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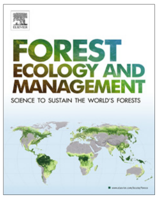

Production and stock of coarse woody debris across a hydro-edaphic gradient of oligotrophic forests in the northern Brazilian Amazon

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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.

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, 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, 2008; Pyle et al., 2008), Amazonas (Martins et al., 2015), Rondônia (Cummings et al., 2002) and Mato Grosso (Pauletto, 2006). Most of these

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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 $\geqslant$ 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 $\geqslant$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

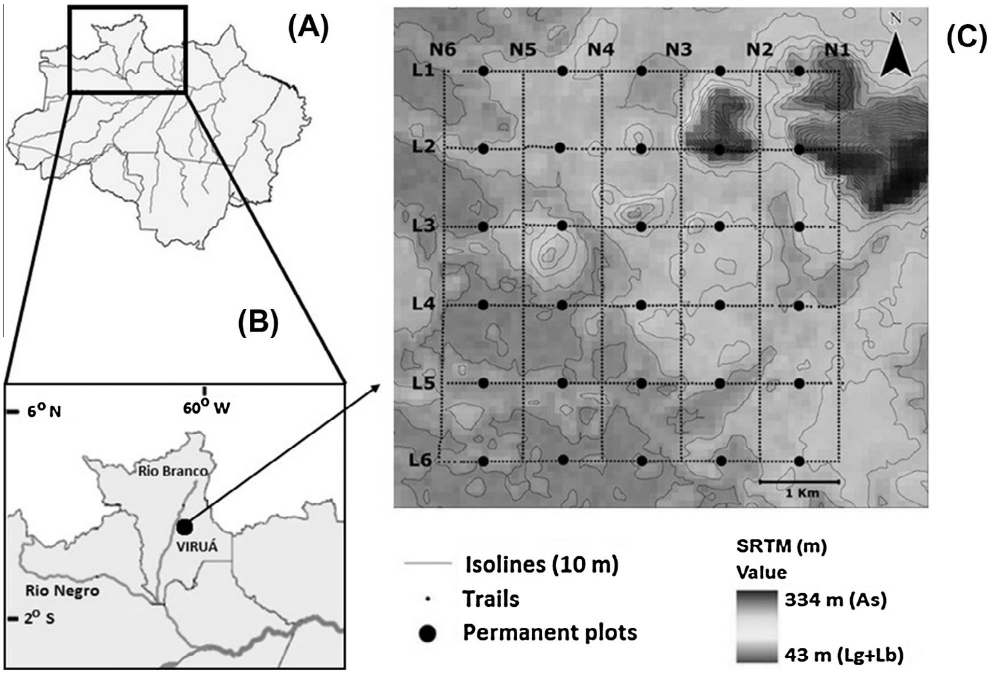

Fig. 1. Study area: (A) Brazilian Amazonia, (B) Rio Negro-Rio Branco basin, (C) PPBio grid system installed in Viruá National Park – SRTM image provided by Brazilian Biodiversity Research Program (PPBio, 2014).

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).

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 ~45 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.

2.2. Sampling design

We estimated production and stock of CWD across a hydro-edaphic gradient spanning six vegetation types (Table 1; Appendix A, Fig. A1), 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).

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 (Appendix A, Fig. A2).

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 (Appendix A, Table A1, Figs. A3 and A4). 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 $\leqslant$ 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:

$$CWD_{input} = \left(\frac{\pi D^2}{4}\right) \times L \times sf \times af \times wd \tag{1}$$

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 $\leqslant$ 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) No CWD production ($\geqslant$10 cm) was found in the "Lg + Lb" vegetation type (grassy-woody).
(3) Lowercase (taxonomic groups and decomposition categories) and uppercase (forest types) indicate significant differences between the means (ANOVA, Tukey test, $\alpha = 0.05$).

where 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 (Appendix A, Table A1, Figs. A3 and A4); 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 ($\geqslant$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:

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

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 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 $\geqslant$ 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 $\geqslant$ 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 $\geqslant$ 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

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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.

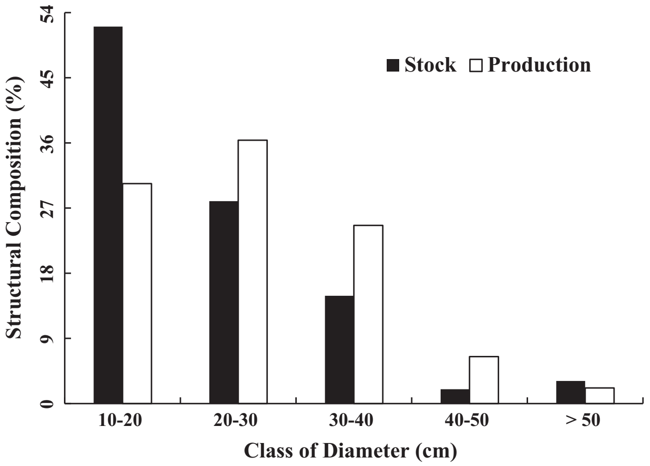

Fig. 2. Structural composition (%) of stock and production of CWD by class of diameter, based on the total amounts of necromass observed for all forest types sampled in Viruá.

Table 3
CWD production (carbon input; ±SD) 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 ± 0.63
Ab	0.15	1.09	1.23	45.93	0.57 ± 0.81
LO	0.11	0.95	1.06	46.29	0.49 ± 1.19
La + Ld	0.44	0.16	0.60	45.91	0.27 ± 0.67
Lb + La	0	0.08	0.08	45.89	0.04 ± 0.08

(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. A1 (Appendix A), where "As" has the lowest restriction.

(2) No CWD production ($\geqslant$10 cm) was found in the "Lg + Lb" vegetation type (grassy-woody).

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) (Appendix A, Table A1).

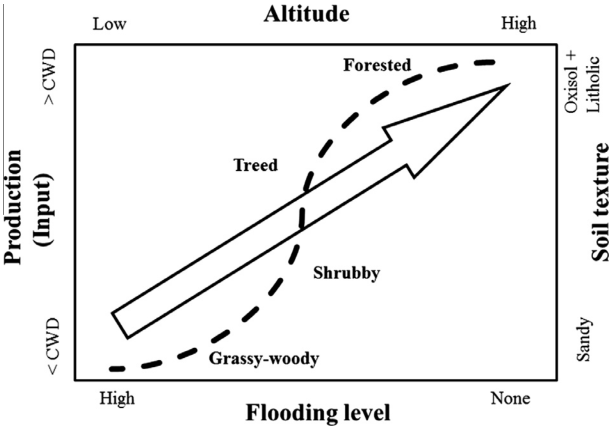

Fig. 3. Conceptual model for production (input) of coarse woody debris (CWD) taking into account hydro-edaphic features in Viruá National Park, Roraima, Brazilian Amazonia.

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 (Figs. 3 and S1).

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).

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 (Appendix A, Table A2). 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

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 (MgC ha^{-1}) (3)	CWD stock Mg ha^{-1} (MgC ha^{-1}) (4)			CWD carbon as % of total tree carbon (live + dead)	Range
				Standing	Fallen	Total		
As	4	179.04 ± 16.99	86.84	0.11 (0.05)	5.82 (2.68)	5.93 ± 5.49 (2.74 ± 2.53)	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±2.04)	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 ± 2.06)	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 ± 1.34)	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 ± 0.30)	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. A1 (Appendix A), where "As" has the lowest restriction.

(2) Tree biomass (±SD) = 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 (±SD) = 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.

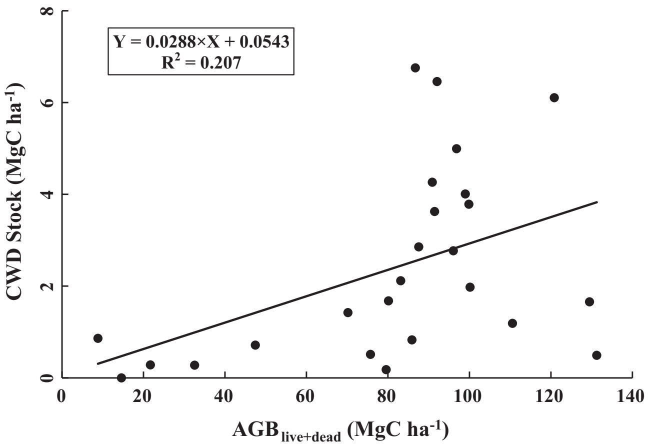

Fig. 4. Linear regression expressing the relationship between the CWD carbon stock and the aboveground tree carbon stock (live + dead; DBH ⩾ 10 cm).

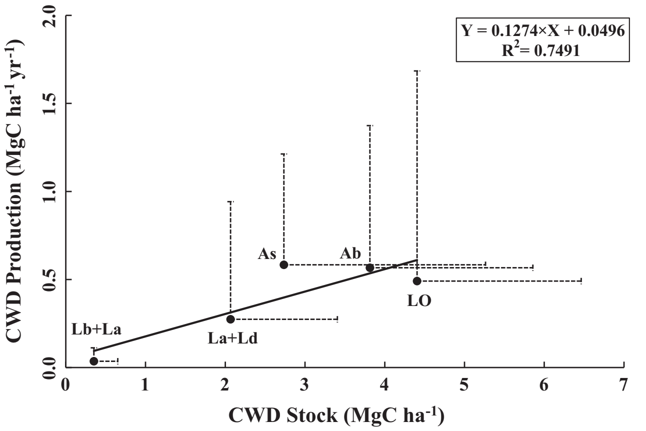

Fig. 5. Relationship between stock and production of coarse woody debris carbon stock in the forest types along a hydro-edaphic gradient in Viruá National Park. Vertical and horizontal bars represent standard deviations.

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.

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%) (Appendix A, Table A2). 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., Appendix A, Table A2). 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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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2015.12.045.

References

Baker, T.R., Honorio Coronado, E.N., Phillips, O.L., Martin, J., van der Heijden, G.M., Garcia, M., Silva Espejo, J., 2007. Low stocks of coarse woody debris in a southwest Amazonian forest. Oecologia 152, 495–504. http://dx.doi.org/10.1007/s00442-007-0667-5.

Baker, T.R., Phillips, O.L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., Erwin, T., Higuchi, N., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Monteagudo, A., Neill, D.A., Vargas, P.N., Pitman, N.C., Silva, J.N., Martinez, R.V., 2004. Increasing biomass in Amazonian forest plots. Philos. Trans. Roy. Soc. Lond., Ser. B: Biol. Sci. 359, 353–365. http://dx.doi.org/10.1098/rstb.2003.1422.

Balch, J.K., Brando, P.M., Nepstad, D.C., Coe, M.T., Silvério, D., Massad, T.J., Davidson, E.A., Lefebvre, P., Oliveira-Santos, C., Rocha, W., Cury, R.T.S., Parsons, A., Carvalho, K.S., 2015. Amazon forests to fire: insights from a large-scale Burn experiment. BioScience 65, 893–905. http://dx.doi.org/10.1093/biosci/biv106.

Barbosa, R.I., 1997. Distribuição das chuvas em Roraima. In: Barbosa, R.I., Ferreira, E., Castellon, E.G. (Eds.), Homem, Ambiente e Ecologia no Estado de Roraima. Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Amazonas, Brazil, pp. 325–335.

Barbosa, R.I., Fearnside, P.M., 1999. Incêndios na Amazônia brasileira: estimativa da emissão de gases do efeito estufa pela queima de diferentes ecossistemas de Roraima na passagem do evento "El Niño" (1997/98). Acta Amazon. 29, 513–534. http://dx.doi.org/10.1590/1809-43921999294534.

Bongers, F., Engelen, D., Klinge, H., 1985. Phytomass structure of natural plant communities on spodosols in southern Venezuela: the Bana woodland. Vegetatio 63, 13–34. http://dx.doi.org/10.1007/BF00032183.

Brazil-IBGE, 2012. Manual técnico da vegetação brasileira: sistema fitogeográfico, inventário das formações florestais e campestres, técnicas e manejo de coleções botânicas, procedimentos para mapeamentos. Instituto Brasileiro de Geografia e Estatística (IBGE), Rio de Janeiro, Brazil.

Brazil-MCT, 2010. Segunda Comunicação Nacional do Brasil à Convenção-Quadro das Nações Unidas sobre Mudança do Clima. In: Coordenação-Geral de Mudanças Globais do Clima, Ministério da Ciência, Tecnologia e Inovação (MCT), Brasília, DF, Brazil. <http://mct.gov.br/index.php/content/view/326988/Texto_Completo_Publicado.html> (accessed 01.07.11).

Brown, S., 2002. Measuring carbon in forests: current status and future challenges. Environ. Pollut. 116, 363–372. http://dx.doi.org/10.1016/S0269-7491(01)00212-3.

Castilho, C.V., Magnusson, W.E., Araújo, R.N.O., Luizão, R.C.C., Luizão, F.J., Lima, A.P., Higuchi, N., 2006. Variation in aboveground tree live biomass in a central Amazonian Forest: effects of soil and topography. For. Ecol. Manage. 234, 85–96. http://dx.doi.org/10.1016/j.foreco.2006.06.024.

Chambers, J.Q., Higuchi, N., Schimel, J.P., Ferreira, L.V., Melack, J.M., 2000. Decomposition and carbon cycling of dead trees in tropical forests of the central Amazon. Oecologia 122, 380–388. http://dx.doi.org/10.1007/s004420050044.

Chambers, J.Q., Negron-Juarez, R.I., Marra, D.M., Vittorio, A.D., Tews, J., Roberts, D., Ribeiro, G.H.P.M., Trumbore, S.E., Higuchi, N., 2013. The steady-state mosaic of disturbance and succession across an old-growth Central Amazon forest landscape. PNAS 110, 3949–3954. http://dx.doi.org/10.1073/pnas.1202894110.

Chambers, J.Q., Santos, J., Ribeiro, R.J., Higuchi, N., 2001. Tree damage, allometric relationships, and above-ground net primary production in Central Amazon forest. For. Ecol. Manage. 152, 73–84. http://dx.doi.org/10.1016/S0378-1127(00)00591-0.

Chao, K.-J., Phillips, O.L., Baker, T.R., 2008. Wood density and stocks of coarse woody debris in a northwestern Amazonian landscape. Can. J. For. Res. 38, 795–805. http://dx.doi.org/10.1139/x07-163.

Chao, K.-J., Phillips, O.L., Baker, T.R., Peacock, J., Lopez-Gonzalez, G., Martinez, R.V., Monteagudo, A., Torres-Lezama, A., 2009. After trees die: quantities and determinants of necromass across Amazonia. Biogeosciences 6, 1615–1626. http://dx.doi.org/10.5194/bg-6-1615-2009.

Chave, J., Andalo, C., Brown, S., Cairns, M.A., Chambers, J.Q., Eamus, D., Fölster, H., Fromard, F., Higuchi, N., Kira, T., Lescure, J.-P., Nelson, B.W., Ogawa, H., Puig, H., Riéra, B., Yamakura, T., 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. Oecologia 145, 87–99. http://dx.doi.org/10.1007/s00442-0050100-x.

Clark, D.B., Clark, D.A., Brown, S., Oberbauer, S.F., Veldkamp, E., 2002. Stocks and flows of coarse wood debris across a tropical rain forest nutrient and topography gradient. For. Ecol. Manage. 164, 237–248. http://dx.doi.org/10.1016/S0378-1127(01)00597-7.

Cummings, D.L., Kauffman, J.B., Perry, D.A., Hughes, R.F., 2002. Aboveground biomass and structure of rainforest in the southwestern Brazilian Amazon. For. Ecol. Manage. 163, 293–307. http://dx.doi.org/10.1016/S0378-1127(01)00587-4.

Damasco, G., Vicentini, A., Castilho, C.V., Pimentel, T.P., Nascimento, H.E.M., 2013. Disentangling the role of edaphic variability, flooding regime and topography of Amazonian white-sand vegetation. J. Veg. Sci. 24, 384–394. http://dx.doi.org/10.1111/j.1654-1103.2012.01464.x.

Delaney, M., Brown, S., Lugo, A.E., Torres-Lezarna, A., Quintero, N.B., 1998. The quantity and turnover of dead wood in permanent forest plots in six Life Zones of Venezuela. Biotropica 30, 2–11. http://dx.doi.org/10.1111/j.1744-7429.1998.tb00364.x.

Doughty, C.E., Metcalfe, D.B., Girardin, C.A., Amezquita, F.F., Cabrera, D.G., Huasco, W.H., Silva-Espejo, J.E., Araujo-Murakami, A., da Costa, M.C., Rocha, W., Feldpausch, T.R., Mendoza, A.L., da Costa, A.C., Meir, P., Phillips, O.L., Malhi, Y.,

2015. Drought impact on forest carbon dynamics and fluxes in Amazonia. Nature 519, 78–82. http://dx.doi.org/10.1038/nature14213.

Ferreira, C.A.C., 2009. Análise comparativa de vegetação lenhosa do ecossistema Campina na Amazônia Brasileira. In: Programa Integrado de Pós-Graduação em Biologia Tropical e Recursos Naturais (PPG-BTRN). Universidade Federal do Amazonas (UFAM), Manaus, Amazonas, Brazil, p. 277.

Gerwing, J.J., 2002. Degradation of forests through logging and fire in the eastern Brazilian Amazon. For. Ecol. Manage. 157, 131–141. http://dx.doi.org/10.1016/S0378-1127(00)00644-7.

Goodman, R.C., Phillips, O.L., del Castillo Torres, D., Freitas, L., Cortese, S.T., Monteagudo, A., Baker, T.R., 2013. Amazon palm biomass and allometry. For. Ecol. Manage. 310, 994–1004. http://dx.doi.org/10.1016/j.foreco.2013.09.045.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, R., Lienkaemper, G.W., Cromack Jr., K., Cummins, K.W., 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. 15, 133–302. http://dx.doi.org/10.1016/S0065-2504(08)60121-X.

Harmon, M.E., Sexton, J., 1996. Guidelines for measurements of woody detritus in forest ecosystems. In: United States Long Term Ecological Research Network Office Publication no. 20. University of Washington, Seattle, Washington, USA.

Houghton, R.A., Lawrence, K.T., Hackler, J.L., Brown, S., 2001. The spatial distribution of forest biomass in the Brazilian Amazon: a comparison of estimates. Glob. Change Biol. 7, 731–746. http://dx.doi.org/10.1111/j.1365-2486.2001.00426.x.

Junk, W.J., Piedade, M.T.F., Schöngart, J., Cohn-Haft, M., Adeney, J.M., Wittmann, F., 2011. A classification of major naturally-occurring Amazonian lowland wetlands. Wetlands 31, 623–640. http://dx.doi.org/10.1007/s13157-011-0190-7.

Kauffman, J.B., Uhl, C., Cummings, D.L., 1988. Fire in the Venezuela Amazon 1: fuel biomass and fire chemistry in the evergreen rainforest of Venezuela. Oikos 53, 167–175. http://dx.doi.org/10.2307/3566059.

Keller, M., Palace, M., Asner, G.P., Pereira, R., Silva, J.N.M., 2004. Coarse woody debris in undisturbed and logged forests in the eastern Brazilian Amazon. Glob. Change Biol. 10, 784–795. http://dx.doi.org/10.1111/j.1529-8817.2003.00770.x.

Klinge, H., Herrera, R., 1983. Phytomass structure of natural plant communities on spodosols in southern Venezuela: the tall Amazon Caatinga forest. Vegetatio 53, 65–84. http://dx.doi.org/10.1007/BF00043025.

Larjavaara, M., Muller-Landau, H.C., 2010. Comparison of decay classification, knife test, and two penetrometers for estimating wood density of coarse woody debris. Can. J. For. Res. 40, 2313–2321. http://dx.doi.org/10.1139/x10-170.

Laurance, W.F., Fearnside, P.M., Laurance, S.G., Delamonica, P., Lovejoy, T.E., Rankin-de-Merona, J.M., Chambers, J.Q., Gascon, C., 1999. Relationship between soils and Amazon forest biomass: a landscape-scale study. For. Ecol. Manage. 18, 127–138. http://dx.doi.org/10.1016/S0378-1127(98)00494-0.

Lewis, S.L., Phillips, O.L., Baker, T.R., Lloyd, J., Malhi, Y., Almeida, S., Higuchi, N., Laurance, W.F., Neill, D.A., Silva, J.N.M., Terborgh, J., Torres Lezama, A., Vasquez Martinez, R., Brown, S., Chave, J., Kuebler, C., Nunez Vargas, P., Vinceti, B., 2004. Concerted changes in tropical forest structure and dynamics: evidence from 50 South American long-term plots. Philos. Trans. Roy. Soc. Lond., Ser. B: Biol. Sci. 359, 421–436. http://dx.doi.org/10.1098/rstb.2003.1431.

Magnusson, W.E., Lima, A.P., Luizão, R., Luizão, F., Costa, F.R.C., Castilho, C.V., Kinupp, V.F., 2005. RAPELD: a modification of the Gentry Method for biodiversity surveys in long-term ecological research sites. Biota Neotrop. 5, 19–24. http://dx.doi.org/10.1590/S1676-06032005000300002.

Malhi, Y., Baker, T.R., Phillips, O.L., Almeida, S., Alvarez, E., Arroyo, L., Chave, J., Czimczik, C.I., Fiore, A.D., Higuchi, N., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Montoya, L.M.M., Monteagudo, A., Neill, D.A., Vargas, P.N., Patino, S., Pitman, N.C.A., Quesada, C.A., Salomao, R., Silva, J.N.M., Lezama, A.T., Martinez, R.V., Terborgh, J., Vinceti, B., Lloyd, J., 2004. The above-ground coarse wood productivity of 104 Neotropical forest plots. Glob. Change Biol. 10, 563–591. http://dx.doi.org/10.1111/j.1529-8817.2003.00778.x.

Malhi, Y., Wood, D., Baker, T.R., Wright, J., Phillips, O.L., Cochrane, T., Meir, P., Chave, J., Almeida, S., Arroyo, L., 2006. The regional variation of aboveground live biomass in old-growth Amazonian forests. Glob. Change Biol. 12, 1107–1138. http://dx.doi.org/10.1111/j.1365-2486.2006.01120.x.

Martins, D.L., Schietti, J., Feldpausch, T.R., Luizão, F.J., Phillips, O.L., Andrade, A., Castilho, C.V., Laurance, S.G., Oliveira, Á., Amaral, I.L., Toledo, J.J., Lugli, L.F., Pinto, J.L.P.V., Mendoza, E.M.O., Quesada, C.A., 2015. Soil-induced impacts on forest structure drive coarse woody debris stocks across central Amazonia. Plant Ecol. Divers. 8, 229–241. http://dx.doi.org/10.1080/17550874.2013.879942.

Martius, C., 1997. Decomposition of wood. In: Junk, W. (Ed.), The Central Amazon Floodplain: Ecology of a Pulsing System. Springer, Heidleberg, Germany, pp. 267–276. http://dx.doi.org/10.1007/978-3-662-03416-3_12.

Martius, C., Bandeira, A.G., 1998. Wood litter stocks in tropical moist forest in Central Amazonia. Ecotropica 4, 115–118.

Mendonça, B.A.F., Fernandes Filho, E.I., Schaefer, C.E.G.R., Simas, F.N.B., Vale Jr., J.F., Lisboa, B.A.R., Mendonça, J.G.F., 2013. Solos e geoambientes do Parque Nacional do Viruá e entorno, Roraima: visão integrada da paisagem e serviços ambiental. Ciência Florest. 23, 427–442.

Mendonça, B.A.F., Simas, F.N.B., Schaefer, C.E.G.R., Fernandes Filho, E.I., Vale Júnior, J.F., Mendonça, J.G.F., 2014. Podzolized soils and paleoenvironmental implications of white-sand vegetation (Campinarana) in the Viruá National Park, Brazil. Geoderma Region. 2–3, 9–20. http://dx.doi.org/10.1016/j.geodrs.2014.09.004.

Montero, J.C., Latrubesse, E.M., 2013. The igapó of the Negro River in central Amazonia: linking late-successional inundation forest with fluvial geomorphology. J. South Am. Earth Sci. 46, 137–149. http://dx.doi.org/10.1016/j.jsames.2013.05.009.

Nascimento, H.E.M., Laurance, W.F., 2004. Biomass dynamics in Amazonian forest fragments. Ecol. Appl. 14, S127–S138. http://dx.doi.org/10.1890/01-6003.

Nogueira, E., Fearnside, P., Nelson, B., Franca, M., 2007. Wood density in forests of Brazil's 'arc of deforestation': implications for biomass and flux of carbon from land-use change in Amazonia. For. Ecol. Manage. 248, 119–135. http://dx.doi.org/10.1016/j.foreco.2007.04.047.

Nogueira, E.M., Yanai, A.M., Fonseca, F.O., Fearnside, P.M., 2015. Carbon stock loss from deforestation through 2013 in Brazilian Amazonia. Glob. Change Biol. 21, 1271–1292. http://dx.doi.org/10.1111/gcb.12798.

Palace, M., Keller, M., Asner, G.P., Silva, J.N.M., Passos, C., 2007. Necromass in undisturbed and logged forests in the Brazilian Amazon. For. Ecol. Manage. 238, 309–318. http://dx.doi.org/10.1016/j.foreco.2006.10.026.

Palace, M., Keller, M., Hurtt, G., Frolking, S., 2012. A review of above ground necromass in tropical forests. In: Sudarshana, P., Nageswara-Rao, M., Soneji, J.R. (Eds.), Tropical Forests. InTech, Rijeka, Croatia, pp. 215–252. http://dx.doi.org/10.5772/1410.

Palace, M., Keller, M., Silva, H., 2008. Necromass production: studies in undisturbed and logged Amazon forests. Ecol. Appl. 18, 873–884. http://dx.doi.org/10.1890/06-2022.1.

Pauletto, D., 2006. Estoque, produção e fluxo de nutrientes da liteira grossa em floresta submetida à exploração seletiva de madeira no noroeste de Mato Grosso. In: Programa de Pós-Graduação em Biologia Tropical e Recursos Naturais. Instituto Nacional de Pesquisas da Amazônia (INPA) and Universidade Federal do Amazonas (UFAM), Manaus, Amazonas, Brazil, p. 78.

Pezzini, F., Melo, P.H.A., Oliveira, D.M.S., Amorim, R.X., Figueiredo, F.O.G., Drucker, D. P., Rodrigues, F.R.O., Zuquim, G., Emilio, T., Costa, F.R.C., Magnusson, W.E., Sampaio, A.F., Lima, A.P., Garcia, A.R.M., Manzatto, A.G., Nogueira, A., Costa, C.P., Barbosa, C.E.A., Bernardes, C., Castilho, C.V., Cunha, C.N., Freitas, C.G., Cavalcante, C.O., Brandão, D.O., Rodrigues, D.J., Santos, E.C.P.R., Baccaro, F.B., Ishida, F.Y., Carvalho, F.A., Moulatlet, G.M., Guillaumet, J.-L.B., Pinto, J.L.P.V., Schietti, J., Vale, J.D., Belger, L., Verdade, L.M., Pansonato, M.P., Nascimento, M.T., Santos, M.C.V., Cunha, M.S., Arruda, R., Barbosa, R.I., Romero, R.L., Pansini, S., Pimentel, T.P., 2012. The Brazilian Program for Biodiversity Research (PPBio) Information System. Biodivers. Ecol. 4, 265–274. http://dx.doi.org/10.7809/b-e.00083.

Phillips, O.L., Baker, T.R., Arroyo, L., Higuchi, N., Killeen, T.J., Laurance, W.F., Lewis, S. L., Lloyd, J., Malhi, Y., Monteagudo, A., Neill, D.A., Vargas, P.N., Silva, J.N., Terborgh, J., Martinez, R.V., Alexiades, M., Almeida, S., Brown, S., Chave, J., Comiskey, J.A., Czimczik, C.I., Di Fiore, A., Erwin, T., Kuebler, C., Laurance, S.G., Nascimento, H.E., Olivier, J., Palacios, W., Patino, S., Pitman, N.C., Quesada, C.A., Saldias, M., Lezama, A.T., Vinceti, B., 2004. Pattern and process in Amazon tree turnover, 1976–2001. Philos. Trans. Roy. Soc. Lond., Ser. B: Biol. Sci. 359, 381–407. http://dx.doi.org/10.1098/rstb.2003.1438.

Phillips, O.L., Higuchi, N., Vieira, S., Chao, T.R.B.K.-J., Lewis, S.L., 2009. Changes in Amazonian forest biomass, dynamics, and composition, 1980–2002. In: Keller, M., Bustamante, M., Gash, J., Dias, P.S. (Eds.), Amazonia and Global Change (Geophysical Monograph Series 186). American Geophysical Union, Washington, DC, USA, pp. 373–387. http://dx.doi.org/10.1029/2008GM000739.

PPBio, 2014. Programa de Pesquisa em Biodiversidade: Repositório de dados do PPBio (Mapas – SIG). In: PPBio, CENBAM, Manaus, AM. <https://ppbio.inpa.gov.br/mapas> (accessed 01.11.14).

Pyle, E.H., Santoni, G.W., Nascimento, H.E.M., Hutyra, L.R., Vieira, S., Curran, D.J., van Haren, J., Saleska, S.R., Chow, V.Y., Carmago, P.B., Laurance, W.F., Wofsy, S.C., 2008. Dynamics of carbon, biomass, and structure in two Amazonian forests. J. Geophys. Res. 113, G00B08. http://dx.doi.org/10.1029/2007jg000592.

R Core Team, 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rice, A.H., Pyle, E.H., Saleska, S.R., Hutyra, L., Palace, M., Keller, M., Camargo, P.B., Portilho, K., Marques, D.F., Wofsy, S.C., 2004. Carbon balance and vegetation dynamics in an old-growth Amazonian forest. Ecol. Appl. 14, S55–S71. http://dx.doi.org/10.1890/02-6006.

Saatchi, S., Houghton, R., Alvalá, R., Soares, J., Yu, Y., 2007. Distribution of aboveground live biomass in the Amazon basin. Glob. Change Biol. 13, 816–837. http://dx.doi.org/10.1111/j.1365-2486.2007.01323.x.

Schaefer, C.E.G.R., Mendonça, B.A.F., Fernandes-Filho, E.I., 2008. Geoambientes e paisagens do Parque Nacional do Viruá – RR: Esboço de integração da geomorfologia, climatologia, solos, hidrologia e ecologia (Zoneamento Preliminar). In: Universidade Federal de Viçosa (UFV), Viçosa, Minas Gerais, Brazil, p. 56.

Scott, D.A., Proctor, J., Thompson, J., 1992. Ecological studies on a lowland evergreen rain forest on Maraca Island, Roraima, Brazil. II. Litter and nutrient cycling. J. Ecol. 80, 705–717. http://dx.doi.org/10.2307/2260861.

Silva, R.P., 2007. Alometria, estoque e dinâmica da biomassa de florestas primárias e secundárias na região de Manaus (AM). In: Programa Integrado de Pós-graduação em Biologia Tropical e Recursos Naturais, Curso de Ciências de Florestas Tropicais. Universidade Federal do Amazonas (UFAM) and Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Amazonas, Brazil, p. 152.

Summers, P.M., 1998. Estoque, decomposição e nutrientes da liteira grossa em florestas de terra-firme na Amazônia Central. In: Programa de Pós-graduação em Ciências de Florestas Tropicais. Instituto Nacional de Pesquisas da Amazônia (INPA) and Universidade do Amazonas (UA), Manaus, Amazonas, Brazil, p. 136.

Targhetta, N., Kesselmeier, J., Wittmann, F., 2015. Effects of the hydroedaphic gradient on tree species composition and aboveground wood biomass of oligotrophic forest ecosystems in the central Amazon basin. Folia Geobot. 50, 185–205. http://dx.doi.org/10.1007/s12224-015-9225-9.

Toledo, J.J., Magnusson, W.E., Castilho, C.V., Nascimento, H.E.M., 2011. How much variation in tree mortality is predicted by soil and topography in Central Amazonia? For. Ecol. Manage. 262, 331–338. http://dx.doi.org/10.1016/j.foreco.2011.03.039.

Trumbore, S., Brando, P., Hartmann, H., 2015. Forest health and global change. Science 349, 814–818. http://dx.doi.org/10.1126/science.aac6759.

Vale, J.D., Zuanon, J., Magnusson, W.E., 2014. The influence of rain in limnological characteristics of Viruá wetlands, Brazilian Amazon. Acta Limnol. Brasil. 26, 254–267. http://dx.doi.org/10.1590/s2179-975x2014000300005.

van Wagner, C.E., 1968. The line intersect method in forest fuel sampling. For. Sci. 14, 20–26.

Vasconcelos, S.S., Fearnside, P.M., Graça, P.M.L.A., Nogueira, E.M., Oliveira, L.C., Figueiredo, E.O., 2013. Forest fires in southwestern Brazilian Amazonia: estimates of area and potential carbon emissions. For. Ecol. Manage. 291, 199–208. http://dx.doi.org/10.1016/j.foreco.2012.11.044.

Zani, H., 2013. Detecção e caracterização do Megaleque Viruá (RR) com dados multisensores e geológicos: influência nos padrões atuais de vegetação. In: Pós-graduação em Sensoriamento Remoto. Instituto Nacional de Pesquisas Espaciais (INPE), São José dos Campos, São Paulo, Brazil, p. 145.