so influencing CWD across large-scale soil gradients.

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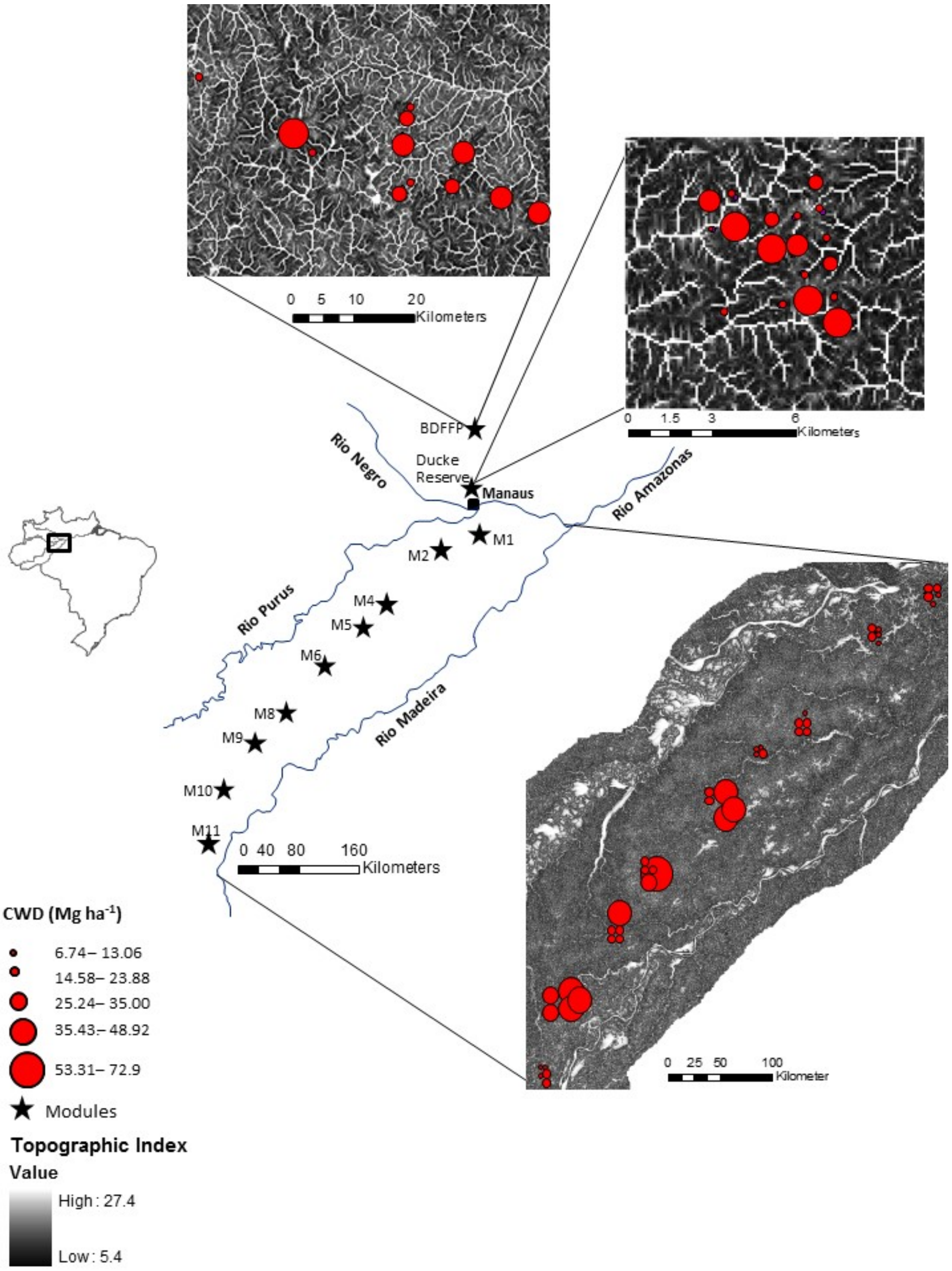


Figure 1 Spatial distribution of coarse woody debris (CWD) stocks and values of the topographyc index (TI). Size of red circles are proportional to variation in CWD stocks. High values of the topographic index (color white) indicate badly drained areas.

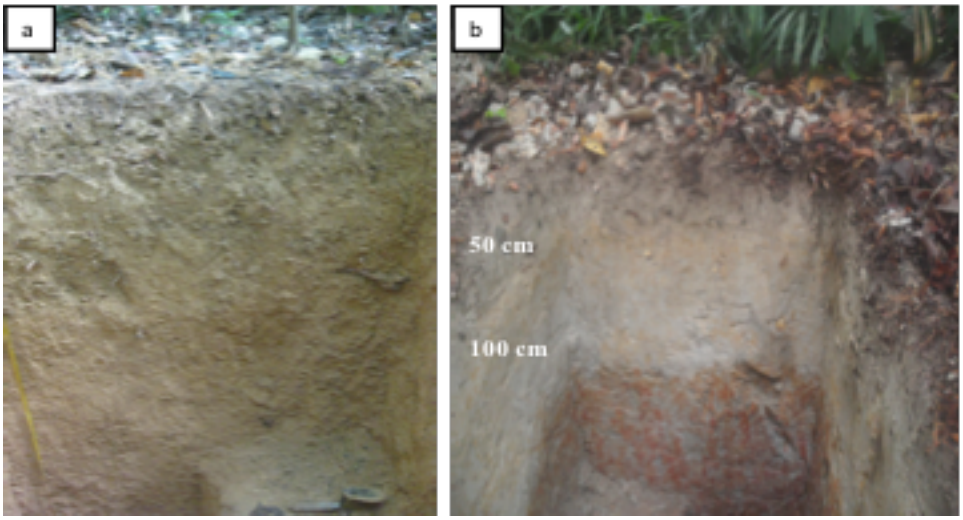
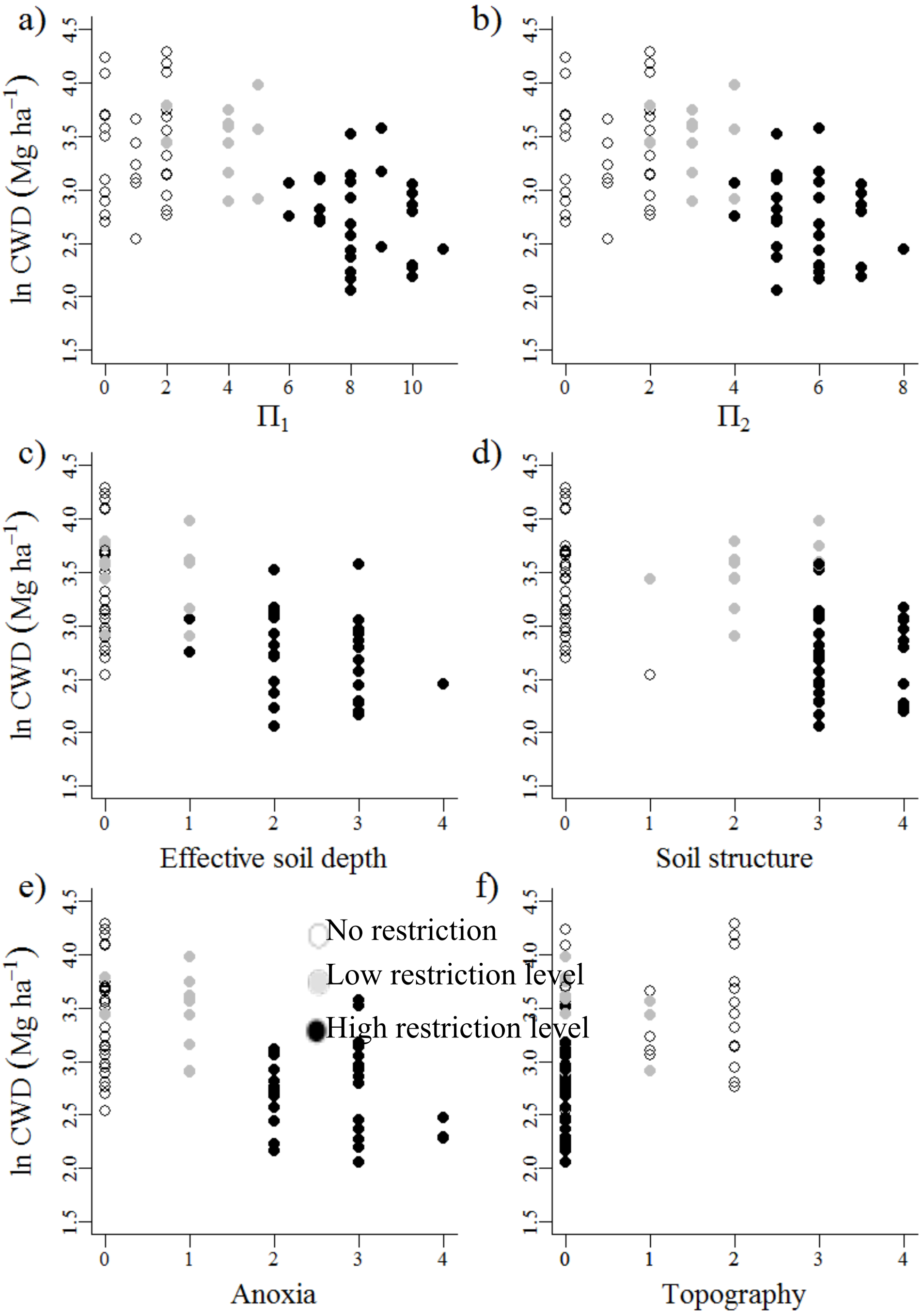
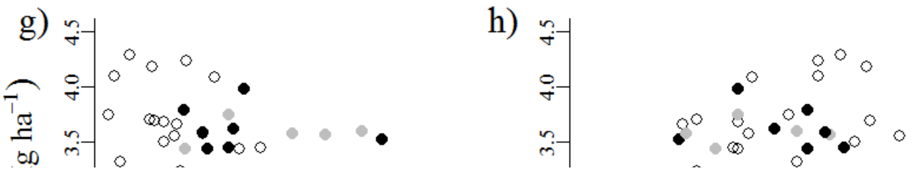


Figure 2 a) Typical Ferralsol for NR sites (BDFFP, Manaus): deep soils presenting good particle aggregation, low bulk density and no physical impediments to root growth such as hardpans and anoxic conditions. b) Typical Plinthosol occurring at the interfluve (Site cluster 1): Soil having short effective depth, and very high bulk density restricting root growth. Soft orange colouration in the first 50 cm and deep mottling showing marks of water fluctuation common to these soils.


a)
b)
c)
d)
e)
f)
ln CWD (Mg ha-1)
1.5
2.0
2.5
3.0
3.5
4.0
4.5
0
2
4
6
8
10
Π1
Π2
0
1
2
3
4
Effective soil depth
Soil structure
Anoxia
Topography
No restriction
Low restriction level
High restriction level


g)
h)
g ha-1)
3.5
4.0
4.5

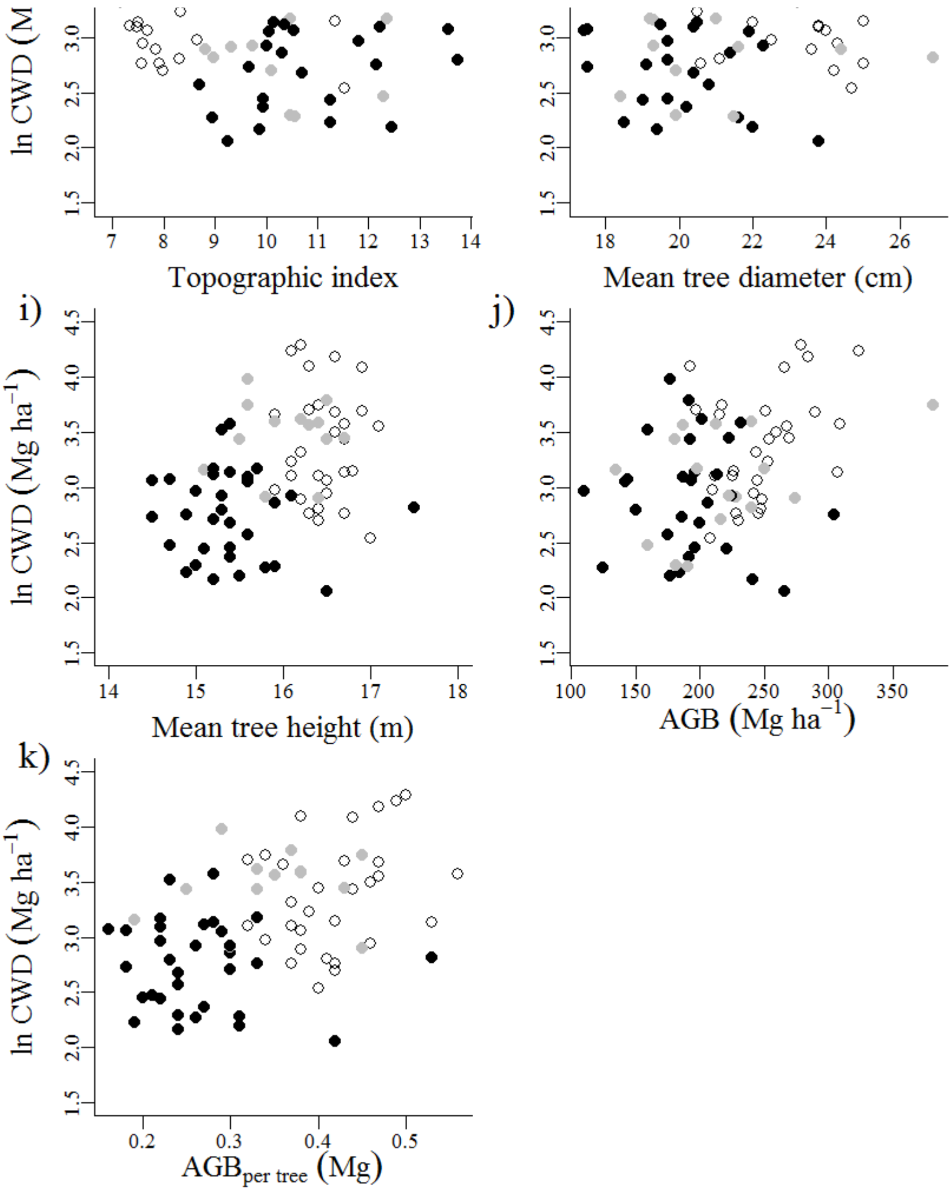


Figure 3. Simple relationships between CWD and environmental variables. All CWD values were ln transformed.

Table 1. Score table for physical soil constraints

Rating categories of soil physical constraints	Score
Effective soil depth (soil depth, presence/ absence of hardpans)	
Shallow soils (< 20 cm)	4
Medium shallow (20 to 50 cm)	3
Hardpan or rock that allows vertical root growth; other soils between 50 and 100 cm deep.	2
Hardpan, rocks or C horizon ≥ 100 cm deep	1
Deep soils ≥ 150 cm	0
Soil structure	
Very dense, very hard, very compact, without aggregation, restrictive to roots	4
Dense, compact, little aggregation, lower root restriction	3
Hard, medium to high density and/or with weak or block-like structure	2
Loose sand, slightly dense; well aggregated in sub angular blocks, discontinuous pans	1
Good aggregation, friable, low density	0
Topography	
Very steep > 45º	4
Steep 20º to 44º	3
Gently undulating 8º to 19º	2
Gently sloping 1º to 8º	1
Flat 0º	0
Anoxic conditions	
Constantly flooded; patches of stagnate water	4
Seasonally flooded; soils with high clay content and very low porosity and/or dominated by plinthite	3
Deep saturated zone (up to 50 cm below surface); redox features	2
Deep saturated zone (maximum height of saturation > 100 cm deep); deep redox features	1
Unsaturated conditions	0

Table 2. Range of soil physical conditions in the three different soil groups. NR, no physical restriction; LRL, low level of physical restriction; and HRL, high level of physical soil restriction; *bulk density was measured at a reference depth of 50 cm. Π_1 - Sum of the four soil parameters, Π_2 - Sum of soil parameters with exception of the Anoxia parameter. See Table1 for score values.

Soil parameter	NR	LRL	HRL
Soil type	Ferralsol/Acrisol	Plinthosol	Gleysol/Plinthosol
Anoxia	0	0-1	2-4
Depth	0	0-2	1-4
Structure	0-1	1-2	2-4
Topography	0-2	0-1	0-1
Bulk densitiy (g cm-3)	0.8-1.2	1.0-1.6	1.2-1.7
Π_1	0-2	2-6	6-11
Π2	0-2	2-6	4-8

Table 3. Mean (± SE) coarse woody debris (CWD) volume, CWD density, and CWD mass in forests on soils with no (NR), low (LRL) and high (HRL) physical soil restriction in central Amazonia. In parentheses is the number of samples.

	NRa, m, x	LRLa, m, x	HRLa, n, y
Wood density (g cm^{-3}) per decay class			
Class 1A	0.68±0.02 (75)	0.67±0.04 (20)	0.61±0.02 (88)
Class 2B	0.55±0.02 (66)	0.53±0.03 (43)	0.48±0.01 (176)
Class 3C	0.32±0.01 (88)	0.34±0.02 (24)	0.33±0.02 (97)
CWD volume (m^3 ha^{-1})			
Class 1M	12.3±3.0	19.8±3.8	6.9±1.2
Class 2N	26.1±4.7	29.9±3.4	15.7±1.3
Class 3N	31.1±3.4	19.8±4.4	11.1±1.2
Total	69.5±11.1	69.5±11.6	33.7±3.7
CWD mass (Mg ha^{-1})			
Class 1X	8.4±2.3	13±3.3	4.2±0.9
Class 2Y	14.4±3.1	15.3±2.7	7.7±0. 8
Class 3X	10.3±1.4	6.8±1.9	4.1±0.7
Total	33.1±7.1	35.1±7.2	16.1±2.6

Uppercase letters indicate statistically significant differences among decay classes (P<0.05): x; lower case letters are for differences among soil groups. Multiple comparison tests (Tukey HSD): are labelled by letters A, B, C, a, b, and c for density in different decay classes; M, N, m and n for CWD volume; X, Y, x and y for CWD mass.

Table 4. Mean (±SE) mass of fallen and standing coarse woody debris (CWD) in forests growing on soils with no (NR), low (LRL) or high (HRL) physical restriction in plots in central Amazonia, north and south of the Rio Amazonas. Statistically significant differences at $P<0.05$ among soil groups (NR, LRL, HRL) are indicated by a and b for total standing CWD; and by x, y and z for total fallen CWD.

	NR a, x	LRL ab, y	HRL b, z
Standing			
Class 1	3.8±1.1	2.7±0.9	1.2±0.3
Class 2	4.2±1.0	2.7±0.7	2.2±0.5
Class 3	2.4±0.5	1.6±0.7	1.0±0.2
Fallen			
Class 1	4.7±1.4	10.6±2.5	3.0±0.6
Class 2	10.2±2.3	13.1±1.4	5.5±0.6
Class 3	7.9±1.2	5.1±1.3	3.2±0.4

Table 5. Average (±SE) above-ground biomass (AGB), stem density, mean tree height and DBH, CWD and CWD:AGB ratio in soils with no (NR), low (LRL) and high (HRL) levels of physical restriction in plots in central Amazonia, north and south of the Rio Amazonas. Different letters indicate significant differences between means ($P<0.05$) in each row. CWD:AGB, ratio of total CWD to AGB for trees>10 cm DBH.

	NR	LRL	HRL
AGB (Mg ha^{-1})	248.2±6.1^{a}	218.8±16.6^{b}	198.8±7.2^{b}
Stems (ha^{-1})	597.9±8.7a	635.3±27.2a	766.2±30.3^{b}
AGB per tree (Mg)	0.42±0.01a	0.35±0.02b	0.26±0.02c
Mean height (m)	16.5±0.1a	16.0±0.1b	15.4±0.1^{c}
DBH (cm)	23.1±0.3a	22.7±0.4a	20.3±0.3b
CWD (Mg ha^{-1})	33.1±3.1^{a}	33.7±2.7a	16.8±1.2b
CWD:AGB	0.13±0.01a	0.14±0.01a	0.08±0.01b

Table 6. Relationships between independent variables and CWD stocks in 75 plots across central Amazonia. AIC, Akaike Information Criterion

Variable	AIC	Fixed effect	Intercept	r^2_m	r^2_c	*P*
CWD with soil physical constraints						
Depth	92.397	-0.258	3.411	0.37	0.37	<0.001
Anoxia	96.682	-0.233	3.421	0.33	0.33	<0.001
Π_1	98.058	-0.084	3.52	0.33	0.33	<0.001
Π_2	101.135	-0.123	3.548	0.32	0.32	<0.001
Structure	104.635	-0.168	3.446	0.29	0.30	<0.001
Topography	109.159	0.112	3.015	0.03	0.34	0.16
CWD:AGB with soil physical constraints						
Depth	98.97	-0.215	-2.094	0.27	0.27	<0.001
Anoxia	102.362	-0.192	-2.089	0.24	0.24	<0.001
Π_1	103.65	-0.068	-2.010	0.22	0.22	<0.001
Π_2	105.81	-0.100	-1.992	0.20	0.20	<0.001
Structure	109.00	-0.130	-2.087	0.16	0.16	0.013
Topography	111.91	0.111	-2.425	0.03	0.24	0.18
CWD with TI	109.76	-0.052	3.565	0.03	0.32	0.217
CWD:AGB with TI	112.91	-0.04	-1.99	0.02	0.23	0.341
CWD with vegetation						
AGB per tree	105.746	1.748	2.498	0.11	0.32	0.013
Stems density	107.132	-0.001	3.773	0.08	0.39	0.05
Wood specific gravity	110.107	-1.137	3.86	0.01	0.37	0.335
Height	110.218	0.119	1.17	0.02	0.30	0.278
AGB	110.419	0.001	2.738	0.01	0.35	0.415
Basal area	110.742	0.01	2.776	0.01	0.35	0.557
DBH	117.31	0.04	2.199	0.03	0.35	0.259
CWD:AGB with vegetation						
AGB per tree	112.82	0.766	-2.633	0.02	0.22	0.288
AGB	110.58	-0.003	-1.720	0.04	0.35	0.077
Stems density	106.04	-0.001	-1.435	0.14	0.29	0.004
Basal area	111.81	-0.025	-1.750	0.03	0.34	0.166
Wood specific gravity	108.52	-2.581	-0.543	0.08	0.31	0.026
DBH	120.97	0.021	-2.854	0.01	0.27	0.538
Height	113.46	0.034	-2.937	0.01	0.23	0.758
CWD with Climate						
Total precipitation	109.655	0.001	1.258	0.05	0.37	0.234
Prec. in the driest quarter	110.937	0.001	2.88	0.01	0.36	0.717
CWD:AGB with Climate						
Total precipitation	113.40	0.000	-3.099	0.01	0.28	0.612
Precipitation in the driest quarter	113.66	0.000	-2.431	0.00	0.28	0.927