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Production and stock of coarse woody debris across a hydro-edaphic gradient of oligotrophic forests in the northern Brazilian Amazon

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Abstract

Most studies on coarse woody debris (CWD) in Brazilian Amazonia have been done in disturbed and undisturbed upland forests. However, oligotrophic forest types occupying seasonal flooding environments have been neglected, although they occupy about one-third of the Amazon region. We examined the effect of an environmental gradient with different hydro-edaphic features on production and stock of CWD in an area of the Rio Negro-Rio Branco basin, in Brazil's state of Roraima. We used 60 km of trails (production) and 30 permanent plots (stock) in a sampling grid established at Viruá National Park. Our study demonstrated that production and stock of CWD carbon are the lowest in all of Amazonia. The highest CWD carbon production was found in open-canopy submontane rainforest (0.58±0.63 MgC ha^{-1} yr^{-1}), which occur in environments that are free of any influence of seasonal flooding. The lowest stocks of CWD carbon (0.35±0.30 MgC ha^{-1}) was associated with low tree biomass in forest types occurring on sandy soils that are strongly influenced by seasonal flooding. CWD stocks in oligotrophic forests at Viruá are partially explained (~21%) by tree biomass, which is determined by different environmental conditions across hydro-edaphic gradients. Reference values (CWD carbon as a percentage of tree carbon) were among the lowest in Amazonia (0.91-4.38%), with lower values being associated with formations with low production and stock of CWD. This finding suggests that values vary among oligotrophic forest types and that separate reference values should be adopted for estimates of undisturbed forest carbon stocks in the different ecosystems in Brazilian Amazonia. Different reference values represent the variability of CWD among forest types and contribute to reducing uncertainties in current estimates of carbon stock in Amazonia.

Keywords: necromass; oligotrophic forests; dead biomass; hydro-edaphic determinants.

1. INTRODUCTION

Coarse woody debris (CWD) is defined as necromass of standing and fallen dead trees and the remains of large branches (diameter ≥ 10 cm) (Harmon *et al.*, 1986; Clark *et al.*, 2002; Palace *et al.*, 2012). CWD estimates are useful for understanding changes in functions and forest services under different natural or anthropogenic disturbances (Phillips *et al.*, 2009; Trumbore *et al.*, 2015). One of the needs for this information is as an input for modeling the flammability of forests due to accumulation of necromass on the ground, which represents fuel for forest fires (Barbosa and Fearnside, 1999; Vasconcelos *et al.*, 2013; Balch *et al.*, 2015). CWD can also reach a high percentage of the entire stock of aboveground tree biomass representing a substantial component of the carbon stored in tropical forests (Houghton *et al.*, 2001; Brown, 2002; Malhi *et al.*, 2004). However, uncertainties are still great, especially in Brazilian Amazonia where necromass estimates have received little attention in greenhouse gas emissions inventories (Brazil-MCT, 2010).

In the Brazilian Amazon, the main studies on production (input) and stock (accumulation) of CWD were carried out in central Amazonia (Martius and Bandeira, 1998; Summers, 1998; Chambers *et al.*, 2000; Chambers *et al.*, 2001; Nascimento and Laurance, 2004) and in the "arc of deforestation," especially in Pará (Gerwing, 2002; Keller *et al.*, 2004; Rice *et al.*, 2004; Palace *et al.*, 2007; Palace *et al.*, 2008; Pyle *et al.*, 2008), Amazonas (Martins *et al.*, 2015), Rondônia (Cummings *et al.*, 2002) and Mato Grosso (Pauletto, 2006). Most of these studies focused their attention on the spatial and temporal distribution of CWD stocks and production in upland forests that were fragmented by deforestation or subjected to selective logging. In all cases, forest structure, species composition, soil type, topography and seasonal flooding are seen as natural predictors of greater weight in the formation of biomass values associated with necromass and wood decomposition processes (Laurance *et al.*, 1999; Castilho *et al.*, 2006; Toledo *et al.*, 2011; Martins *et al.*, 2015).

Despite improved understanding of environmental conditions affecting the process of necromass formation, the Brazilian Amazon still has low sampling representativeness in different disturbed and undisturbed forest ecosystems, even when compared to other countries in South America (Malhi *et al.*, 2004). This is because vast forest areas represent great gaps of information on CWD stock and production across latitudinal and longitudinal gradients in the region (Chao *et al.*, 2009; Palace *et al.*, 2012). This sparse spatial representation increases uncertainty about CWD carbon stocks and inputs when they are extrapolated as reference values (necromass / aboveground biomass ratio or CWD carbon as a percentage of tree carbon) to large forest areas under different stages of succession and environmental conditions (Chambers *et al.*, 2013).

One of these gaps is the Rio Negro-Rio Branco basin, which occupies ~600.000 km^2 of Amazonia (Montero and Latrubesse, 2013). Overall, this is a lowland ecoregion that is subject to seasonal flooding and is characterized by a mosaic of upland forests and oligotrophic ecosystems (*campinas* and *campinaranas*), which are vegetation types that often occur on low-fertility sandy soils (Ferreira, 2009; Junk *et al.*, 2011; Mendonça *et al.*, 2014). The phyto-physionomic structures of this ecoregion are directly related to the hydro-edaphic gradient that is determined by different topographical features, soils and flooding levels (Damasco *et al.*, 2013; Targhetta *et al.*, 2015). In this Amazonian ecoregion, few studies have been carried out with the objective of estimating CWD, such as Martius (1997) in flooded forests near Manaus, Amazonas (5.9–11.4 Mg ha^{-1}) and Scott *et al.* (1992) in forests on sandy soils on Maracá Island, Roraima (3.8 Mg ha^{-1}; palms+trees ≥ 10 cm in diameter). Both studies adopted small sampling scales. In a recent review, Nogueira *et al.* (2015) estimated necromass for this ecoregion based on the few existing studies, most of which were from outside the Brazilian Amazon, especially from southern Venezuela (Klinge and Herrera, 1983; Bongers *et al.*, 1985; Kauffman *et al.*, 1988). The lack of regional values leads to greater uncertainty in calculations of carbon stocks and fluxes in Amazon forest. It is therefore important to improve our understanding of the role of this forest compartment in Amazonian ecosystems by investigating the effect of macro-environmental conditions on CWD production and stock. This will provide adjustment options for the Brazilian greenhouse-gas emissions inventories with direct implications for estimates of global carbon flows and pools.

The present study aims to estimate production and stock of CWD in undisturbed forest types in the Rio Negro-Rio Branco basin, in the northern portion of Brazilian Amazonia. The specific objectives of the study were to associate estimates of CWD stock, CWD production, and reference values (% of CWD carbon in relation to aboveground tree carbon [live + dead]) for a mosaic of upland forests with oligotrophic forest types dispersed along an environmental gradient defined by distinct hydro-edaphic conditions.

2. MATERIALS AND METHODS

2.1 Study area

We sampled CWD (standing and fallen dead wood pieces ≥ 10 cm in diameter) for stock and production estimates at a Biodiversity Research Program (PPBio) research site (25 km^2) in Viruá National Park (1º 36' N, 61º 13' W), which is a federal protected area located in the state of Roraima (Fig. 1). Viruá has high environmental heterogeneity with oligotrophic ecosystems (*campinas and campinaranas*) occupying hydromorphic soils, alluvial forests along major watercourses and upland ombrophilous forests scattered in isolated mountain ranges (Damasco *et al.*, 2013). This 215,917-ha park is set in a climatic transition zone (Aw-Am under the Köppen classification system), and the climate is characterized by a dry season (December to March), a wet season (May to August), and an average annual rainfall ranging from 1750 to 2000 mm (Barbosa, 1997; Schaefer *et al.*, 2008). The sampling period (December 2007-December 2008) was a year with ~2100 mm of rainfall, considering the climatological station (Brazilian Institute of Meteorology) located ~35 km from Viruá in the city of Caracaraí. Strong storms with winds occurred naturally in September and October, a period that encompasses the end of rainy season and the beginning of the dry season in this part of the Amazon region.

*** Figure 1

2.2 Sampling design

We estimated production and stock of CWD across a hydro-edaphic gradient spanning six vegetation types (Table 1; Fig. S1, Supplementary Material), varying with respect to soil, topography, flood height, and flooded period (Schaefer *et al.*, 2008; Mendonça *et al.*, 2013; Vale *et al.*, 2014). Vegetation types occurring below 55 m a.s.l. are periodically flooded and are controlled by depositional processes including: (i) recent active sedimentation (Middle Holocene) covered by non-forest vegetation, and (ii) paleo-aeolian dunes and paleo-river bars covered by forest (Zani, 2013). Vegetation types between 55 and 300 m a.s.l. are characterized by presence of *inselbergs*, hills and dissected slopes covered by open-canopy rainforests and forested ecotones. We characterized all vegetation types according to the Brazilian vegetation classification system (Brazil-IBGE, 2012). Sampling was linked to the PPBio grid, a network of 12 trails (6 north-south and 6 east-west; each 1 m in width and 5 km in length) and 30 permanent plots (each 250 m in length) distributed systematically along the 6 east-west trails (Magnusson *et al.*, 2005; Pezzini *et al.*, 2012). We relied on the entire 25-km^2 PPBio grid to obtain robust estimates of CWD stock (sampled in the 30 permanent plots) and of CWD production (sampled along the 12 trails).

*** Table 1

CWD production was estimated in a 6-ha sampling area formed by the sum of all trails crossing the grid (60,000 m × 1 m). The sampling area for each forest type was estimated based on geo-environmental divisions defined by Schaefer *et al.* (2008) (Table 1). All dead branches and trunks (fallen and standing) were removed from the grid trails in December 2007 (t_0) and in December 2008 (t_1) we conducted a census of all new fallen and standing dead pieces on the trails (Fig. S2, Supplementary Material).

The length of each fallen piece was measured up to the limits of the sampling area. For standing-dead trees (no leaves; no small branches or twigs) we measured DBH (diameter at breast height: 1.3 m above the ground) and estimated the biomass of trees by the "moist-forest" model (Chave *et al.*, 2005), discounting 10% for leaves, small branches and twigs, as adopted by Nascimento and Laurance (2004) to calculate necromass volume (m^3). For residual stems (broken trunks) we measured height and stem diameter to estimate the necromass volume based on the formula for a cylinder. In both cases we estimated the percentage of the standing tree or residual stem projected onto the trail limits in order to adjust their participation to represent only material inside the sampling area, as suggested by Harmon and Sexton (1996). For each dead piece we recorded the dominant forest type, the taxonomic group (Arecaceae and Dicotyledons) and the location on the grid taking in account georeferenced landmarks (UTM) established on all trails.

A sample disk was collected from each dead piece to estimate hollow spaces (physical mass loss) and wood density (g cm^{-3}) because the degree of decomposition varies for each dead wood piece, therefore requiring a separate calculation (Supplementary Material: Table S1, Figs. S3 and S4). To determine the degree of decomposition we used categories established by Delaney *et al.* (1998), adjusted in this study by the percentage of physical mass loss: P1 (sound) – pieces with no perceptible deterioration, recently fallen and resistant to microorganism attack (net loss of mass ≤ 10%), P2 (intermediate) – pieces with few signs of insect and/or fungal attacks, deterioration in the initial stage (11-30% lost) and P3 (rotten) – pieces in advanced stage of decomposition, breaking or shattering to the touch (> 30% lost). The necromass estimate was determined following Keller *et al.* (2004), calculating the solid volume for each piece and adjusting this value for wood-density reduction and physical loss:

$$CWD_{input} = \left(\frac{\pi D^2}{4}\right) \times L \times sf \times af \times wd$$

Where: **CWD$_{\mathbf{input}}$** = necromass of each piece (Mg); **D** = diameter of each piece in meters (averaging the measurements made at the ends of each fallen piece, DBH for standing trees or diameter for residual stems); **L** = length (or height of residual stem) of each piece in meters; **sf** = solid fraction of the piece (Supplementary Material: Table S1, Figs. S3 and S4); **af** = adjustment factor for standing dead trees only (percentage of dead parts within the sampling area limits); **wd** = wood density (g cm^{-3}).

The stock of CWD of standing dead trees was calculated in the same way as CWD production taking into account dead trees and residual stems that were partially or entirely within of the 1-m width limit along the central line of each permanent plot. The stock of fallen pieces was estimated indirectly based on the line intersect sampling (LIS) method (van Wagner, 1968), with the central line of each permanent plot corresponding to the sampling transect. In each transect we measured the diameters of all the fallen pieces (≥ 10 cm in diameter) that touched a stretched line along the transect in each permanent plot. Wood pieces arranged longitudinally in relation to the central line were not sampled because they cannot undergo the process of mathematical integration between the diameter and the plot length. The volume[1] of each of the fallen pieces was calculated as defined below:

$$V = \frac{\pi^2 \times D^2}{8 \times L}$$

Where: **V** = solid necromass volume of a unit of area; **D** = diameter of each piece touching the sampling line; **L** = length of sampling line.

All pieces were classified by degree of decomposition (tactile and visual) based on the same categories as those defined for CWD production. We assumed a correspondence with

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[1] The LIS method (van Wagner, 1968) can estimate the wood volume of any area by means of a line that crosses fallen trunks (cylinders) of different lengths, diameters and orientations. The sum of the series of vertical elliptical cross sections that are formed by the line crossing provides an estimate of wood volume per unit area as a function of cross-sectional area per unit length of line.

the measured values for CWD production to calculate the average physical mass loss and wood density for each piece accumulated in the plots, taking into account the taxonomic group and the degree of decomposition. This assumption was intended to simplify the calculation and maintain the representativeness of parts that were not sampled directly (Larjavaara and Muller-Landau, 2010). The mass of each piece was estimated based on volume calculated by the LIS method, discounted by the fraction of the physical mass loss corresponding to the degree of decomposition, followed by multiplication by the wood density (defined by taxonomic group).

All sample disks were individually milled to estimate carbon concentration (%C). Approximately 10 g of each sample was sent for analysis in the Soil and Plant Thematic Laboratory of the National Institute for Research in Amazonia (LTSP-INPA), Manaus, Amazonas, Brazil. Analyses were performed using a CHN Auto Analyzer (Vario MAX, Elementar Instruments, Hanau, Germany).

2.3 Data analysis

Production and stock of CWD were calculated for each forest type defined in Table 1. Normality tests and analysis of variance (ANOVA; Tukey Test; $\alpha = 0.05$) were applied to the set of the wood density data associated with the taxonomic group and the degree of decomposition. All values of CWD (production and stock) were transformed into carbon per unit of time and area based on the results of the analysis of carbon concentration (%C). Reference values (% of stock of CWD carbon in relation to carbon in aboveground tree biomass [live+dead]; DBH ≥ 10 cm) were estimated from the forest inventory carried out by C.V. de Castilho in all permanent plots in the PPBio grid at Viruá. All trees with DBH ≥ 10 cm (Dicotyledons) were transformed into aboveground live tree biomass using the "moist-forest" model (Chave *et al.*, 2005) and a value of 0.642 g cm^{-3} for wood density (Nogueira *et al.*, 2007). Palm biomass (Arecaceae) was calculated using the model of Goodman *et al.* (2013). Carbon in aboveground live tree biomass was estimated using 48.5% C as measured by Silva (2007) for Amazon trees. Correlation analysis (Pearson; $\alpha = 0.05$) and linear regression were performed between carbon in aboveground tree biomass (live+dead; DBH ≥ 10 cm) and the carbon stock in CWD as the response variable. All analyses were performed with R software (R Core Team, 2014).

3. RESULTS

3.1 Data description

Estimates of CWD production (60 km of trails = 5.36 ha of forest and 0.64 ha of non-forest vegetation) were based on observation of 201 pieces (190 fallen and 11 standing): 182 (90.5%) of Dicotyledons and 19 (9.5%) of Arecaceae (Table 2). The largest number of pieces (67.7%) were classified as having no perceptible deterioration (P1), indicating that production during the study period was characterized by intact pieces in the early stages of decomposition. To estimate CWD stock we observed 317 pieces (293 fallen and 24 standing): 294 (92.7%) of Dicotyledons and 23 (7.3%) of Arecaceae. In contrast to the production of CWD, most of the pieces in the CWD stock were classified as P3 (69.1%), followed by P2 (17.0%) and P1 (13.9%). Pieces 10-30 cm in diameter (structure) dominated both the production (66.8%) and the stock (80.0%), taking into account the total necromass estimated for all sampled forest types (Fig. 2). Wood density was higher in P1 (0.531 ± 0.132 g cm^{-3}) as compared to other decomposition categories (Tukey test, $p < 0.01$). Wood density of the

Dicotyledons group (0.516 ± 0.126 g cm^{-3}) was higher than that of the Arecaceae group (0.403 ± 0.146 g cm^{-3}) (t test; $p < 0.0047$), but density did not differ among forest types (ANOVA, $p > 0.493$; $F = 0.854$). The mean values for physical mass loss taking into account the decomposition classes, were 1.4% (P1), 15.9% (P2) and 56.6% (P3) (Supplementary Material: Table S1).

*** Table 2

*** Figure 2

3.2 Production and Stock

The annual input of carbon of CWD was higher in open-canopy rainforests (As = 0.58±0.63 MgC ha^{-1} yr^{-1} and Ab = 0.57±0.81 MgC ha^{-1} yr^{-1}) and ecotones (LO = 0.49±1.19 MgC ha^{-1} yr^{-1}) found in environments with little or no influence of seasonal flooding (Table 3). Mosaics of forested *campinaranas* (La+Ld = 0.27±0.67 MgC ha^{-1} yr^{-1}) and shrubby+treed *campinaranas* (Lb+La = 0.04±0.08 MgC ha^{-1} yr^{-1}), located on white-sand hydromorphic soils had the lowest values. The CWD production pattern indicates an association with the hydro-edaphic gradient at Viruá, where the largest CWD inputs are in forest types occurring in topographical zones free of long flooding periods and with better soil conditions as compared to the forest types in areas with greater hydro-edaphic restrictions (Fig. 3, Fig. S1).

*** Table 3

*** Figure 3

The largest CWD stocks were observed in ecotones (LO=9.52±4.45 Mg ha^{-1}) and open-canopy rainforest on non-flooding lowlands (Ab=8.30±4.45 Mg ha^{-1}) (Table 4). Most CWD stock was fallen necromass (92%) and was characterized by high variability (range: 0.77-8.58 Mg ha^{-1}) among all forest types. Carbon in the CWD stock in all forest types analyzed ranged from 0.35 to 4.41 MgC ha^{-1}, corresponding to reference values from 0.91% (shrubby+treed *campinaranas*) to 4.38% (ecotone). The correlation between carbon in aboveground tree biomass (live + dead) and carbon in CWD stock was positive and significant (r_p=0.455; p=0.022), indicating that higher CWD carbon accumulation is partially explained ($R^2 \approx 0.21$) by forest types with little or no influence from fluctuations in groundwater levels along the hydro-edaphic gradient (Fig. 4).

*** Table 4

*** Figure 4

4. DISCUSSION

CWD production in the forest types at Viruá is lower than in all other studies in disturbed and undisturbed forest areas in the central and eastern Amazon (Supplementary Material: Table S2). The highest values for input of CWD carbon at Viruá (0.49-0.58 MgC ha^{-1} yr^{-1}) were six-fold lower when compared with the average value of 3.1 MgC ha^{-1} yr^{-1} estimated for Pan Amazonia as a whole (Malhi *et al.*, 2004). The lower CWD production determined in our study is best explained by the fact that most mature and more productive forests (which have higher tree turnover) in Amazonia are in the central and eastern portions of the region (Phillips *et al.*, 2004; Malhi *et al.*, 2006). These differ from the seasonally flooded oligotrophic environments (*campinas* and *campinaranas*) of the Rio Negro-Rio Branco region in northwestern Amazonia.

Since higher hydro-edaphic restrictions determine lower tree biomass content in oligotrophic forests (Targhetta *et al.*, 2015), naturally lower CWD production at Viruá also decreased in association with forest types with lower tree biomass on poor sandy soils that are subject to frequent flooding and high groundwater levels (anoxia). These ecological distinctions are important because in most spatial macro-analyses in Amazonia (e.g., benchmark maps) the oligotrophic forest types occupying hydromorphic soils are not distinguished due to the map scales used, and in this ecoregion these vegetation types are presented as forest conglomerates (Malhi *et al.*, 2004; Saatchi *et al.*, 2007; Chao *et al.*, 2009). This causes an upward bias when CWD production values are used from other regions where there are fewer restrictions (higher biomass and higher production), or when information is used from sites located outside of Brazilian Amazonia (not representative).

CWD stock at Viruá follows a trend similar to the results for production, with the largest stocks being partially explained by forest type with higher tree biomass occurring where hydro-edaphic restrictions are smaller (Fig. 4). The relationship between tree biomass and CWD stock was also suggested by Chao *et al.* (2008) studying lowland forests (flooding and non-flooding) in Peruvian Amazonia, and by Martins *et al.* (2015) in areas with different edaphic restrictions in Central Amazonia. Although there are disagreements about the effect of forest structure on the CWD stock (e.g., Chao *et al.*, 2009), our results suggest that stocks of CWD at Viruá are partly determined by the forest types that are conditioned by hydro-edaphic features across the environmental gradient.

Since CWD stock is roughly controlled by the input derived from tree biomass (Baker *et al.*, 2004), the relationship between production and stock of CWD can be considered to apply to other parts of the Rio Negro-Rio Branco region, which is where most oligotrophic ecosystems are located in northwest Brazilian Amazonia (Fig. 5). On the other hand, oligotrophic forest types do not necessarily imply lower turnover rates of CWD as compared to other forest ecosystems in Amazonia. This is because the relationship between input and stock is well known and is affected by tree mortality under climatic stress (Lewis *et al.*, 2004; Doughty *et al.*, 2015) or natural and anthropic disturbances (Gerwing, 2002; Nascimento and Laurance, 2004; Rice *et al.*, 2004). In this case, we can assume a steady-state between production, stock and rate of decomposition, estimating 5-10 years as the residence time of CWD in all of the forest types investigated at Viruá. This range follows the pattern expected in forests in central Amazonia (~6 years; Chambers *et al.*, 2000). The CWD residence time in oligotrophic forest types at Viruá indicates that these rates are not affected by environmental variability, and necromass accumulation is approximately stable over time, independent of the position on the environmental gradient.

*** Figure 5

The lower reference values determined for all forest types at Viruá were associated with the formations with low production and stock of CWD. In general, our findings were among the lowest in Amazonia, such as those estimated by Chao *et al.* (2008) for forests on soils with frequent flooding (6.4-15.4%) or those derived from Martins *et al.* (2015) for environments with different hydro-edaphic restrictions (7.8-13.3%) (Supplementary Material: Table S2). These discrepancies indicate great variability among the forest types and environmental conditions with direct impact on estimates of flows and forest carbon stocks in the Amazon region. This debate is important because it involves the use of a single reference value (3%) for all forest types in Brazil’s second national greenhouse-gas inventory (Brazil-

MCT, 2010) to adjust the total biomass using the percentage of necromass. Use of a default value makes the calculations easy but linearizes the dynamics of mortality for all forest types. This generates uncertainties in the estimates of current carbon stocks in undisturbed Amazonian ecosystems because forest types have different areas and aboveground carbon stock in trees. Thus, differences of a few percentage points tend to produce discrepancies in individual necromass stocks, and the discrepancy will be greater the larger the area that the ecosystem occupies in the Brazilian Amazon.

The value currently adopted by Brazil should be changed and separate necromass / aboveground biomass ratios (or CWD carbon as a percentage of tree carbon) should be used for each forest type or large formation (e.g., rainforests, seasonal forests, ecotones, etc.), taking advantage of investigations that have already been carried out in different undisturbed ecosystems in the Brazilian Amazon (e.g., Supplementary Material: Table S2). Even understanding that this relationship needs to be better understood based on structural variability of the ecosystems (Pyle *et al.*, 2008), forest dynamics (Chao *et al.*, 2009) and environmental conditions (Baker *et al.*, 2007), there is no doubt that carbon-stock estimates in Amazonian forests would be improved and would gain due the reduction of uncertainties.

5. CONCLUSIONS

Based on our results, we conclude that the environmental gradient at Viruá has a direct effect on production and stock of coarse woody debris (CWD). Forest types located in topographic zones with lower hydro-edaphic restrictions support higher tree biomass and have higher production and stock of CWD. Reference values indicated that formations with low production and stock of CWD are associated with the higher hydro-edaphic restrictions where sandy soils predominate and there is strong influence from seasonal flooding.

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FIGURES

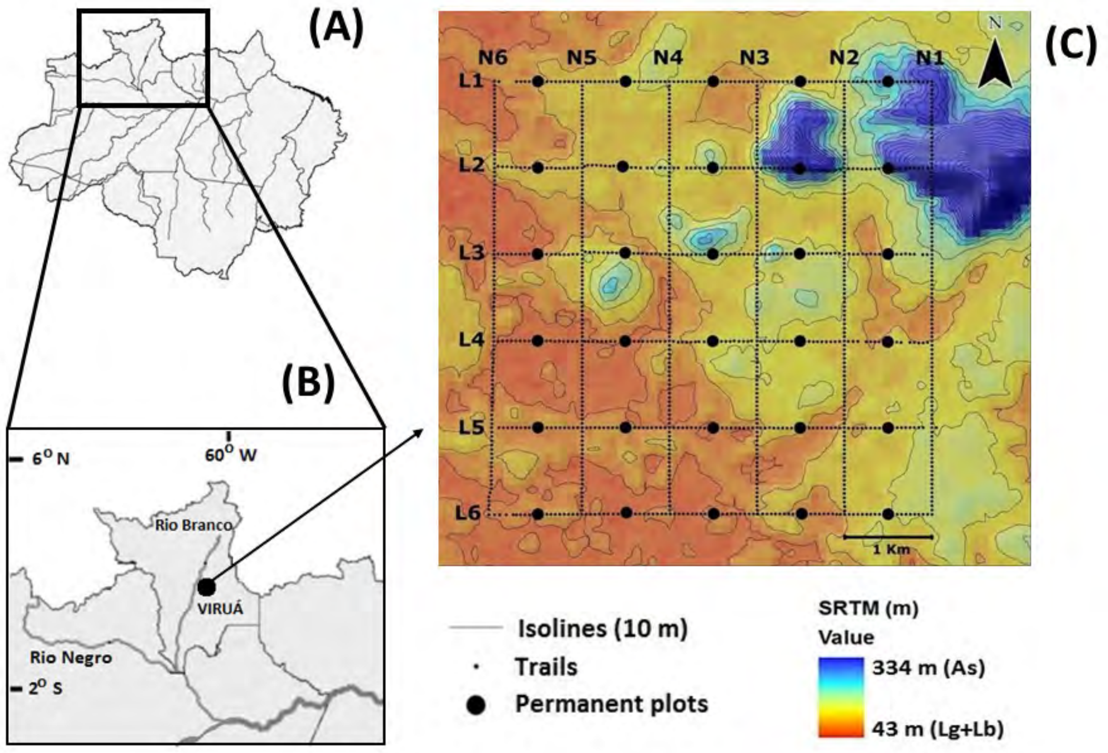

Figure 1 – Study area: (A) Brazilian Amazonia, (B) Rio Negro-Rio Branco Basin, (C) PPBio grid system installed in Viruá National Park - SRTM image provided by Brazilian Biodiversity Research Program (PPBio, 2014).

<u>Online version in color and printed version in black-and-white</u>**.

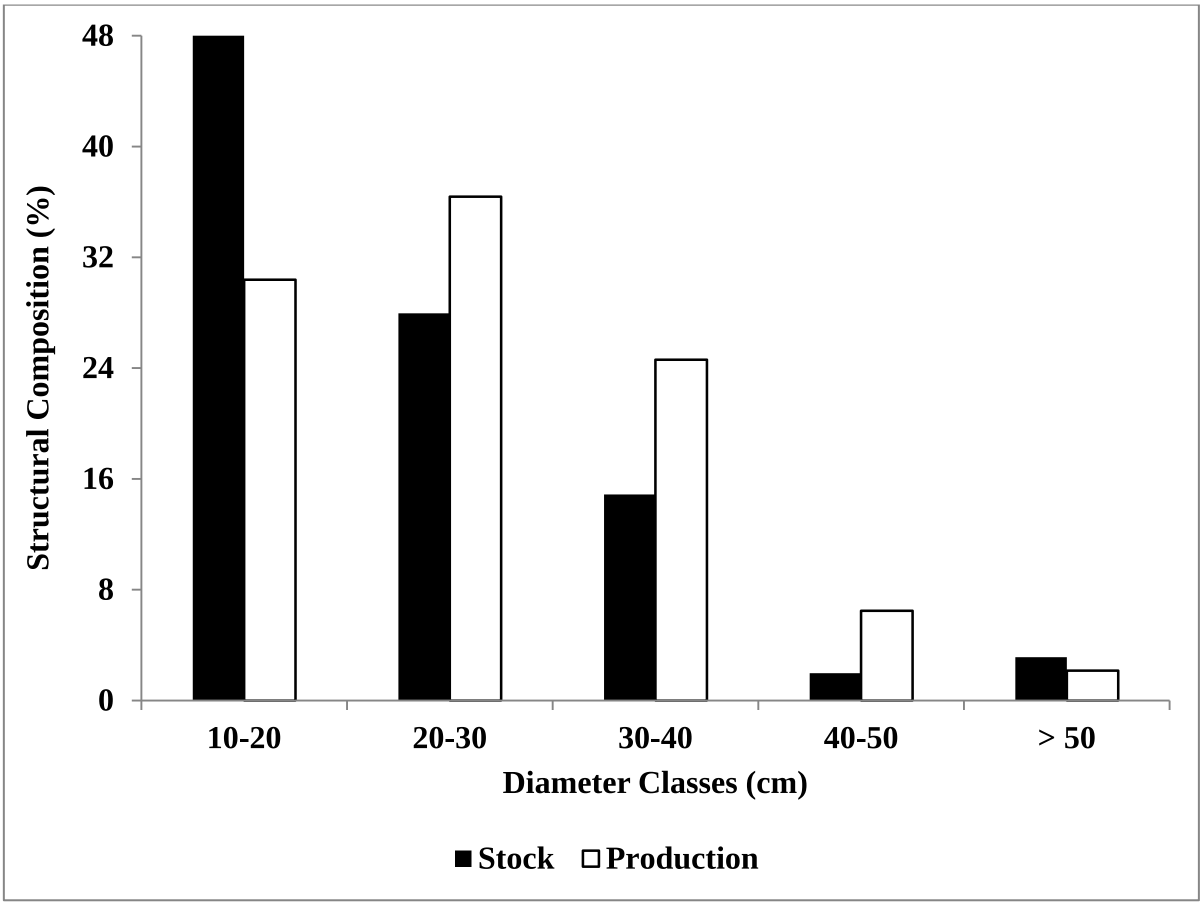

Figure 2 – Structural composition (%) of stock and production of CWD by diameter classes, based on the total amounts of necromass observed for all forest types sampled.

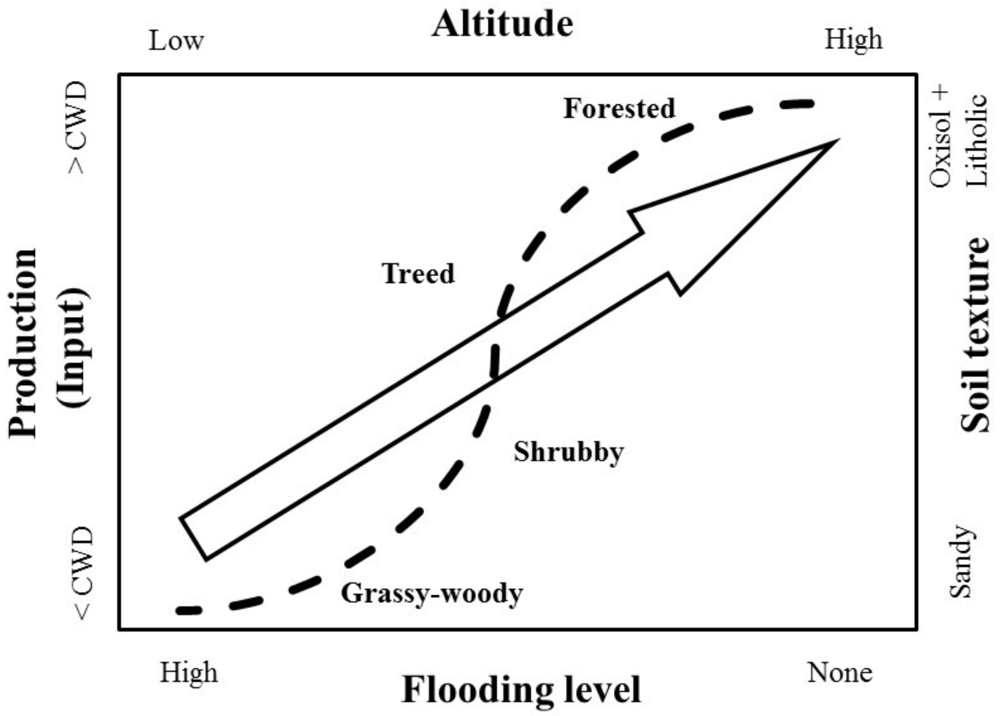

Figure 3 – Conceptual model for production (input) of coarse woody debris (CWD) taking into account hydro-edaphic features in Viruá National Park, Roraima, Brazilian Amazonia.

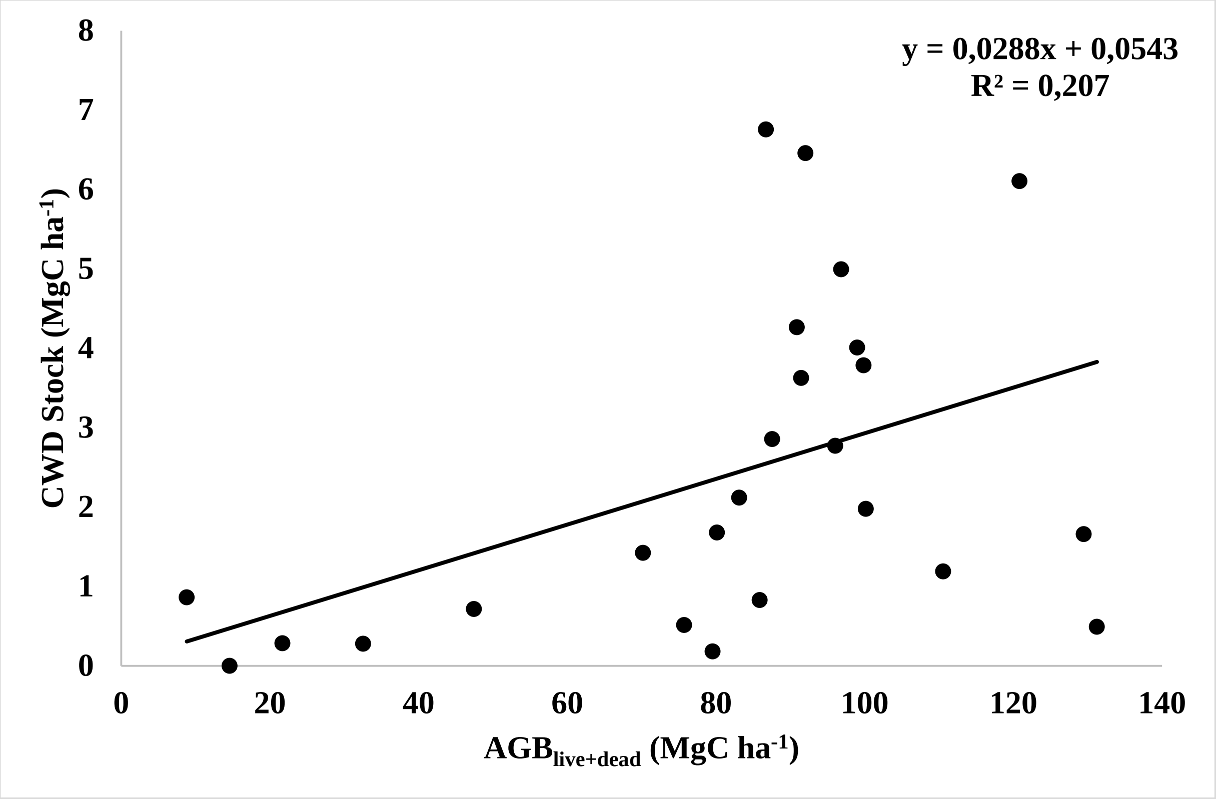

Figure 4 – Linear regression expressing the relationship between the CWD carbon stock and the aboveground tree carbon stock (live + dead; DBH ≥ 10 cm).

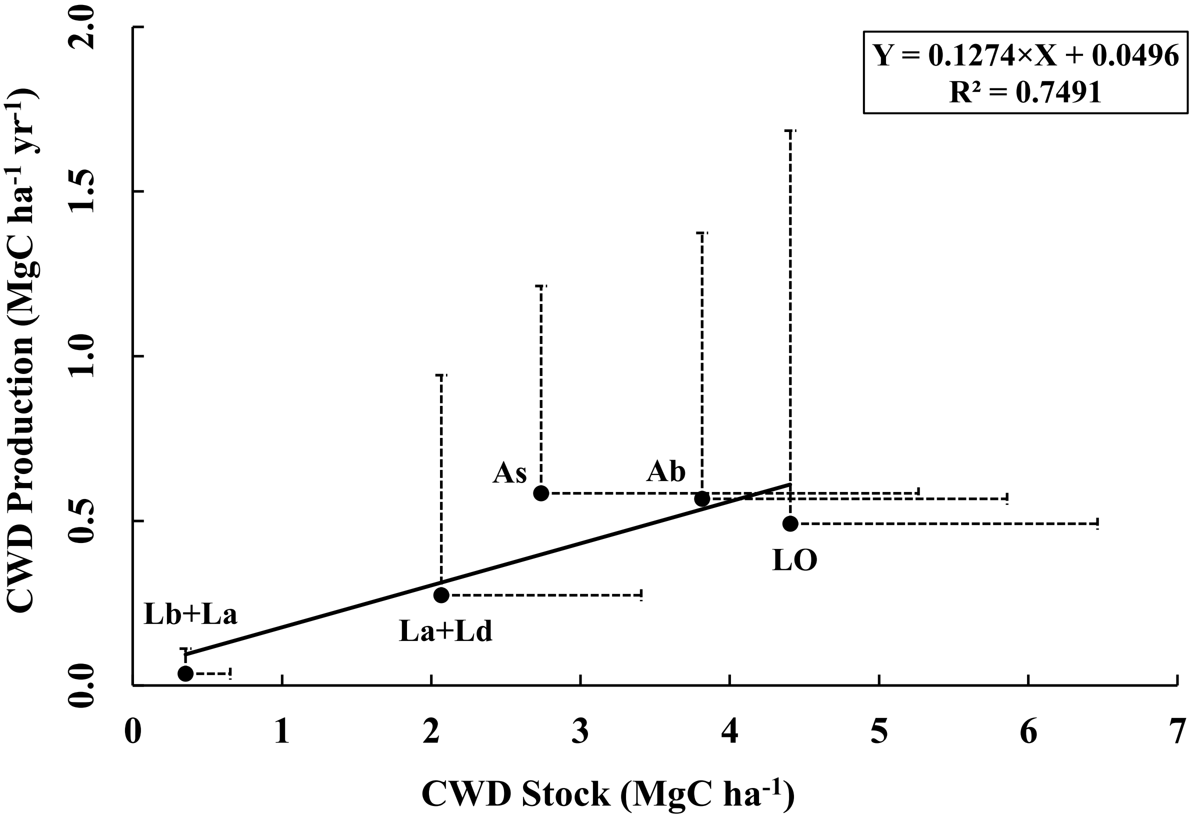

Figure 5 - Relationship between stock and production of coarse woody debris carbon stock in the forest types along a hydro-edaphic gradient in Viruá National Park. Vertical and horizontal bars represent standard deviations.

TABLES

Table 1 – Vegetation types dispersed along the hydro-edaphic gradient at Viruá National Park, Roraima, Brazilian Amazonia.

Vegetation Types (1)	Brazilian Code (IBGE) (3)	Hydroedaphic Gradient Description (3)	Trail Length (km)	Altitude (m) (Mean±SD)	Mean groundwater level (cm) (4)
Open-canopy submontane rainforest	As	Low mountains and Inselbergs on Oxisols, Inseptisols and Leptsols	5.1	106.9±40.9	0
Open-canopy rainforest on non-flooding lowlands	Ab	Hills and Dissected Forested Slopes on Inseptisols and Oxisols; Open-canopy rainforest on Yellow Oxisols	10.3	57.3±3.6	0
Contact between *campinarana* and rainforest	LO	Ramps and pediplained surfaces in ecotone areas covered by open-canopy rainforest on Oxisols and Inseptisols; Ecotones (open-canopy rainforest of palms and lianas / Forested *campinarana*); Geological transition areas between Forested *campinarana* (white-sand forest) and Open rainforest associated with regions with hills and sandy plateaus with forested *campinarana*	6.9	52.6±2.0	0-20
Mosaic (Treed shade-loving *campinarana* and Forested shade-loving *campinarana*)	La+Ld	Drainage area of the Iruá River on hydromorphic soils; Geological transition areas at the edges of Forested *campinaranas* following the transition soils of the geological transition areas covered by Treed and Shrubby *campinaranas*	21.9	50.3±1.6	20-40
Mosaic (Shrubby shade-loving *campinarana* and Treed shade-loving *campinarana*)	Lb+La	Sandy plain covered by Treed and Shrubby *campinaranas*; Mosaic of sandy flooding lowland surfaces covered by Shrubby *campinarana* and areas covered by Treed and Forested *campinaranas*	9.4	49.7±0.5	40-80
Mosaic (Grassy-woody shade-loving *campinarana* and Shrubby shade-loving *campinarana*)	Lg+Lb	Valleys and depressions with swampy fields and semi-aquatic vegetation on hydromorphic sandy soils; Sandy swampy fields with Grassy-woody *campinarana* on Spodosols	6.25	49.6±0.6	40-80
Water	A	Aquatic environments (small rivers and lakes)	0.15	49.2±0.4	-

(1) Vegetation types as described by Nogueira *et al.* (2015) following the official Brazilian classification (Brazil, IBGE, 2012); (2) Brazilian vegetation codes (Brazil, IBGE, 2012); (3) hydro-edaphic gradient as described by Schaefer *et al.* (2008) and Mendonça *et al*. (2013) using geo-environmental conditions; (4) mean groundwater level in the flooding period estimated of the data Vale *et al.* (2014).

Table 2 – Wood density (g cm^{-3}; mean ± SD) of necromass by decomposition category, forest type (as shown in Table 1) and taxonomic group in Viruá National Park. Values in parentheses represent the number of sample disks used to estimate the means.

Decomposition Categories (1)	Forest Types (2)					Taxonomic Groups		Mean (3)
	As	Ab	LO	La+Ld	Lb+La	Dicotyledons	Arecaceae	
P1	0.519 (18)	0.560 (41)	0.534 (19)	0.535 (43)	0.551 (2)	0.541±0.127 (123)	0.434±0.142 (13)	0.531±0.132^{b} (136)
P2	0.467 (10)	0.480 (5)	0.513 (2)	0.428 (7)	0.505 (3)	0.458±0.103 (27)	0.385±0.152 (3)	0.449±0.108^{a} (30)
P3	0.326 (5)	0.511 (8)	0.530 (1)	0.450 (14)	0.479 (4)	0.450±0.108 (32)	0.231±0.009 (3)	0.434±0.119^{a} (35)
Mean (3)	0.479±0.137^{A} (33)	0.524±0.130^{A} (54)	0.511±0.148^{A} (22)	0.509±0.124^{A} (64)	0.504±0.083^{A} (9)	0.516±0.126^{a} (182)	0.403±0.146^{b} (19)	0.506±0.132 (201)

(1) P1 (sound) – pieces with no perceptible deterioration, recently fallen and resistant to microorganism attack (net loss of mass ≤ 10%), P2 (intermediate) – pieces with few signs of insect and/or fungal attack, deterioration in the initial stage (11-30% lost) and P3 (rotten) – pieces in advanced stage of decomposition, breaking or shattering to the touch (> 30% lost); (2) It was not found CWD production and stock (≥ 10 cm) in the "Lg+Lb" vegetation type (3) Lowercase (taxonomic groups and decomposition categories) and uppercase (forest types) indicate significant differences between the means (ANOVA, Tukey test, α=0.05).

Table 3 – CWD production (carbon input) in different forest types in Viruá National Park, Roraima.

Forest Types (1)	CWD Production (Mg ha^{-1} yr^{-1}) (2)			%C	Carbon Input (MgC ha^{-1} yr^{-1})
	Standing	Fallen	Annual Input		
As	0.14	1.13	1.27	46.09	0.58
Ab	0.15	1.09	1.23	45.93	0.57
LO	0.11	0.95	1.06	46.29	0.49
La+Ld	0.44	0.16	0.60	45.91	0.27
Lb+La	0	0.08	0.08	45.89	0.04

(1) Forest types are ordered along a hydro-edaphic gradient varying with respect to soil, topography, flood height, and flooded period by topographic zone as described in Table 1 and diagrammed in Fig. S1 (Supplementary Material), where As has the lowest restriction and Lb+La has the highest restriction.

(2) (2) No CWD production (≥ 10 cm) was found in the Lg+Lb vegetation type.

Table 4 – CWD carbon stock and CWD carbon as a percentage (%) of aboveground tree carbon (live + dead).

Forest Types (1)	Permanent Plots	Tree biomass (Mg ha^{-1}) (2)	Tree carbon (Mg C ha^{-1}) (3)	CWD Stock Mg ha^{-1} (MgC ha^{-1})			CWD carbon as % of total tree carbon (live+dead)	Range
				Standing	Fallen	Total (4)		
As	4	179.04±16.99	86.84	0.11 (0.05)	5.82 (2.68)	5.93±5.49 (2.74)	3.05	0.96-7.01
Ab	5	187.92±23.82	91.14	1.18 (0.54)	7.12 (3.27)	8.30±4.45 (3.81)	4.02	1.07-7.79
LO	4	198.37±29.00	96.21	0.94 (0.44)	8.58 (3.97)	9.52±4.45 (4.41)	4.38	2.55-5.16
La+Ld	7	191.85±61.87	93.05	0.15 (0.07)	4.50 (2.00)	4.50±2.92 (2.07)	2.17	0.37-3.96
Lb+La	6	79.34±64.24	38.48	0.00 (0.00)	0.77 (0.35)	0.77±0.65 (0.35)	0.91	0.00-9.76
Lg+Lb	3	5.28±7.67	2.56	-	-	-	-	-
Aquatic environments	1	-	-	-	-	-	-	-

(1) Forest types are ordered along a hydro-edaphic gradient varying with respect to soil, topography, flood height, and flooded period by topographic zone as described in Table 1 and diagrammed in Fig. S1 (Supplementary Material), where As has the lowest restriction and Lg+Lb has the highest restriction.

(2) Tree biomass = aboveground live tree biomass (DBH ≥ 10 cm) calculated from a forest inventory conducted by C.V. de Castilho in 30 permanent plots in the PPBio grid at Viruá

(3) Tree carbon = estimates of the carbon contained in live aboveground tree biomass calculated based on a concentration of 48.5% C for Amazonian trees (Silva, 2007).

(4) Total CWD = stock of CWD (fallen + standing) and carbon contained in CWD (in parentheses; MgC ha^{-1}) calculated by forest type taking into account the %C values in Table 3.

SUPPLEMENTARY MATERIAL

Production and stock of coarse woody debris across a hydro-edaphic gradient of oligotrophic forests in the northern Brazilian Amazon

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Table S1 – Physical mass loss (% hollows) observed in CWD pieces collected on the grid trails is Viruá National Park, by decomposition category, forest type and taxonomic group. Values in parentheses represent standard deviations (± SD).

Decomposition Categories	Lb+La	La+Ld	LO	Ab	As	Mass loss (%)		Mean (%)
						Dicotyledons	Arecaceae	
P1 (< 10%)	1.0	1.5	1.0	0.9	2.2	1.3	1.4	1.4
	(1.4)	(2.8)	(3.0)	(2.0)	(3.5)	(2.7)	(3.0)	(2.7)
P2 (11-30%)	21.9	15.9	13.9	19.4	17.5	17.7	14.4	15.9
	(7.1)	(7.2)	(6.2)	(5.8)	(5.1)	(6.1)	(3.0)	(7.9)
P3 (> 31%)	49.6	61.9	65.1	47.5	52.8	56.1	61.3	56.6
	(14.7)	(21.8)	-	(19.4)	(20.0)	(19.3)	(22.2)	(19.2)
Mean (%)	31.9	14.9	5.1	10.3	16.9	13.4	12.9	13.1
	(25.9)	(24.8)	(13.6)	(19.9)	(22.8)	(22.3)	(23.4)	(22.4)

(1) To calculate necromass of the CWD pieces we used the basic wood density (g cm^{-3}) of each sample collected in the field (see Table 1). The volume of each sample (disk) was calculated multiplying the area (cm^2) of each piece (determined by scanning) by its average of thickness (cm). After this step, all wood pieces were dried in an electric oven at ~100 °C until they reached constant weight. Basic wood density was calculated by dividing dry weight (g) by wet volume (cm^3) following Fearnside (1997).

$$D_b = \frac{P_s}{V_s}$$

Where:

D_b = wood density (g cm^{-3});

P_S = dry weight of each piece (g);

V_S = volume of each piece (cm^3), considering field water saturation.

(2) To adjust the solid volume calculation of each sample, discounted physical losses by decomposition we scanned all collected pieces. A drawing of the contour of each piece was made on paper showing the perimeter of the piece. The thickness of each sample disk was recorded at four points (see Figure S3). The purpose of this task was to obtain an average thickness closer for subsequent calculation of wood density. Each drawing had as its main interest the representation of all lost and residual portions of each sample piece (see Figure S4). Scanning was performed with a Digital Scanner at 1200 dpi to obtain high-resolution images. The estimate of the number of pixels (residual wood and lost mass) was obtained with a digital image manipulation computer program as in Chao *et al.* (2008). After this stage, all results were placed in a database to estimate the percentage of physical loss in each piece by taxonomic group, category of decomposition and forest type.

Table S2 - Production and stock of coarse woody debris (CWD) in different forest formations of the Brazilian Amazon. AGB_{live} = live tree aboveground biomass (DBH ≥ 10 cm). Reference Value = stock of CWD as % of tree biomass (AGB_{live} + CWD stock).

Number	**Brazilian state**	**Locality**	**Latitude**	**Longitude**	**Dominant phyto-physiognomy**	**Treatment**	**Input CWD (Mg ha^{-1} yr)**	**Stock CWD (Mg ha^{-1})**	**AGB$_{live}$ (Mg ha^{-1})**	**Reference Value (%)**	**Note**	**Fonte**
1	Roraima	PARNA Viruá	01° 36' N	61° 13' W	Open-canopy rainforest submontane	Undisturbed	0.58	2.74	86.8	3.05	Based in carbon values (AGB to DBH ≥ 10 cm)	This study
2	Roraima	PARNA Viruá	01° 36' N	61° 13' W	Open-canopy rainforest on non-flooding lowlands	Undisturbed	0.57	3.81	91.1	4.02	Based in carbon values (AGB to DBH ≥ 10 cm)	This study
3	Roraima	PARNA Viruá	01° 36' N	61° 13' W	Contact between campinarana and rainforest	Undisturbed	0.49	4.41	96.2	4.38	Based in carbon values (AGB to DBH ≥ 10 cm)	This study
4	Roraima	PARNA Viruá	01° 36' N	61° 13' W	Mosaic Treed *campinarana* and Forested *campinarana*	Undisturbed	0.27	2.07	93.0	2.17	Based in carbon values (AGB to DBH ≥ 10 cm)	This study
5	Roraima	PARNA Viruá	01° 36' N	61° 13' W	Mosaic Shrubby *campinarana* and Treed *campinarana*	Undisturbed	0.04	0.35	38.5	0.91	Based in carbon values (AGB to DBH ≥ 10 cm)	This study
6	Roraima	ESEC Maracá	-	-	Upland forest	Undisturbed	-	3.81	-	-	Estimated taking into account the total of necromass / Project Maracá (1987/88)	Scott *et al.* (1992)
7	Amazonas	BR 319	-	-	Forests on soils with no physical restriction	Undisturbed	-	33.10	248.2	11.77	Permanent plots dispersed along BR 319	Martins *et al.*(2015)
8	Amazonas	BR 319	-	-	Forests on soils with low physical restriction	Undisturbed	-	33.70	218.8	13.35	Permanent plots dispersed along BR 319	Martins *et al.*(2015)
9	Amazonas	BR 319	-	-	Forests on soils with high physical restriction	Undisturbed	-	16.80	198.8	7.79	Permanent plots dispersed along BR 319	Martins *et al.*(2015)
10	Amazonas	Experimental Station for Forest Management (INPA)	02° 37' - 02° 38' S	60° 11' W	Upland forest	Undisturbed	2.23	25.10	362.2	6.48	Production estimated taking into account unpublished data	Summers (1998)

11	Amazonas	Experimental Station for Forest Management (INPA)	02º 37' a 02º 38' S	60º 11' W	Upland forest	Undisturbed	1.45	11.40	384.2	2.88	Production estimated taking into account unpublished data	Summers (1998)
12	Amazonas	Experimental Station for Forest Management (INPA)	02º 37' a 02º 38' S	60º 11' W	Upland forest	Undisturbed	4.49	52.60	328.8	13.79	Production estimated taking into account unpublished data	Summers (1998)
13	Amazonas	PDBFF and Experimental Station for Forest Management (INPA)	02º 30' S	60º W	Dense-canopy rainforest	Undisturbed	3.60	21.00	-	-	Production based on tree mortality and on the assumption that 85% of the dead pieces have diameter ≥ 10 cm	Chambers *et al.* (2000)
14	Amazonas	PDBFF and Experimental Station for Forest Management (INPA)	02º 30' S	60º W	Dense-canopy rainforest	Undisturbed	0.9 (0.3-1.6)	-	324.0	-	Structural loss of trees (branch and crown) ≥ 10 cm in diameter, without accounting for tree mortality	Chambers *et al.* (2001)
15	Amazonas	ZF-Manaus	-	-	Dense-canopy rainforest	Fragmented forest edge	6.63	34.13	320.5	9.62	Production based on tree mortality plus (tree structural loss) multiplied by 0.85 (pieces ≥ in diameter).	Nascimento and Laurance (2004)
16	Amazonas	ZF-Manaus	-	-	Dense-canopy rainforest	Fragmented forest interior	4.00	25.43	329.4	7.17	Production based on tree mortality plus (tree structural loss) multiplied by 0.85 (pieces ≥ in diameter).	Nascimento and Laurance (2004)
17	Mato Grosso	Juruena	10º 28' S	58º 30' W	Open-canopy rainforest	Undisturbed	5.30	31.17	276-313	9.57	CWD measured by difference between years (indirect measured). Standing dead trees were not accounted.	Pauletto (2006)
18	Mato Grosso	Juruena	10º 28' S	58º 30' W	Open-canopy rainforest	Logged (2 years)	0.70	17.22	276-313	5.52	CWD measured by difference between years (indirect measured). Standing dead trees were not accounted.	Pauletto (2006)
19	Mato Grosso	Juruena	10º 28' S	58º 30' W	Open-canopy rainforest	Logged (6-7 years)	1.70	16.90	276-313	5.43	CWD measured by difference between years (indirect measured). Standing dead trees were not accounted.	Pauletto (2006)

20	Mato Grosso	Juruena	10° 28' S	58° 30' W	Open-canopy rainforest	Logged (11-12 years)	4.70	22.81	276-313	7.19	CWD measured by difference between years (indirect measured). Standing dead trees were not accounted.	Pauletto (2006)
21	Mato Grosso	Juruena	10.48° S	58.47° W	Open forest	Undisturbed	-	43.20	263.0	14.11	-	Palace *et al.* (2007)
22	Mato Grosso	Juruena	10.48° S	58.47° W	Open forest	Logging	-	67.30	263.0	20.38	-	Palace *et al.* (2007)
23	Pará	Cauaxi	3.23° S	48.29° W	Dense-canopy rainforest	Undisturbed	-	43.80	-	-	Stock based only on fallen necromass	Keller *et al.* (2004)
24	Pará	Cauaxi	3.23° S	48.29° W	Dense-canopy rainforest	Undisturbed	-	52.70	-	-	Stock based only on fallen necromass	Keller *et al.* (2004)
25	Pará	Cauaxi	3.23° S	48.29° W	Dense-canopy rainforest	Reduced impact logging	-	61.60	-	-	Stock based only on fallen necromass	Keller *et al.* (2004)
26	Pará	Cauaxi	3.23° S	48.29° W	Dense-canopy rainforest	Reduced impact logging	-	67.50	-	-	Stock based only on fallen necromass	Keller *et al.* (2004)
27	Pará	Cauaxi	3.23° S	48.29° W	Dense-canopy rainforest	Conventional logging	-	105.90	-	-	Stock based only on fallen necromass	Keller *et al.* (2004)
28	Pará	Cauaxi	3.23° S	48.29° W	Dense-canopy rainforest	Conventional logging	-	88.60	-	-	Stock based only on fallen necromass	Keller *et al.* (2004)
29	Pará	FLONA Tapajós	3.04° S	54.55° W	Dense-canopy rainforest	Undisturbed	-	45.10	282.0	13.79	Stock based only on fallen necromass	Keller *et al.* (2004)
30	Pará	FLONA Tapajós	3.04° S	54.55° W	Dense-canopy rainforest	Undisturbed	-	44.40	282.0	13.60	Stock based only on fallen necromass	Keller *et al.* (2004)
31	Pará	FLONA Tapajós	3.04° S	54.55° W	Dense-canopy rainforest	Reduced impact logging	-	66.40	282.0	19.06	Stock based only on fallen necromass	Keller *et al.* (2004)
32	Pará	FLONA Tapajós	3.04° S	54.55° W	Dense-canopy rainforest	Reduced impact Logging	-	48.40	282.0	14.65	Stock based only on fallen necromass	Keller *et al.* (2004)
33	Pará	FLONA Tapajós	02° 51' S	54° 58' W	Dense-canopy rainforest	Undisturbed	-	43.30	143.7	23.16	Values presented as Carbon (AGB to DBH ≥ 10 cm). Using LIS and permanent plots for different CWD diameter.	Rice *et al.* (2004)
34	Pará	FLONA Tapajós	3.08° S	54.94° W	Dense forest	Undisturbed	-	52.40	282.0	15.67	-	Palace *et al.* (2007)

35	Pará	FLONA Tapajós	3.08° S	54.94° W	Dense forest	Logging	-	70.30	282.0	19.95	-	Palace *et al.* (2007)
36	Pará	FLONA Tapajós	3.08° S	54.94° W	Dense forest	Undisturbed	4.70	44.40	282.0	13.60	Mean (4.5 years)	Palace *et al.* (2008)
37	Pará	FLONA Tapajós	3.08° S	54.94° W	Dense forest	Logging	6.40	79.70	282.0	22.03	Mean (4.5 years)	Palace *et al.* (2008)
38	Pará	Paragominas	03° S	50° W	Evergreen forest	Undisturbed	-	55.00	364.0	13.13	AGB total (live+dead)	Gerwing (2002)
39	Pará	Paragominas	03° S	50° W	Evergreen forest	Moderately logged	-	76.00	321.0	19.14	AGB total (live+dead)	Gerwing (2002)
40	Pará	Paragominas	03° S	50° W	Evergreen forest	Heavily logged	-	149.00	317.0	31.97	AGB total (live+dead)	Gerwing (2002)
41	Pará	Paragominas	03° S	50° W	Evergreen forest	Logged and lightly burned	-	101.00	279.0	26.58	AGB total (live+dead)	Gerwing (2002)
42	Pará	Paragominas	03° S	50° W	Evergreen forest	Logged and heavily burned	-	128.00	178.0	41.83	AGB total (live+dead)	Gerwing (2002)
43	Pará	FLONA Tapajós	02° 51' S	54° 58' W	Dense forest	Undisturbed	-	40.7	197.0	17.12	Values presented as Carbon (AGB to DBH ≥ 10 cm). Using transects.	Pyle *et al.* (2008)
44	Amazonas	ZF-Manaus	02° 30' S	60° W	Dense forest	Fragmented	-	16.2	190.0	7.86	Values presented as Carbon (AGB to DBH ≥ 10 cm). Using permanent plots.	Pyle *et al.* (2008)
45	-	E Amazonia	-	-	Upland forest	Undisturbed	-	36.00	284.7	11.23	Mean for the Eastern of the Pan-Amazon	Chao *et al.* (2009)
46	-	NE Amazonia	-	-	Upland forest	Undisturbed	-	39.90	328.9	10.82	Mean for the Northeastern of the Pan-Amazon	Chao *et al.* (2009)
47	-	NW Amazonia	-	-	Upland forest	Undisturbed	-	24.50	238.2	9.33	Mean for the Northwestern of the Pan-Amazon	Chao *et al.* (2009)
48	-	S Amazonia	-	-	Upland forest	Undisturbed	-	17.40	206.7	7.76	Mean for the Southern of the Pan-Amazon	Chao *et al.* (2009)
49	-	SW Amazonia	-	-	Upland forest	Undisturbed	-	17.50	216.5	7.48	Mean for the Southwestern of the Pan-Amazon	Chao *et al.* (2009)
50	-	Amazonia	-	-	Upland forest	Undisturbed	-	33.00	275.5	10.70	Mean for the entire Pan-Amazon	Chao *et al.* (2009)
51	-	104 Neotropical studies	-	-	Neotropical forests	Neotropical forests	3.10	-	-	-	Production based on Carbon. Range from 1.5 to 5.5 tC ha^{-1} (CWD ≥ 10 cm)	Malhi *et al.* (2004)

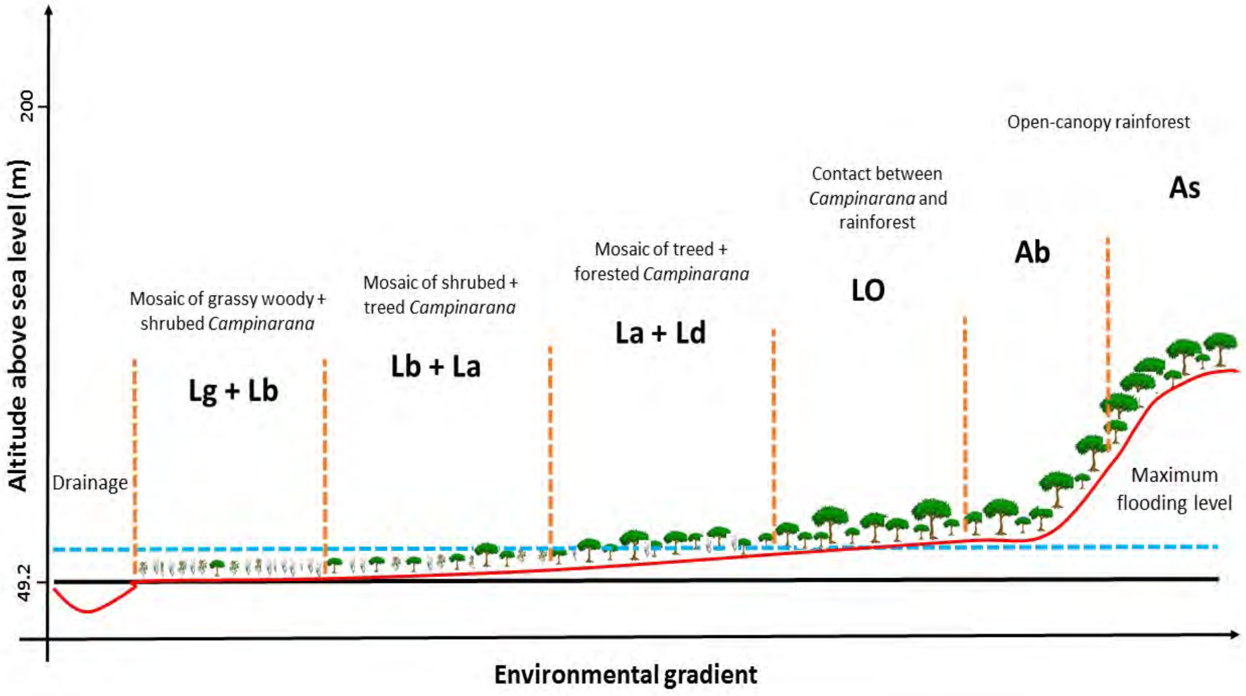

Figure S1 – Vegetation types associated with the conceptual hydro-edaphic gradient in Viruá National Park, Roraima.

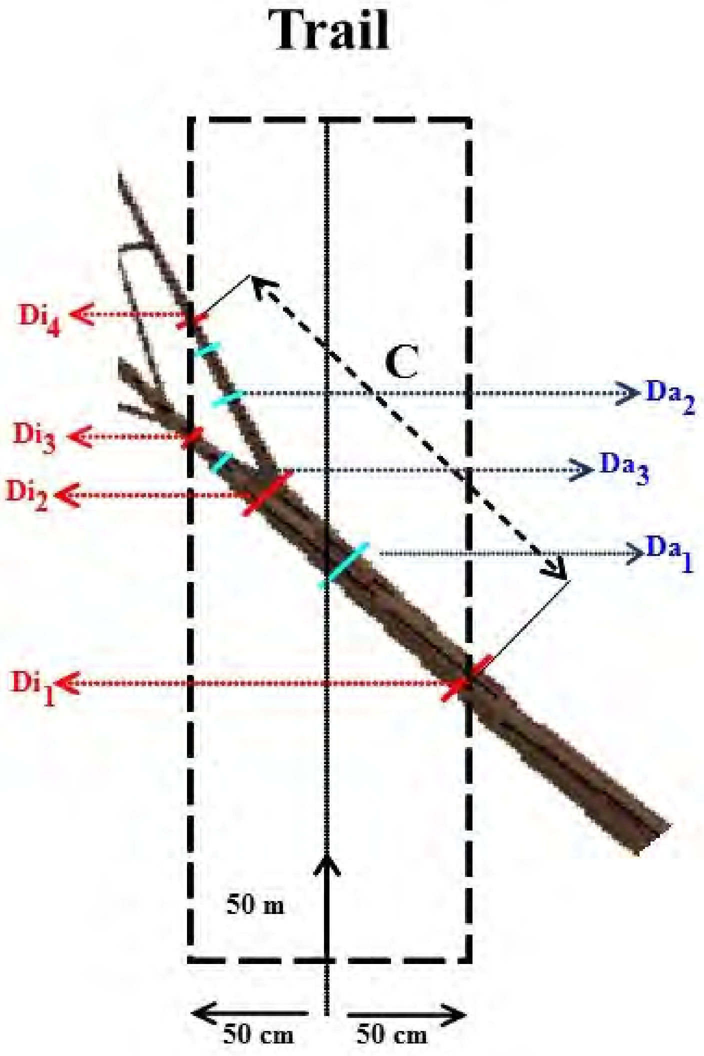

Figure S2 – Sampling scheme for measuring wood pieces (branches and trunks) and collect of the sampling disks (i) Di$_1$ and Di$_2$ = diameters of the first wood piece; Di$_2$ and Di$_3$ = diameters of the second wood piece (1st bifurcation); Di$_2$ and Di$_4$ = diameters of the third wood piece (2nd bifurcation); (ii) Da$_1$, Da$_2$ and Da$_3$ = place of collection of the three sampling disks (a single tree can contain several sampling disks) and (iii) C = length of the piece.

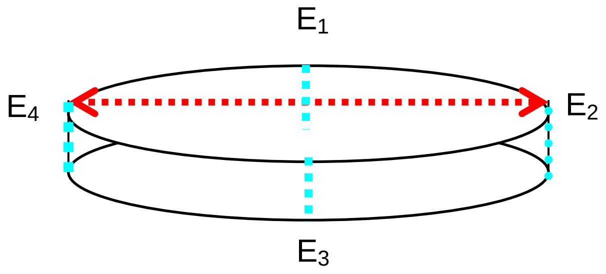

Figure S3 – Schematic drawing showing sampling disk and the location of the workpiece thickness measured positions. E_1 and E_2 are measurements smaller diameter positions, and E3 and E4 are measurements larger diameter positions.

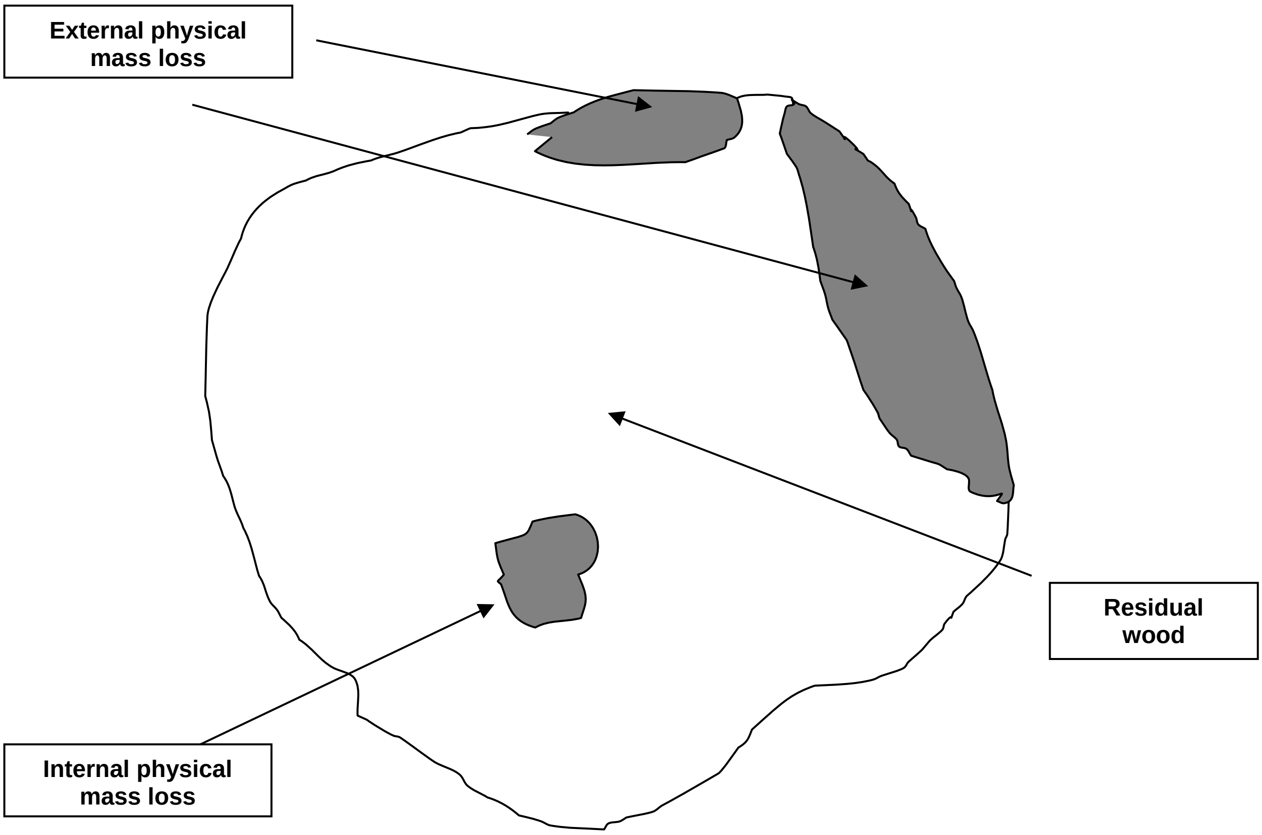

Figure S4 – Schematic drawing of the cross section of a wood piece collected as a sample disk of CWD.

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Production and stock of coarse woody debris across a hydro-edaphic gradient of oligotrophic forests in the northern Brazilian Amazon

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Abstract

Most studies on coarse woody debris (CWD) in Brazilian Amazonia have been done in disturbed and undisturbed upland forests. However, oligotrophic forest types occupying seasonal flooding environments have been neglected, although they occupy about one-third of the Amazon region. We examined the effect of an environmental gradient with different hydro-edaphic features on production and stock of CWD in an area of the Rio Negro-Rio Branco basin, in Brazil's state of Roraima. We used 60 km of trails (production) and 30 permanent plots (stock) in a sampling grid established at Viruá National Park. Our study demonstrated that production and stock of CWD carbon are the lowest in all of Amazonia. The highest CWD carbon production was found in open-canopy submontane rainforest (0.58±0.63 MgC ha^{-1} yr^{-1}), which occur in environments that are free of any influence of seasonal flooding. The lowest stocks of CWD carbon (0.35±0.30 MgC ha^{-1}) was associated with low tree biomass in forest types occurring on sandy soils that are strongly influenced by seasonal flooding. CWD stocks in oligotrophic forests at Viruá are partially explained (~21%) by tree biomass, which is determined by different environmental conditions across hydro-edaphic gradients. Reference values (CWD carbon as a percentage of tree carbon) were among the lowest in Amazonia (0.91-4.38%), with lower values being associated with formations with low production and stock of CWD. This finding suggests that values vary among oligotrophic forest types and that separate reference values should be adopted for estimates of undisturbed forest carbon stocks in the different ecosystems in Brazilian Amazonia. Different reference values represent the variability of CWD among forest types and contribute to reducing uncertainties in current estimates of carbon stock in Amazonia.

Keywords: necromass; oligotrophic forests; dead biomass; hydro-edaphic determinants.

1. INTRODUCTION

Coarse woody debris (CWD) is defined as necromass of standing and fallen dead trees and the remains of large branches (diameter ≥ 10 cm) (Harmon *et al.*, 1986; Clark *et al.*, 2002; Palace *et al.*, 2012). CWD estimates are useful for understanding changes in functions and forest services under different natural or anthropogenic disturbances (Phillips *et al.*, 2009; Trumbore *et al.*, 2015). One of the needs for this information is as an input for modeling the flammability of forests due to accumulation of necromass on the ground, which represents fuel for forest fires (Barbosa and Fearnside, 1999; Vasconcelos *et al.*, 2013; Balch *et al.*, 2015). CWD can also reach a high percentage of the entire stock of aboveground tree biomass representing a substantial component of the carbon stored in tropical forests (Houghton *et al.*, 2001; Brown, 2002; Malhi *et al.*, 2004). However, uncertainties are still great, especially in Brazilian Amazonia where necromass estimates have received little attention in greenhouse gas emissions inventories (Brazil-MCT, 2010).

In the Brazilian Amazon, the main studies on production (input) and stock (accumulation) of CWD were carried out in central Amazonia (Martius and Bandeira, 1998; Summers, 1998; Chambers *et al.*, 2000; Chambers *et al.*, 2001; Nascimento and Laurance, 2004) and in the "arc of deforestation," especially in Pará (Gerwing, 2002; Keller *et al.*, 2004; Rice *et al.*, 2004; Palace *et al.*, 2007; Palace *et al.*, 2008; Pyle *et al.*, 2008), Amazonas (Martins *et al.*, 2015), Rondônia (Cummings *et al.*, 2002) and Mato Grosso (Pauletto, 2006). Most of these studies focused their attention on the spatial and temporal distribution of CWD stocks and production in upland forests that were fragmented by deforestation or subjected to selective logging. In all cases, forest structure, species composition, soil type, topography and seasonal flooding are seen as natural predictors of greater weight in the formation of biomass values associated with necromass and wood decomposition processes (Laurance *et al.*, 1999; Castilho *et al.*, 2006; Toledo *et al.*, 2011; Martins *et al.*, 2015).

Despite improved understanding of environmental conditions affecting the process of necromass formation, the Brazilian Amazon still has low sampling representativeness in different disturbed and undisturbed forest ecosystems, even when compared to other countries in South America (Malhi *et al.*, 2004). This is because vast forest areas represent great gaps of information on CWD stock and production across latitudinal and longitudinal gradients in the region (Chao *et al.*, 2009; Palace *et al.*, 2012). This sparse spatial representation increases uncertainty about CWD carbon stocks and inputs when they are extrapolated as reference values (necromass / aboveground biomass ratio or CWD carbon as a percentage of tree carbon) to large forest areas under different stages of succession and environmental conditions (Chambers *et al.*, 2013).

One of these gaps is the Rio Negro-Rio Branco basin, which occupies ~600.000 km^2 of Amazonia (Montero and Latrubesse, 2013). Overall, this is a lowland ecoregion that is subject to seasonal flooding and is characterized by a mosaic of upland forests and oligotrophic ecosystems (*campinas* and *campinaranas*), which are vegetation types that often occur on low-fertility sandy soils (Ferreira, 2009; Junk *et al.*, 2011; Mendonça *et al.*, 2014). The phyto-physionomic structures of this ecoregion are directly related to the hydro-edaphic gradient that is determined by different topographical features, soils and flooding levels (Damasco *et al.*, 2013; Targhetta *et al.*, 2015). In this Amazonian ecoregion, few studies have been carried out with the objective of estimating CWD, such as Martius (1997) in flooded forests near Manaus, Amazonas (5.9–11.4 Mg ha^{-1}) and Scott *et al.* (1992) in forests on sandy soils on Maracá Island, Roraima (3.8 Mg ha^{-1}; palms+trees ≥ 10 cm in diameter). Both studies adopted small sampling scales. In a recent review, Nogueira *et al.* (2015) estimated necromass for this ecoregion based on the few existing studies, most of which were from outside the Brazilian Amazon, especially from southern Venezuela (Klinge and Herrera, 1983; Bongers *et al.*, 1985; Kauffman *et al.*, 1988). The lack of regional values leads to greater uncertainty in calculations of carbon stocks and fluxes in Amazon forest. It is therefore important to improve our understanding of the role of this forest compartment in Amazonian ecosystems by investigating the effect of macro-environmental conditions on CWD production and stock. This will provide adjustment options for the Brazilian greenhouse-gas emissions inventories with direct implications for estimates of global carbon flows and pools.

The present study aims to estimate production and stock of CWD in undisturbed forest types in the Rio Negro-Rio Branco basin, in the northern portion of Brazilian Amazonia. The specific objectives of the study were to associate estimates of CWD stock, CWD production, and reference values (% of CWD carbon in relation to aboveground tree carbon [live + dead]) for a mosaic of upland forests with oligotrophic forest types dispersed along an environmental gradient defined by distinct hydro-edaphic conditions.

2. MATERIALS AND METHODS

2.1 Study area

We sampled CWD (standing and fallen dead wood pieces ≥ 10 cm in diameter) for stock and production estimates at a Biodiversity Research Program (PPBio) research site (25 km^2) in Viruá National Park (1° 36' N, 61° 13' W), which is a federal protected area located in the state of Roraima (Fig. 1). Viruá has high environmental heterogeneity with oligotrophic ecosystems (*campinas and campinaranas*) occupying hydromorphic soils, alluvial forests along major watercourses and upland ombrophilous forests scattered in isolated mountain ranges (Damasco *et al.*, 2013). This 215,917-ha park is set in a climatic transition zone (Aw-Am under the Köppen classification system), and the climate is characterized by a dry season (December to March), a wet season (May to August), and an average annual rainfall ranging from 1750 to 2000 mm (Barbosa, 1997; Schaefer *et al.*, 2008). The sampling period (December 2007-December 2008) was a year with ~2100 mm of rainfall, considering the climatological station (Brazilian Institute of Meteorology) located ~35 km from Viruá in the city of Caracaraí. Strong storms with winds occurred naturally in September and October, a period that encompasses the end of rainy season and the beginning of the dry season in this part of the Amazon region.

*** Figure 1

2.2 Sampling design

We estimated production and stock of CWD across a hydro-edaphic gradient spanning six vegetation types (Table 1; Fig. S1, Supplementary Material), varying with respect to soil, topography, flood height, and flooded period (Schaefer *et al.*, 2008; Mendonça *et al.*, 2013; Vale *et al.*, 2014). Vegetation types occurring below 55 m a.s.l. are periodically flooded and are controlled by depositional processes including: (i) recent active sedimentation (Middle Holocene) covered by non-forest vegetation, and (ii) paleo-aeolian dunes and paleo-river bars covered by forest (Zani, 2013). Vegetation types between 55 and 300 m a.s.l. are characterized by presence of *inselbergs*, hills and dissected slopes covered by open-canopy rainforests and forested ecotones. We characterized all vegetation types according to the Brazilian vegetation classification system (Brazil-IBGE, 2012). Sampling was linked to the PPBio grid, a network of 12 trails (6 north-south and 6 east-west; each 1 m in width and 5 km in length) and 30 permanent plots (each 250 m in length) distributed systematically along the 6 east-west trails (Magnusson *et al.*, 2005; Pezzini *et al.*, 2012). We relied on the entire 25-km^2 PPBio grid to obtain robust estimates of CWD stock (sampled in the 30 permanent plots) and of CWD production (sampled along the 12 trails).

*** Table 1

CWD production was estimated in a 6-ha sampling area formed by the sum of all trails crossing the grid (60,000 m × 1 m). The sampling area for each forest type was estimated based on geo-environmental divisions defined by Schaefer *et al.* (2008) (Table 1). All dead branches and trunks (fallen and standing) were removed from the grid trails in December 2007 (t_0) and in December 2008 (t_1) we conducted a census of all new fallen and standing dead pieces on the trails (Fig. S2, Supplementary Material).

The length of each fallen piece was measured up to the limits of the sampling area. For standing-dead trees (no leaves; no small branches or twigs) we measured DBH (diameter at breast height: 1.3 m above the ground) and estimated the biomass of trees by the "moist-forest" model (Chave *et al.*, 2005), discounting 10% for leaves, small branches and twigs, as adopted by Nascimento and Laurance (2004) to calculate necromass volume (m^3). For residual stems (broken trunks) we measured height and stem diameter to estimate the necromass volume based on the formula for a cylinder. In both cases we estimated the percentage of the standing tree or residual stem projected onto the trail limits in order to adjust their participation to represent only material inside the sampling area, as suggested by Harmon and Sexton (1996). For each dead piece we recorded the dominant forest type, the taxonomic group (Arecaceae and Dicotyledons) and the location on the grid taking in account georeferenced landmarks (UTM) established on all trails.

A sample disk was collected from each dead piece to estimate hollow spaces (physical mass loss) and wood density (g cm^{-3}) because the degree of decomposition varies for each dead wood piece, therefore requiring a separate calculation (Supplementary Material: Table S1, Figs. S3 and S4). To determine the degree of decomposition we used categories established by Delaney *et al.* (1998), adjusted in this study by the percentage of physical mass loss: P1 (sound) – pieces with no perceptible deterioration, recently fallen and resistant to microorganism attack (net loss of mass ≤ 10%), P2 (intermediate) – pieces with few signs of insect and/or fungal attacks, deterioration in the initial stage (11-30% lost) and P3 (rotten) – pieces in advanced stage of decomposition, breaking or shattering to the touch (> 30% lost). The necromass estimate was determined following Keller *et al.* (2004), calculating the solid volume for each piece and adjusting this value for wood-density reduction and physical loss:

$$CWD_{input} = \left(\frac{\pi D^2}{4}\right) \times L \times sf \times af \times wd$$

Where: $\mathbf{CWD_{input}}$ = necromass of each piece (Mg); **D** = diameter of each piece in meters (averaging the measurements made at the ends of each fallen piece, DBH for standing trees or diameter for residual stems); **L** = length (or height of residual stem) of each piece in meters; **sf** = solid fraction of the piece (Supplementary Material: Table S1, Figs. S3 and S4); **af** = adjustment factor for standing dead trees only (percentage of dead parts within the sampling area limits); **wd** = wood density (g cm^{-3}).

The stock of CWD of standing dead trees was calculated in the same way as CWD production taking into account dead trees and residual stems that were partially or entirely within of the 1-m width limit along the central line of each permanent plot. The stock of fallen pieces was estimated indirectly based on the line intersect sampling (LIS) method (van Wagner, 1968), with the central line of each permanent plot corresponding to the sampling transect. In each transect we measured the diameters of all the fallen pieces (≥ 10 cm in diameter) that touched a stretched line along the transect in each permanent plot. Wood pieces arranged longitudinally in relation to the central line were not sampled because they cannot undergo the process of mathematical integration between the diameter and the plot length. The volume[1] of each of the fallen pieces was calculated as defined below:

$$V = \frac{\pi^2 \times D^2}{8 \times L}$$

Where: **V** = solid necromass volume of a unit of area; **D** = diameter of each piece touching the sampling line; **L** = length of sampling line.

All pieces were classified by degree of decomposition (tactile and visual) based on the same categories as those defined for CWD production. We assumed a correspondence with

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[1] The LIS method (van Wagner, 1968) can estimate the wood volume of any area by means of a line that crosses fallen trunks (cylinders) of different lengths, diameters and orientations. The sum of the series of vertical elliptical cross sections that are formed by the line crossing provides an estimate of wood volume per unit area as a function of cross-sectional area per unit length of line.

the measured values for CWD production to calculate the average physical mass loss and wood density for each piece accumulated in the plots, taking into account the taxonomic group and the degree of decomposition. This assumption was intended to simplify the calculation and maintain the representativeness of parts that were not sampled directly (Larjavaara and Muller-Landau, 2010). The mass of each piece was estimated based on volume calculated by the LIS method, discounted by the fraction of the physical mass loss corresponding to the degree of decomposition, followed by multiplication by the wood density (defined by taxonomic group).

All sample disks were individually milled to estimate carbon concentration (%C). Approximately 10 g of each sample was sent for analysis in the Soil and Plant Thematic Laboratory of the National Institute for Research in Amazonia (LTSP-INPA), Manaus, Amazonas, Brazil. Analyses were performed using a CHN Auto Analyzer (Vario MAX, Elementar Instruments, Hanau, Germany).

2.3 Data analysis

Production and stock of CWD were calculated for each forest type defined in Table 1. Normality tests and analysis of variance (ANOVA; Tukey Test; $\alpha = 0.05$) were applied to the set of the wood density data associated with the taxonomic group and the degree of decomposition. All values of CWD (production and stock) were transformed into carbon per unit of time and area based on the results of the analysis of carbon concentration (%C). Reference values (% of stock of CWD carbon in relation to carbon in aboveground tree biomass [live+dead]; DBH $\geq$ 10 cm) were estimated from the forest inventory carried out by C.V. de Castilho in all permanent plots in the PPBio grid at Viruá. All trees with DBH $\geq$ 10 cm (Dicotyledons) were transformed into aboveground live tree biomass using the "moist-forest" model (Chave *et al.*, 2005) and a value of 0.642 g cm^{-3} for wood density (Nogueira *et al.*, 2007). Palm biomass (Arecaceae) was calculated using the model of Goodman *et al.* (2013). Carbon in aboveground live tree biomass was estimated using 48.5% C as measured by Silva (2007) for Amazon trees. Correlation analysis (Pearson; $\alpha = 0.05$) and linear regression were performed between carbon in aboveground tree biomass (live+dead; DBH $\geq$ 10 cm) and the carbon stock in CWD as the response variable. All analyses were performed with R software (R Core Team, 2014).

3. RESULTS

3.1 Data description

Estimates of CWD production (60 km of trails = 5.36 ha of forest and 0.64 ha of non-forest vegetation) were based on observation of 201 pieces (190 fallen and 11 standing): 182 (90.5%) of Dicotyledons and 19 (9.5%) of Arecaceae (Table 2). The largest number of pieces (67.7%) were classified as having no perceptible deterioration (P1), indicating that production during the study period was characterized by intact pieces in the early stages of decomposition. To estimate CWD stock we observed 317 pieces (293 fallen and 24 standing): 294 (92.7%) of Dicotyledons and 23 (7.3%) of Arecaceae. In contrast to the production of CWD, most of the pieces in the CWD stock were classified as P3 (69.1%), followed by P2 (17.0%) and P1 (13.9%). Pieces 10-30 cm in diameter (structure) dominated both the production (66.8%) and the stock (80.0%), taking into account the total necromass estimated for all sampled forest types (Fig. 2). Wood density was higher in P1 (0.531 ± 0.132 g cm^{-3}) as compared to other decomposition categories (Tukey test, $p < 0.01$). Wood density of the

Dicotyledons group (0.516 ± 0.126 g cm^{-3}) was higher than that of the Arecaceae group (0.403 ± 0.146 g cm^{-3}) (t test; $p < 0.0047$), but density did not differ among forest types (ANOVA, $p > 0.493$; $F = 0.854$). The mean values for physical mass loss taking into account the decomposition classes, were 1.4% (P1), 15.9% (P2) and 56.6% (P3) (Supplementary Material: Table S1).

*** Table 2

*** Figure 2

3.2 Production and Stock

The annual input of carbon of CWD was higher in open-canopy rainforests (As = 0.58±0.63 MgC ha^{-1} yr^{-1} and Ab = 0.57±0.81 MgC ha^{-1} yr^{-1}) and ecotones (LO = 0.49±1.19 MgC ha^{-1} yr^{-1}) found in environments with little or no influence of seasonal flooding (Table 3). Mosaics of forested *campinaranas* (La+Ld = 0.27±0.67 MgC ha^{-1} yr^{-1}) and shrubby+treed *campinaranas* (Lb+La = 0.04±0.08 MgC ha^{-1} yr^{-1}), located on white-sand hydromorphic soils had the lowest values. The CWD production pattern indicates an association with the hydro-edaphic gradient at Viruá, where the largest CWD inputs are in forest types occurring in topographical zones free of long flooding periods and with better soil conditions as compared to the forest types in areas with greater hydro-edaphic restrictions (Fig. 3, Fig. S1).

*** Table 3

*** Figure 3

The largest CWD stocks were observed in ecotones (LO=9.52±4.45 Mg ha^{-1}) and open-canopy rainforest on non-flooding lowlands (Ab=8.30±4.45 Mg ha^{-1}) (Table 4). Most CWD stock was fallen necromass (92%) and was characterized by high variability (range: 0.77-8.58 Mg ha^{-1}) among all forest types. Carbon in the CWD stock in all forest types analyzed ranged from 0.35 to 4.41 MgC ha^{-1}, corresponding to reference values from 0.91% (shrubby+treed *campinaranas*) to 4.38% (ecotone). The correlation between carbon in aboveground tree biomass (live + dead) and carbon in CWD stock was positive and significant (r_p=0.455; p=0.022), indicating that higher CWD carbon accumulation is partially explained ($R^2 \approx 0.21$) by forest types with little or no influence from fluctuations in groundwater levels along the hydro-edaphic gradient (Fig. 4).

*** Table 4

*** Figure 4

4. DISCUSSION

CWD production in the forest types at Viruá is lower than in all other studies in disturbed and undisturbed forest areas in the central and eastern Amazon (Supplementary Material: Table S2). The highest values for input of CWD carbon at Viruá (0.49-0.58 MgC ha^{-1} yr^{-1}) were six-fold lower when compared with the average value of 3.1 MgC ha^{-1} yr^{-1} estimated for Pan Amazonia as a whole (Malhi *et al.*, 2004). The lower CWD production determined in our study is best explained by the fact that most mature and more productive forests (which have higher tree turnover) in Amazonia are in the central and eastern portions of the region (Phillips *et al.*, 2004; Malhi *et al.*, 2006). These differ from the seasonally flooded oligotrophic environments (*campinas* and *campinaranas*) of the Rio Negro-Rio Branco region in northwestern Amazonia.

Since higher hydro-edaphic restrictions determine lower tree biomass content in oligotrophic forests (Targhetta *et al.*, 2015), naturally lower CWD production at Viruá also decreased in association with forest types with lower tree biomass on poor sandy soils that are subject to frequent flooding and high groundwater levels (anoxia). These ecological distinctions are important because in most spatial macro-analyses in Amazonia (e.g., benchmark maps) the oligotrophic forest types occupying hydromorphic soils are not distinguished due to the map scales used, and in this ecoregion these vegetation types are presented as forest conglomerates (Malhi *et al.*, 2004; Saatchi *et al.*, 2007; Chao *et al.*, 2009). This causes an upward bias when CWD production values are used from other regions where there are fewer restrictions (higher biomass and higher production), or when information is used from sites located outside of Brazilian Amazonia (not representative).

CWD stock at Viruá follows a trend similar to the results for production, with the largest stocks being partially explained by forest type with higher tree biomass occurring where hydro-edaphic restrictions are smaller (Fig. 4). The relationship between tree biomass and CWD stock was also suggested by Chao *et al.* (2008) studying lowland forests (flooding and non-flooding) in Peruvian Amazonia, and by Martins *et al.* (2015) in areas with different edaphic restrictions in Central Amazonia. Although there are disagreements about the effect of forest structure on the CWD stock (e.g., Chao *et al.*, 2009), our results suggest that stocks of CWD at Viruá are partly determined by the forest types that are conditioned by hydro-edaphic features across the environmental gradient.

Since CWD stock is roughly controlled by the input derived from tree biomass (Baker *et al.*, 2004), the relationship between production and stock of CWD can be considered to apply to other parts of the Rio Negro-Rio Branco region, which is where most oligotrophic ecosystems are located in northwest Brazilian Amazonia (Fig. 5). On the other hand, oligotrophic forest types do not necessarily imply lower turnover rates of CWD as compared to other forest ecosystems in Amazonia. This is because the relationship between input and stock is well known and is affected by tree mortality under climatic stress (Lewis *et al.*, 2004; Doughty *et al.*, 2015) or natural and anthropic disturbances (Gerwing, 2002; Nascimento and Laurance, 2004; Rice *et al.*, 2004). In this case, we can assume a steady-state between production, stock and rate of decomposition, estimating 5-10 years as the residence time of CWD in all of the forest types investigated at Viruá. This range follows the pattern expected in forests in central Amazonia (~6 years; Chambers *et al.*, 2000). The CWD residence time in oligotrophic forest types at Viruá indicates that these rates are not affected by environmental variability, and necromass accumulation is approximately stable over time, independent of the position on the environmental gradient.

*** Figure 5

The lower reference values determined for all forest types at Viruá were associated with the formations with low production and stock of CWD. In general, our findings were among the lowest in Amazonia, such as those estimated by Chao *et al.* (2008) for forests on soils with frequent flooding (6.4-15.4%) or those derived from Martins *et al.* (2015) for environments with different hydro-edaphic restrictions (7.8-13.3%) (Supplementary Material: Table S2). These discrepancies indicate great variability among the forest types and environmental conditions with direct impact on estimates of flows and forest carbon stocks in the Amazon region. This debate is important because it involves the use of a single reference value (3%) for all forest types in Brazil's second national greenhouse-gas inventory (Brazil-

MCT, 2010) to adjust the total biomass using the percentage of necromass. Use of a default value makes the calculations easy but linearizes the dynamics of mortality for all forest types. This generates uncertainties in the estimates of current carbon stocks in undisturbed Amazonian ecosystems because forest types have different areas and aboveground carbon stock in trees. Thus, differences of a few percentage points tend to produce discrepancies in individual necromass stocks, and the discrepancy will be greater the larger the area that the ecosystem occupies in the Brazilian Amazon.

The value currently adopted by Brazil should be changed and separate necromass / aboveground biomass ratios (or CWD carbon as a percentage of tree carbon) should be used for each forest type or large formation (e.g., rainforests, seasonal forests, ecotones, etc.), taking advantage of investigations that have already been carried out in different undisturbed ecosystems in the Brazilian Amazon (e.g., Supplementary Material: Table S2). Even understanding that this relationship needs to be better understood based on structural variability of the ecosystems (Pyle *et al.*, 2008), forest dynamics (Chao *et al.*, 2009) and environmental conditions (Baker *et al.*, 2007), there is no doubt that carbon-stock estimates in Amazonian forests would be improved and would gain due the reduction of uncertainties.

5. CONCLUSIONS

Based on our results, we conclude that the environmental gradient at Viruá has a direct effect on production and stock of coarse woody debris (CWD). Forest types located in topographic zones with lower hydro-edaphic restrictions support higher tree biomass and have higher production and stock of CWD. Reference values indicated that formations with low production and stock of CWD are associated with the higher hydro-edaphic restrictions where sandy soils predominate and there is strong influence from seasonal flooding.

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FIGURES

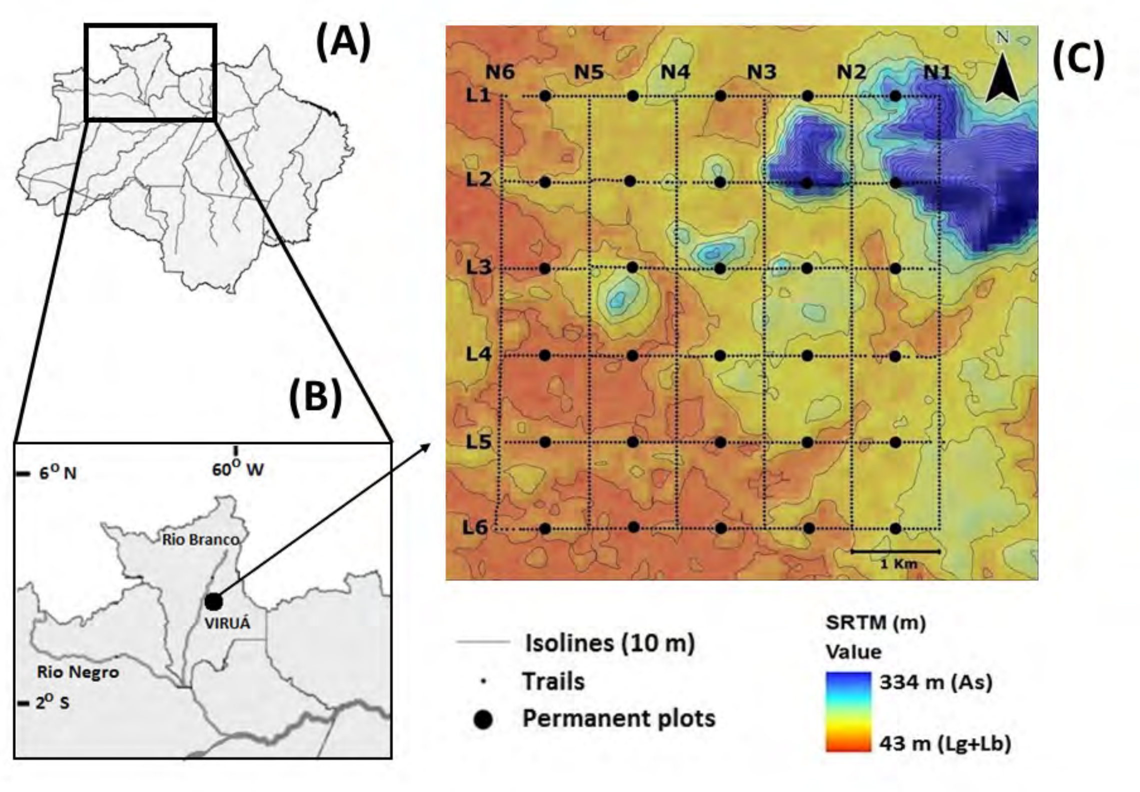

Figure 1 – Study area: (A) Brazilian Amazonia, (B) Rio Negro-Rio Branco Basin, (C) PPBio grid system installed in Viruá National Park - SRTM image provided by Brazilian Biodiversity Research Program (PPBio, 2014).

<u>Online version in color and printed version in black-and-white</u>**.

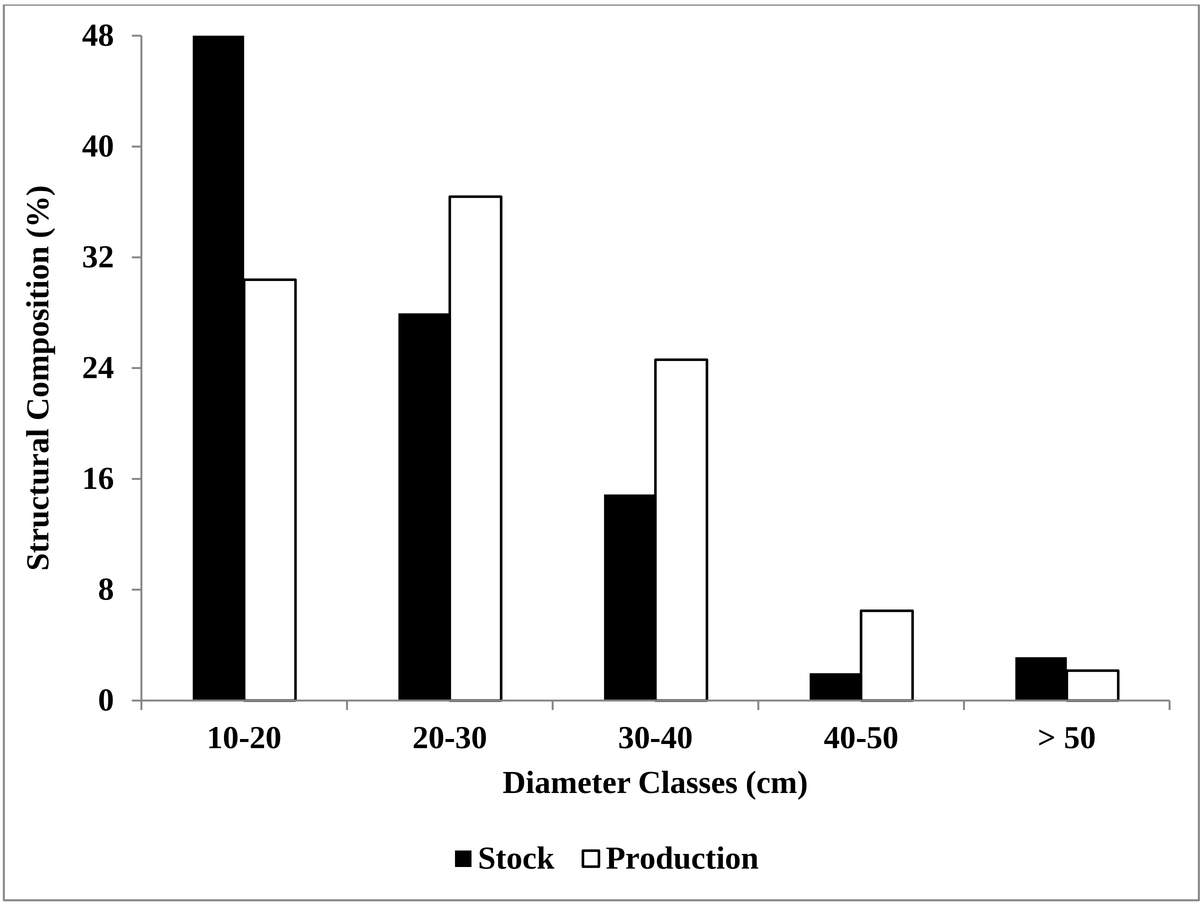

Figure 2 – Structural composition (%) of stock and production of CWD by diameter classes, based on the total amounts of necromass observed for all forest types sampled.

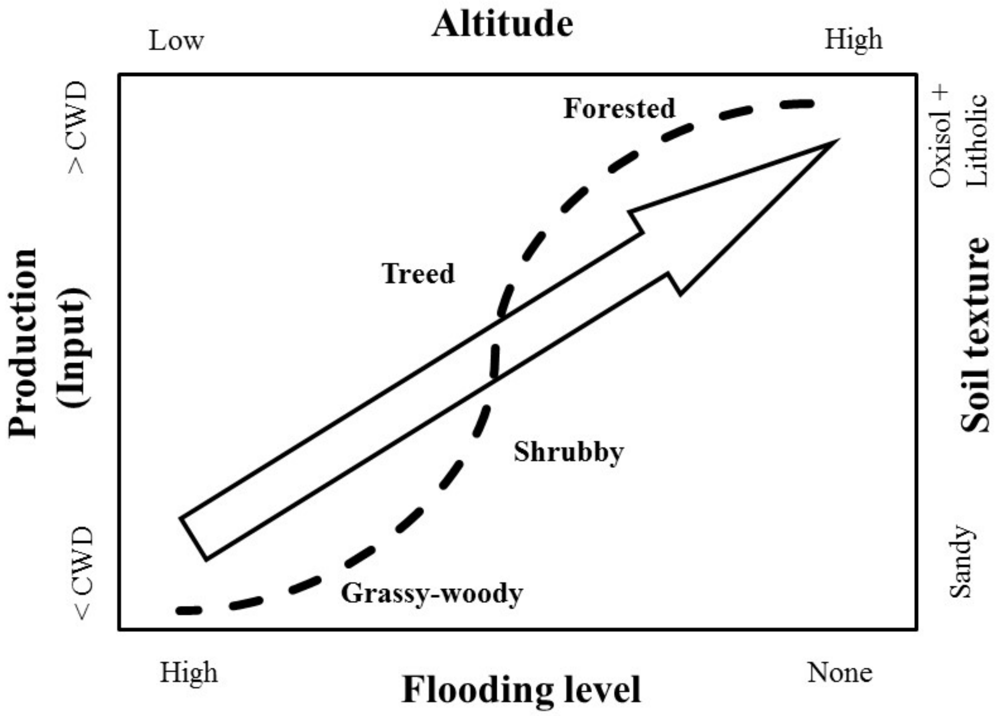

Figure 3 – Conceptual model for production (input) of coarse woody debris (CWD) taking into account hydro-edaphic features in Viruá National Park, Roraima, Brazilian Amazonia.

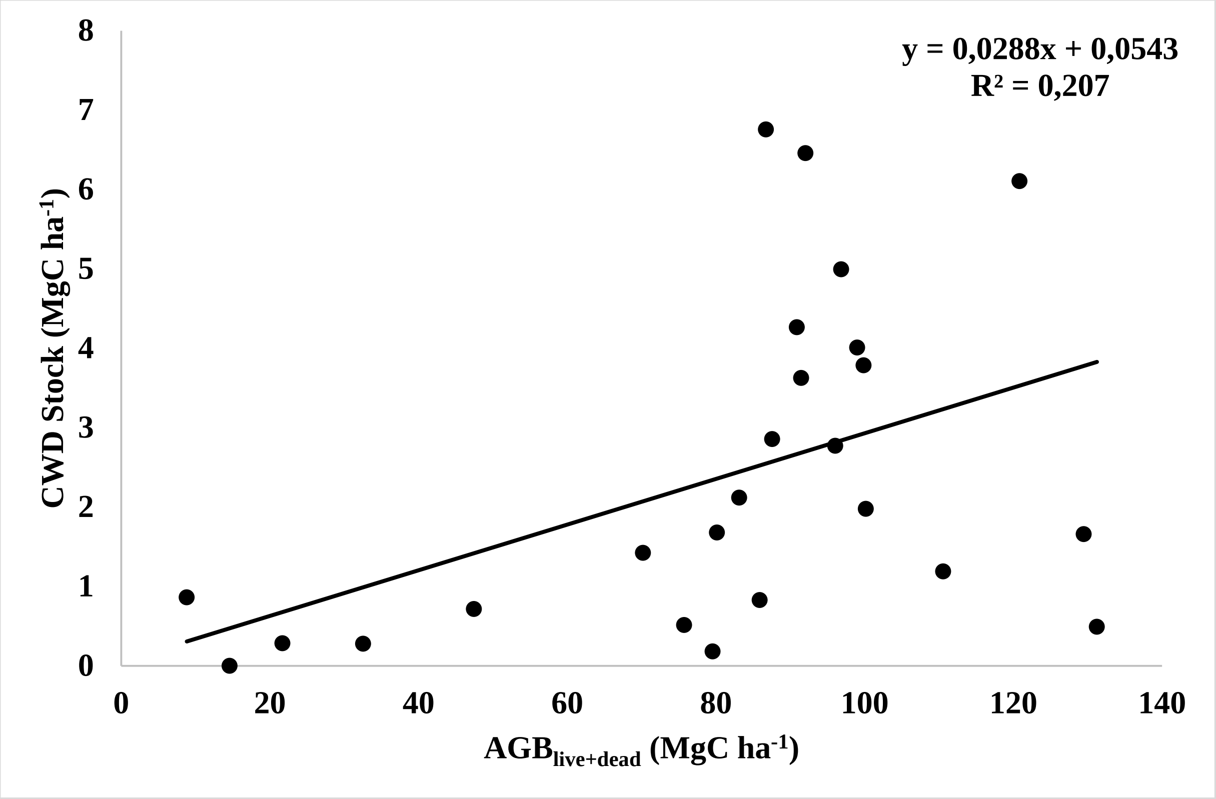

Figure 4 – Linear regression expressing the relationship between the CWD carbon stock and the aboveground tree carbon stock (live + dead; DBH ≥ 10 cm).

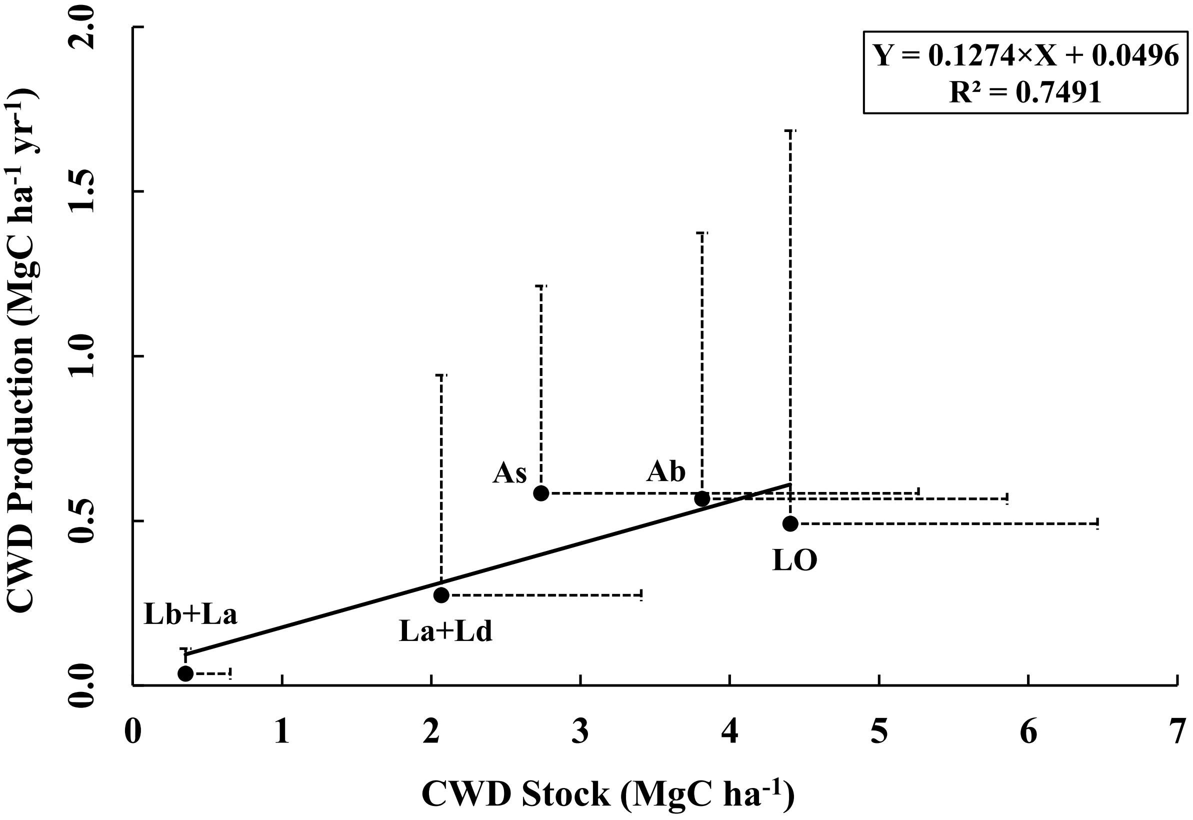

Figure 5 - Relationship between stock and production of coarse woody debris carbon stock in the forest types along a hydro-edaphic gradient in Viruá National Park. Vertical and horizontal bars represent standard deviations.

TABLES

Table 1 – Vegetation types dispersed along the hydro-edaphic gradient at Viruá National Park, Roraima, Brazilian Amazonia.

Vegetation Types (1)	Brazilian Code (IBGE) (3)	Hydroedaphic Gradient Description (3)	Trail Length (km)	Altitude (m) (Mean±SD)	Mean groundwater level (cm) (4)
Open-canopy submontane rainforest	As	Low mountains and Inselbergs on Oxisols, Inseptisols and Leptsols	5.1	106.9±40.9	0
Open-canopy rainforest on non-flooding lowlands	Ab	Hills and Dissected Forested Slopes on Inseptisols and Oxisols; Open-canopy rainforest on Yellow Oxisols	10.3	57.3±3.6	0
Contact between *campinarana* and rainforest	LO	Ramps and pediplained surfaces in ecotone areas covered by open-canopy rainforest on Oxisols and Inseptisols; Ecotones (open-canopy rainforest of palms and lianas / Forested *campinarana*); Geological transition areas between Forested *campinarana* (white-sand forest) and Open rainforest associated with regions with hills and sandy plateaus with forested *campinarana*	6.9	52.6±2.0	0-20
Mosaic (Treed shade-loving *campinarana* and Forested shade-loving *campinarana*)	La+Ld	Drainage area of the Iruá River on hydromorphic soils; Geological transition areas at the edges of Forested *campinaranas* following the transition soils of the geological transition areas covered by Treed and Shrubby *campinaranas*	21.9	50.3±1.6	20-40
Mosaic (Shrubby shade-loving *campinarana* and Treed shade-loving *campinarana*)	Lb+La	Sandy plain covered by Treed and Shrubby *campinaranas*; Mosaic of sandy flooding lowland surfaces covered by Shrubby *campinarana* and areas covered by Treed and Forested *campinaranas*	9.4	49.7±0.5	40-80
Mosaic (Grassy-woody shade-loving *campinarana* and Shrubby shade-loving *campinarana*)	Lg+Lb	Valleys and depressions with swampy fields and semi-aquatic vegetation on hydromorphic sandy soils; Sandy swampy fields with Grassy-woody *campinarana* on Spodosols	6.25	49.6±0.6	40-80
Water	A	Aquatic environments (small rivers and lakes)	0.15	49.2±0.4	-

(1) Vegetation types as described by Nogueira *et al.* (2015) following the official Brazilian classification (Brazil, IBGE, 2012); (2) Brazilian vegetation codes (Brazil, IBGE, 2012); (3) hydro-edaphic gradient as described by Schaefer *et al.* (2008) and Mendonça *et al*. (2013) using geo-environmental conditions; (4) mean groundwater level in the flooding period estimated of the data Vale *et al.* (2014).

Table 2 – Wood density (g cm^{-3}; mean ± SD) of necromass by decomposition category, forest type (as shown in Table 1) and taxonomic group in Viruá National Park. Values in parentheses represent the number of sample disks used to estimate the means.

Decomposition Categories (1)	Forest Types (2)					Taxonomic Groups		Mean (3)
	As	Ab	LO	La+Ld	Lb+La	Dicotyledons	Arecaceae	
P1	0.519 (18)	0.560 (41)	0.534 (19)	0.535 (43)	0.551 (2)	0.541±0.127 (123)	0.434±0.142 (13)	0.531 ± 0.132^{b} (136)
P2	0.467 (10)	0.480 (5)	0.513 (2)	0.428 (7)	0.505 (3)	0.458±0.103 (27)	0.385±0.152 (3)	0.449 ± 0.108^{a} (30)
P3	0.326 (5)	0.511 (8)	0.530 (1)	0.450 (14)	0.479 (4)	0.450±0.108 (32)	0.231±0.009 (3)	0.434 ± 0.119^{a} (35)
Mean (3)	0.479 ± 0.137^{A} (33)	0.524 ± 0.130^{A} (54)	0.511 ± 0.148^{A} (22)	0.509 ± 0.124^{A} (64)	0.504 ± 0.083^{A} (9)	0.516 ± 0.126^{a} (182)	0.403 ± 0.146^{b} (19)	0.506±0.132 (201)

(1) P1 (sound) – pieces with no perceptible deterioration, recently fallen and resistant to microorganism attack (net loss of mass ≤ 10%), P2 (intermediate) – pieces with few signs of insect and/or fungal attack, deterioration in the initial stage (11-30% lost) and P3 (rotten) – pieces in advanced stage of decomposition, breaking or shattering to the touch (> 30% lost); (2) It was not found CWD production and stock (≥ 10 cm) in the “Lg+Lb” vegetation type (3) Lowercase (taxonomic groups and decomposition categories) and uppercase (forest types) indicate significant differences between the means (ANOVA, Tukey test, α=0.05).

Table 3 – CWD production (carbon input) in different forest types in Viruá National Park, Roraima.

Forest Types (1)	CWD Production (Mg ha^{-1} yr^{-1}) (2)			%C	Carbon Input (MgC ha^{-1} yr^{-1})
	Standing	Fallen	Annual Input		
As	0.14	1.13	1.27	46.09	0.58
Ab	0.15	1.09	1.23	45.93	0.57
LO	0.11	0.95	1.06	46.29	0.49
La+Ld	0.44	0.16	0.60	45.91	0.27
Lb+La	0	0.08	0.08	45.89	0.04

(1) Forest types are ordered along a hydro-edaphic gradient varying with respect to soil, topography, flood height, and flooded period by topographic zone as described in Table 1 and diagrammed in Fig. S1 (Supplementary Material), where As has the lowest restriction and Lb+La has the highest restriction.

(2) (2) No CWD production (≥ 10 cm) was found in the Lg+Lb vegetation type.

Table 4 – CWD carbon stock and CWD carbon as a percentage (%) of aboveground tree carbon (live + dead).

Forest Types (1)	Permanent Plots	Tree biomass (Mg ha^{-1}) (2)	Tree carbon (Mg C ha^{-1}) (3)	CWD Stock Mg ha^{-1} (MgC ha^{-1})			CWD carbon as % of total tree carbon (live+dead)	Range
				Standing	Fallen	Total (4)		
As	4	179.04±16.99	86.84	0.11 (0.05)	5.82 (2.68)	5.93±5.49 (2.74)	3.05	0.96-7.01
Ab	5	187.92±23.82	91.14	1.18 (0.54)	7.12 (3.27)	8.30±4.45 (3.81)	4.02	1.07-7.79
LO	4	198.37±29.00	96.21	0.94 (0.44)	8.58 (3.97)	9.52±4.45 (4.41)	4.38	2.55-5.16
La+Ld	7	191.85±61.87	93.05	0.15 (0.07)	4.50 (2.00)	4.50±2.92 (2.07)	2.17	0.37-3.96
Lb+La	6	79.34±64.24	38.48	0.00 (0.00)	0.77 (0.35)	0.77±0.65 (0.35)	0.91	0.00-9.76
Lg+Lb	3	5.28±7.67	2.56	-	-	-	-	-
Aquatic environments	1	-	-	-	-	-	-	-

(1) Forest types are ordered along a hydro-edaphic gradient varying with respect to soil, topography, flood height, and flooded period by topographic zone as described in Table 1 and diagrammed in Fig. S1 (Supplementary Material), where As has the lowest restriction and Lg+Lb has the highest restriction.
(2) Tree biomass = aboveground live tree biomass (DBH ≥ 10 cm) calculated from a forest inventory conducted by C.V. de Castilho in 30 permanent plots in the PPBio grid at Viruá
(3) Tree carbon = estimates of the carbon contained in live aboveground tree biomass calculated based on a concentration of 48.5% C for Amazonian trees (Silva, 2007).
(4) Total CWD = stock of CWD (fallen + standing) and carbon contained in CWD (in parentheses; MgC ha^{-1}) calculated by forest type taking into account the %C values in Table 3.

SUPPLEMENTARY MATERIAL

Production and stock of coarse woody debris across a hydro-edaphic gradient of oligotrophic forests in the northern Brazilian Amazon

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Table S1 – Physical mass loss (% hollows) observed in CWD pieces collected on the grid trails is Viruá National Park, by decomposition category, forest type and taxonomic group. Values in parentheses represent standard deviations (± SD).

Decomposition Categories	Lb+La	La+Ld	LO	Ab	As	Mass loss (%)		Mean (%)
						Dicotyledons	Arecaceae	
P1 (< 10%)	1.0	1.5	1.0	0.9	2.2	1.3	1.4	1.4
	(1.4)	(2.8)	(3.0)	(2.0)	(3.5)	(2.7)	(3.0)	(2.7)
P2 (11-30%)	21.9	15.9	13.9	19.4	17.5	17.7	14.4	15.9
	(7.1)	(7.2)	(6.2)	(5.8)	(5.1)	(6.1)	(3.0)	(7.9)
P3 (> 31%)	49.6	61.9	65.1	47.5	52.8	56.1	61.3	56.6
	(14.7)	(21.8)	-	(19.4)	(20.0)	(19.3)	(22.2)	(19.2)
Mean (%)	31.9	14.9	5.1	10.3	16.9	13.4	12.9	13.1
	(25.9)	(24.8)	(13.6)	(19.9)	(22.8)	(22.3)	(23.4)	(22.4)

(1) To calculate necromass of the CWD pieces we used the basic wood density (g cm^{-3}) of each sample collected in the field (see Table 1). The volume of each sample (disk) was calculated multiplying the area (cm^{2}) of each piece (determined by scanning) by its average of thickness (cm). After this step, all wood pieces were dried in an electric oven at ~100 °C until they reached constant weight. Basic wood density was calculated by dividing dry weight (g) by wet volume (cm^{3}) following Fearnside (1997).

$$D_b = \frac{P_s}{V_s}$$

Where:

D_b = wood density (g cm^{-3});

P_S = dry weight of each piece (g);

V_S = volume of each piece (cm^{3}), considering field water saturation.

(2) To adjust the solid volume calculation of each sample, discounted physical losses by decomposition we scanned all collected pieces. A drawing of the contour of each piece was made on paper showing the perimeter of the piece. The thickness of each sample disk was recorded at four points (see Figure S3). The purpose of this task was to obtain an average thickness closer for subsequent calculation of wood density. Each drawing had as its main interest the representation of all lost and residual portions of each sample piece (see Figure S4). Scanning was performed with a Digital Scanner at 1200 dpi to obtain high-resolution images. The estimate of the number of pixels (residual wood and lost mass) was obtained with a digital image manipulation computer program as in Chao *et al.* (2008). After this stage, all results were placed in a database to estimate the percentage of physical loss in each piece by taxonomic group, category of decomposition and forest type.

Table S2 - Production and stock of coarse woody debris (CWD) in different forest formations of the Brazilian Amazon. AGB$_{live}$ = live tree aboveground biomass (DBH ≥ 10 cm). Reference Value = stock of CWD as % of tree biomass (AGB$_{live}$ + CWD stock). Values for Viruá (this study), Rice *et al.* (2004) and Pyle *et al.* (2008) are presented as C stock of CWD in the “Stock CWD” column and as % of tree carbon in the “AGB$_{live}$ + CWD stock” column. Differences in the calculation of reference values are presented in the “Notes” column.

Number	**Brazilian state**	**Locality**	**Latitude**	**Longitude**	**Dominant phyto-physiognomy**	**Treatment**	**Input CWD (Mg ha^{-1} yr)**	**Stock CWD (Mg ha^{-1})**	**AGB (Mg ha^{-1})**	**Reference Value (%)**	**Notes**	**Reference**
1	Roraima	Viruá	01^{o} 36' N	61^{o} 13' W	Open-canopy rainforest submontane	Undisturbed	**0.58**	**2.74**	**86.8**	**3.05**	**Based in carbon values (AGB for DBH ≥ 10 cm)**	**This study**
2	Roraima	Viruá	01^{o} 36' N	61^{o} 13' W	Open-canopy rainforest on non-flooding lowlands	Undisturbed	**0.57**	**3.81**	**91.1**	**4.02**	**Based in carbon values (AGB for DBH ≥ 10 cm)**	**This study**
3	Roraima	Viruá	01^{o} 36' N	61^{o} 13' W	Contact between campinarana and rainforest	Undisturbed	**0.49**	**4.41**	**96.2**	**4.38**	**Based in carbon values (AGB for DBH ≥ 10 cm)**	**This study**
4	Roraima	Viruá	01^{o} 36' N	61^{o} 13' W	Mosaic Treed *campinarana* and Forested *campinarana*	Undisturbed	**0.27**	**2.07**	**93.0**	**2.17**	**Based in carbon values (AGB for DBH ≥ 10 cm)**	**This study**
5	Roraima	Viruá	01^{o} 36' N	61^{o} 13' W	Mosaic Shrubby *campinarana* and Treed *campinarana*	Undisturbed	**0.04**	**0.35**	**38.5**	**0.91**	**Based in carbon values (AGB for DBH ≥ 10 cm)**	**This study**
6	Roraima	ESEC Maracá	-	-	Upland forest	Undisturbed	-	3.81	-	-	Estimated taking into account the total of necromass / Project Maracá (1987/88)	Scott *et al.* (1992)
7	Amazonas	BR 319	-	-	Forests on soils with no physical restriction	Undisturbed	-	33.10	248.2	11.77	Permanent plots dispersed along BR 319	Martins *et al.*(2015)
8	Amazonas	BR 319	-	-	Forests on soils with low physical restriction	Undisturbed	-	33.70	218.8	13.35	Permanent plots dispersed along BR 319	Martins *et al.*(2015)
9	Amazonas	BR 319	-	-	Forests on soils with high physical restriction	Undisturbed	-	16.80	198.8	7.79	Permanent plots dispersed along BR 319	Martins *et al.*(2015)

10	Amazonas	Experimental Station for Forest Management (INPA)	02^{o} 37' - 02^{o} 38' S	60^{o} 11' W	Upland forest	Undisturbed	2.23	25.10	362.2	6.48	Production estimated taking into account unpublished data	Summers (1998)
11	Amazonas	Experimental Station for Forest Management (INPA)	02^{o} 37' a 02^{o} 38' S	60^{o} 11' W	Upland forest	Undisturbed	1.45	11.40	384.2	2.88	Production estimated taking into account unpublished data	Summers (1998)
12	Amazonas	Experimental Station for Forest Management (INPA)	02^{o} 37' a 02^{o} 38' S	60^{o} 11' W	Upland forest	Undisturbed	4.49	52.60	328.8	13.79	Production estimated taking into account unpublished data	Summers (1998)
13	Amazonas	PDBFF and Experimental Station for Forest Management (INPA)	02^{o} 30' S	60^{o} W	Dense-canopy rainforest	Undisturbed	3.60	21.00	-	-	Production based on tree mortality and on the assumption that 85% of the dead pieces have diameter ≥ 10 cm	Chambers *et al.* (2000)
14	Amazonas	PDBFF and Experimental Station for Forest Management (INPA)	02^{o} 30' S	60^{o} W	Dense-canopy rainforest	Undisturbed	0.9 (0.3-1.6)	-	324.0	-	Structural loss of trees (branch and crown) ≥ 10 cm in diameter, without accounting for tree mortality	Chambers *et al.* (2001)
15	Amazonas	ZF-Manaus	-	-	Dense-canopy rainforest	Fragmented forest edge	6.63	34.13	320.5	9.62	Production based on tree mortality plus (tree structural loss) multiplied by 0.85 (pieces ≥ in diameter).	Nascimento and Laurance (2004)
16	Amazonas	ZF-Manaus	-	-	Dense-canopy rainforest	Fragmented forest interior	4.00	25.43	329.4	7.17	Production based on tree mortality plus (tree structural loss) multiplied by 0.85 (pieces ≥ in diameter).	Nascimento and Laurance (2004)
17	Mato Grosso	Juruena	10^{o} 28' S	58^{o} 30' W	Open-canopy rainforest	Undisturbed	5.30	31.17	276-313	9.57	CWD measured by difference between years (indirect measured). Standing dead trees were not accounted.	Pauletto (2006)
18	Mato Grosso	Juruena	10^{o} 28' S	58^{o} 30' W	Open-canopy rainforest	Logged (2 years)	0.70	17.22	276-313	5.52	CWD measured by difference between years (indirect measured). Standing dead trees were not accounted.	Pauletto (2006)
19	Mato Grosso	Juruena	10^{o} 28' S	58^{o} 30' W	Open-canopy rainforest	Logged (6-7 years)	1.70	16.90	276-313	5.43	CWD measured by difference between years (indirect measured). Standing dead trees were not accounted.	Pauletto (2006)

20	Mato Grosso	Juruena	10º 28' S	58º 30' W	Open-canopy rainforest	Logged (11-12 years)	4.70	22.81	276-313	7.19	CWD measured by difference between years (indirect measured). Standing dead trees were not accounted.	Pauletto (2006)
21	Mato Grosso	Juruena	10.48º S	58.47º W	Open forest	Undisturbed	-	43.20	263.0	14.11	-	Palace *et al.* (2007)
22	Mato Grosso	Juruena	10.48º S	58.47º W	Open forest	Logging	-	67.30	263.0	20.38	-	Palace *et al.* (2007)
23	Pará	Cauaxi	3.23º S	48.29º W	Dense-canopy rainforest	Undisturbed	-	43.80	-	-	Stock based only on fallen necromass	Keller *et al.* (2004)
24	Pará	Cauaxi	3.23º S	48.29º W	Dense-canopy rainforest	Undisturbed	-	52.70	-	-	Stock based only on fallen necromass	Keller *et al.* (2004)
25	Pará	Cauaxi	3.23º S	48.29º W	Dense-canopy rainforest	Reduced impact Logging	-	61.60	-	-	Stock based only on fallen necromass	Keller *et al.* (2004)
26	Pará	Cauaxi	3.23º S	48.29º W	Dense-canopy rainforest	Reduced impact Logging	-	67.50	-	-	Stock based only on fallen necromass	Keller *et al.* (2004)
27	Pará	Cauaxi	3.23º S	48.29º W	Dense-canopy rainforest	Conventional logging	-	105.90	-	-	Stock based only on fallen necromass	Keller *et al.* (2004)
28	Pará	Cauaxi	3.23º S	48.29º W	Dense-canopy rainforest	Conventional logging	-	88.60	-	-	Stock based only on fallen necromass	Keller *et al.* (2004)
29	Pará	FLONA Tapajós	3.04º S	54.55º W	Dense-canopy rainforest	Undisturbed	-	45.10	282.0	13.79	Stock based only on fallen necromass	Keller *et al.* (2004)
30	Pará	FLONA Tapajós	3.04º S	54.55º W	Dense-canopy rainforest	Undisturbed	-	44.40	282.0	13.60	Stock based only on fallen necromass	Keller *et al.* (2004)
31	Pará	FLONA Tapajós	3.04º S	54.55º W	Dense-canopy rainforest	Reduced impact Logging	-	66.40	282.0	19.06	Stock based only on fallen necromass	Keller *et al.* (2004)
32	Pará	FLONA Tapajós	3.04º S	54.55º W	Dense-canopy rainforest	Reduced impact Logging	-	48.40	282.0	14.65	Stock based only on fallen necromass	Keller *et al.* (2004)
33	Pará	FLONA Tapajós	02º 51' S	54º 58' W	Dense-canopy rainforest	Undisturbed	-	43.30	143.7	23.16	Values presented as Carbon (AGB for DBH ≥ 10 cm). Using LIS and permanent plots for different CWD diameter.	Rice *et al.* (2004)
34	Pará	FLONA Tapajós	3.08º S	54.94º W	Dense forest	Undisturbed	-	52.40	282.0	15.67	-	Palace *et al.* (2007)

35	Pará	FLONA Tapajós	3.08^{o} S	54.94^{o} W	Dense forest	Logging	-	70.30	282.0	19.95	-	Palace *et al.* (2007)
36	Pará	FLONA Tapajós	3.08^{o} S	54.94^{o} W	Dense forest	Undisturbed	4.70	44.40	282.0	13.60	Mean (4.5 years)	Palace *et al.* (2008)
37	Pará	FLONA Tapajós	3.08^{o} S	54.94^{o} W	Dense forest	Logging	6.40	79.70	282.0	22.03	Mean (4.5 years)	Palace *et al.* (2008)
38	Pará	Paragominas	03^{o} S	50^{o} W	Evergreen forest	Undisturbed	-	55.00	364.0	13.13	AGB total (live+dead)	Gerwing (2002)
39	Pará	Paragominas	03^{o} S	50^{o} W	Evergreen forest	Moderately logged	-	76.00	321.0	19.14	AGB total (live+dead)	Gerwing (2002)
40	Pará	Paragominas	03^{o} S	50^{o} W	Evergreen forest	Heavily logged	-	149.00	317.0	31.97	AGB total (live+dead)	Gerwing (2002)
41	Pará	Paragominas	03^{o} S	50^{o} W	Evergreen forest	Logged and lightly burned	-	101.00	279.0	26.58	AGB total (live+dead)	Gerwing (2002)
42	Pará	Paragominas	03^{o} S	50^{o} W	Evergreen forest	Logged and heavily burned	-	128.00	178.0	41.83	AGB total (live+dead)	Gerwing (2002)
43	Pará	FLONA Tapajós	02^{o} 51' S	54^{o} 58' W	Dense forest	Undisturbed	-	40.7	197.0	17.12	Values presented as Carbon (AGB for DBH ≥ 10 cm). Using transects.	Pyle *et al.* (2008)
44	Amazonas	ZF-Manaus	02^{o} 30' S	60^{o} W	Dense forest	Fragmented	-	16.2	190.0	7.86	Values presented as Carbon (AGB for DBH ≥ 10 cm). Using permanent plots.	Pyle *et al.* (2008)
45	-	E Amazonia	-	-	Upland forest	Undisturbed	-	36.00	284.7	11.23	Mean for the Eastern of the Pan-Amazon	Chao *et al.* (2009)
46	-	NE Amazonia	-	-	Upland forest	Undisturbed	-	39.90	328.9	10.82	Mean for the Northeastern of the Pan-Amazon	Chao *et al.* (2009)
47	-	NW Amazonia	-	-	Upland forest	Undisturbed	-	24.50	238.2	9.33	Mean for the Northwestern of the Pan-Amazon	Chao *et al.* (2009)
48	-	S Amazonia	-	-	Upland forest	Undisturbed	-	17.40	206.7	7.76	Mean for the Southern of the Pan-Amazon	Chao *et al.* (2009)
49	-	SW Amazonia	-	-	Upland forest	Undisturbed	-	17.50	216.5	7.48	Mean for the Southwestern of the Pan-Amazon	Chao *et al.* (2009)
50	-	Amazonia	-	-	Upland forest	Undisturbed	-	33.00	275.5	10.70	Mean for the entire Pan-Amazon	Chao *et al.* (2009)
51	-	104 Neotropical studies	-	-	Neotropical forests	Neotropical forests	3.10	-	-	-	Production based on Carbon. Range from 1.5 to 5.5 tC ha^{-1} (CWD ≥ 10 cm)	Malhi *et al.* (2004)

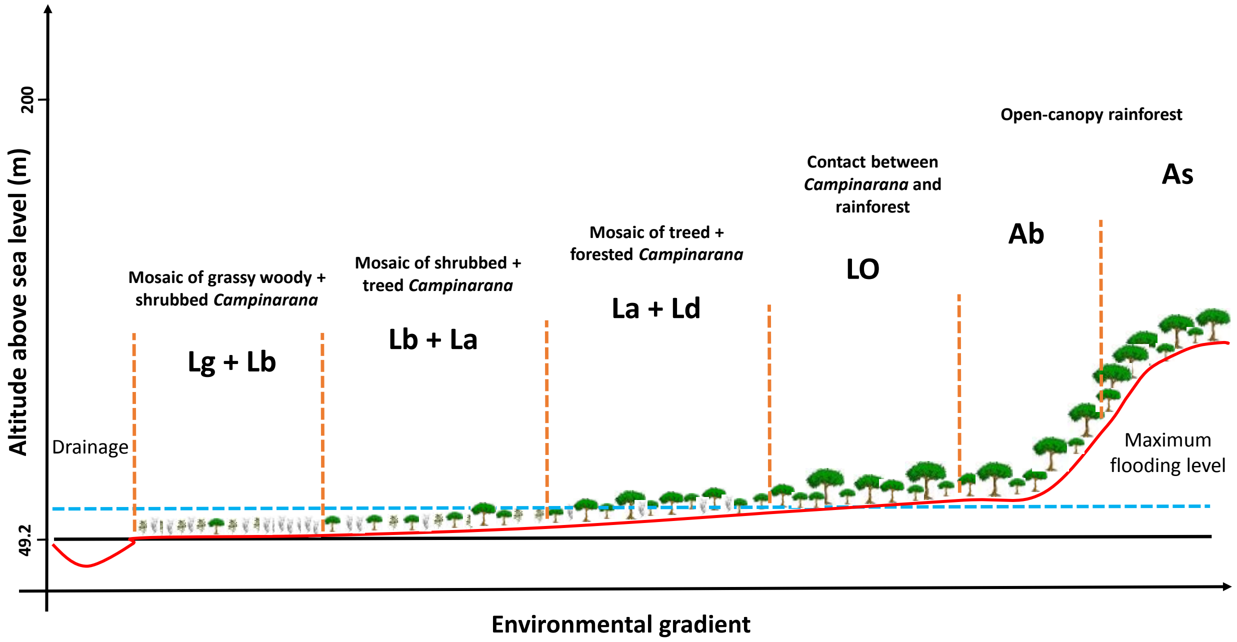

Figure S1 – Vegetation types associated with the conceptual hydro-edaphic gradient in Viruá National Park, Roraima.

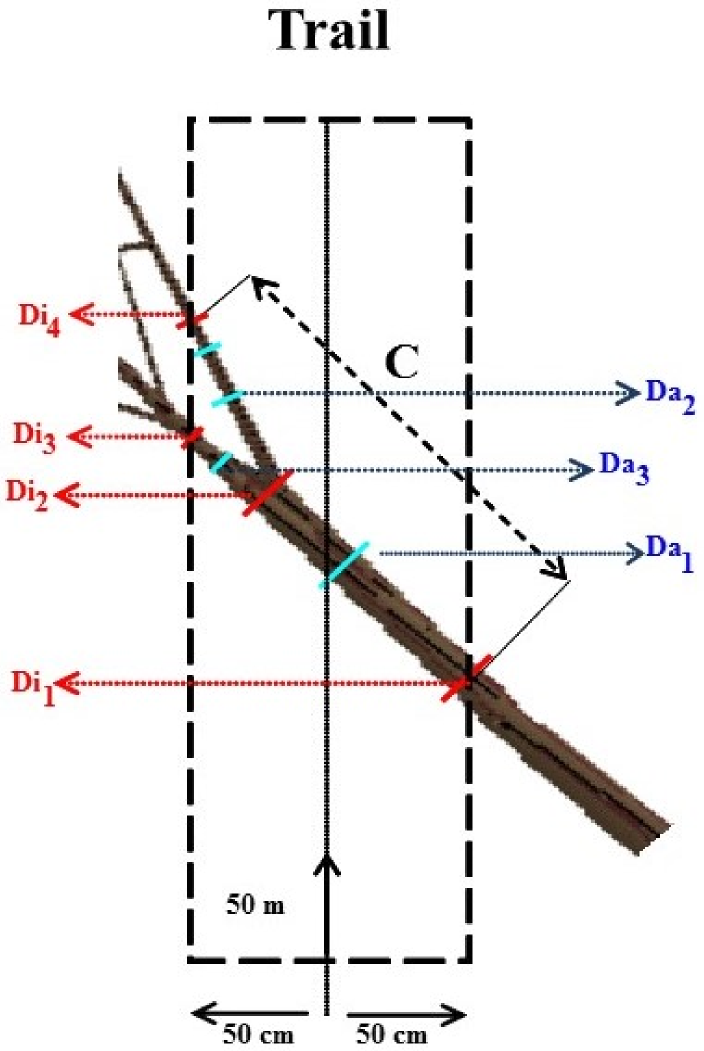

Figure S2 – Sampling scheme for measuring wood pieces (branches and trunks) and collect of the sampling disks (i) Di_1 and Di_2 = diameters of the first wood piece; Di_2 and Di_3 = diameters of the second wood piece (1st bifurcation); Di_2 and Di_4 = diameters of the third wood piece (2nd bifurcation); (ii) Da_1, Da_2 and Da_3 = place of collection of the three sampling disks (a single tree can contain several sampling disks) and (iii) C = length of the piece.

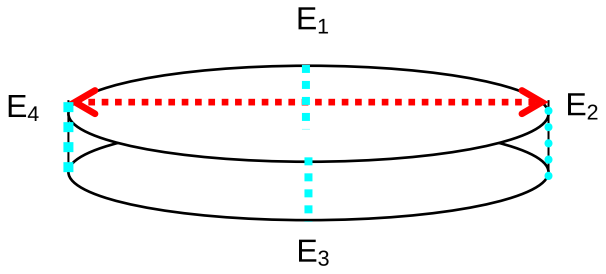

Figure S3 – Schematic drawing showing sampling disk and the location of the workpiece thickness measured positions. E_1 and E_2 are measurements smaller diameter positions, and E3 and E4 are measurements larger diameter positions.

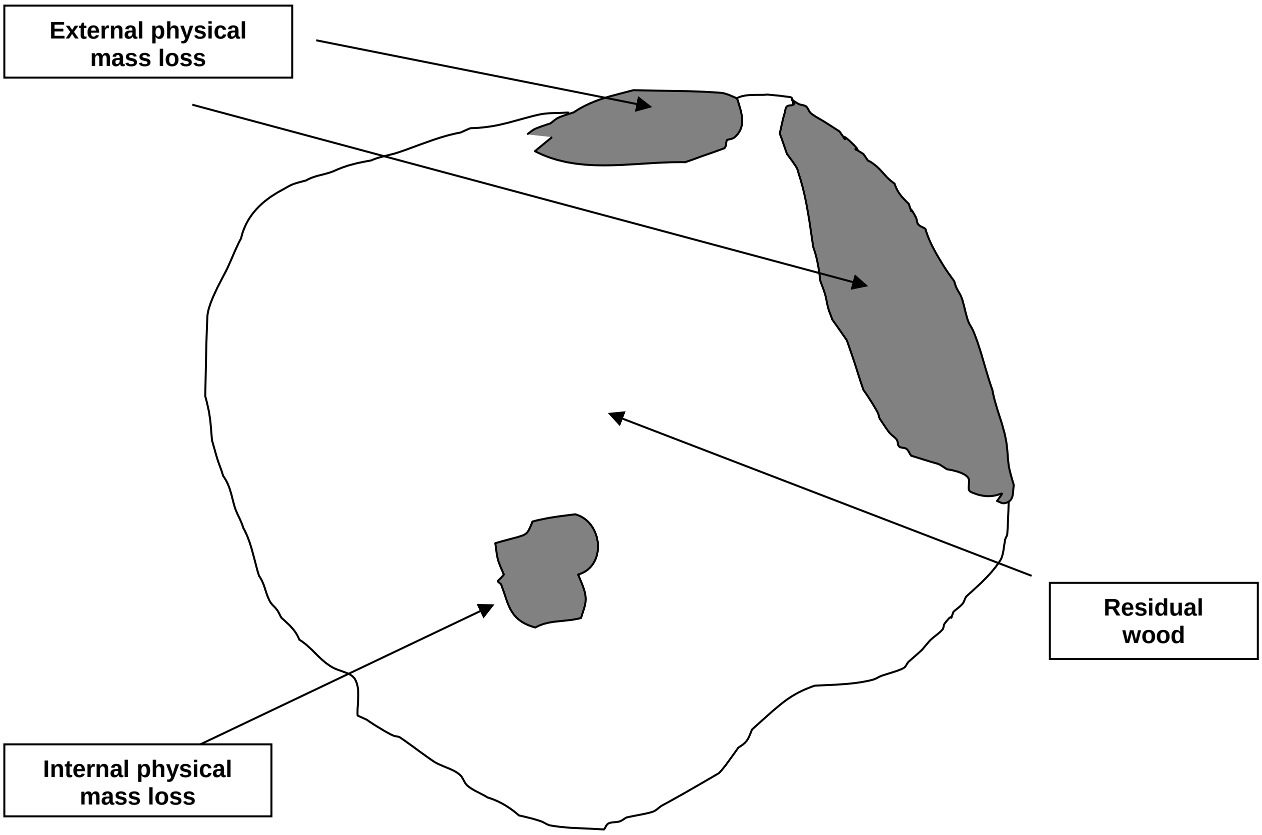

Figure S4 – Schematic drawing of the cross section of a wood piece collected as a sample disk of CWD.

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