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Decomposition rates of coarse woody debris in undisturbed Amazonian seasonally flooded and unflooded forests in the Rio Negro-Rio Branco Basin in Roraima, Brazil

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Estimates of carbon-stock changes in forest ecosystems require information on dead wood decomposition rates. In the Amazon, the lack of data is dramatic due to the small number of studies and the large range of forest types. The aim of this study was to estimate the decomposition rate of coarse woody debris (CWD) in two oligotrophic undisturbed forest formations of the northern Brazilian Amazon: seasonally flooded and unflooded. We analyzed 20 arboreal individuals (11 tree species and 3 palm species) with distinct wood-density categories. The mean annual decomposition rate of all samples independent of forest formation ranged from 0.044 to 0.963 yr^{-1}, considering two observation periods (12 and 24 months). The highest rate (0.732 ± 0.206 [SD] yr^{-1}) was observed for the lowest wood-density class of palms, whereas the lowest rate (0.119 ± 0.101 yr^{-1}) was determined for trees with high wood density. In terms of forest formation, the rates values differ when weighted by the wood-density classes, indicating that unflooded forest (0.181 ± 0.083 [SE] yr^{-1}; mean decay time 11–30 years) has a decomposition rate ~19% higher than the seasonally flooded formations (0.152 ± 0.072 yr^{-1}; 13–37 years). This result reflects the dominance of species with high wood density in seasonally flooded formations. In both formations 95% of the dead wood is expected to disappear within 30–40 years. Based on our results, we conclude that the CWD decomposition in the studied area is slower in forests on nutrient-poor seasonally flooded soils, where structure and species composition result in ~40% of the aboveground biomass being in tree species with high wood density. Thus, it is estimated that CWD in seasonally flooded forest formations has longer residence time and slower carbon release by decomposition (respiration) than in unflooded forests. These results improve our ability to model stocks and fluxes of carbon derived from decomposition of dead wood in undisturbed oligotrophic forests in the Rio Negro-Rio Branco Basin, northern Brazilian Amazon.

1. Introduction

Greenhouse gases are emitted from tropical forests not only from deforestation but also from standing forests, both disturbed and undisturbed. Emissions from standing forest have received much less research attention than deforestation. The December 2015 Paris Accords on climate change (UNFCCC, 2015) make it critical to gain better understanding of emissions from standing forest, including the time path of these emissions. The Paris Accords call for preventing mean global temperature from passing a limit "well below" 2 °C the pre-industrial mean, and to "pursue efforts" to keep mean temperature within 1.5 °C of the pre-industrial level.

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This means that the net total of all greenhouse gas fluxes, whether anthropogenic or not, must be reduced within a period of approximately 20 years such that the atmospheric concentrations are held close to their present levels (e.g., Rogelj et al., 2016). This requires faster action and greater attention to the time path of emissions than the previous criterion, which defined the limit in terms of a longterm "stabilization" of greenhouse gas concentrations (UNFCCC, 1992, Article 2).

One of the major ways that standing tropical forests emit greenhouse gases is by the death and decomposition of trees, which may be caused by disturbances such as logging, forest fires, invasion by plants such as lianas and bamboos, or by extreme droughts or floods. These disturbances may be either "directly human induced" (in the terms of the Kyoto Protocol: UNFCCC, 1998) or not, as in extreme events influenced by climate change. Coarse woody debris (CWD, diameter $\geq$ 10 cm) represents a key forest ecosystem compartment in carbon fluxes from standing forest. The carbon stock in this compartment is also important in quantifying the emissions of deforestation, and cannot be simply defined away on the bases of 'necromass' not being considered to be 'biomass' (e.g., IPCC, 1997); as was done in Brazil's first and second inventories of greenhouse gases (Brazil-MCT, 2004; Brazil-MCTI, 2010). In the standing forest, the carbon stock in CWD and its decomposition rate will determine the annual carbon budget from this compartment (Harmon et al., 1986).

The CWD decomposition rate (k) is an important biological metric. It is influenced by environmental conditions, wood density and the quality of the soil substrate (Li et al., 2007; Harmon et al., 2011; Russell et al., 2015). Due to slow decomposition and sporadic mortality of trees in forest environments, few studies have addressed the variability in CWD decomposition rates, although this process is a great source of uncertainty in the context of forest dynamics (Harmon et al., 1995; Chambers et al., 2001; Palace et al., 2012). Accurate measurements of CWD decomposition rates are important for determining the magnitude of the carbon stock and the residence time in this forest compartment, providing crucial data for accurate modeling of the effects of climate change on these stocks and on global carbon fluxes (IPCC, 2006; Zell et al., 2009; Bradford et al., 2014).

The paucity of data on CWD decomposition is particularly acute in Amazonia due to the small number of studies, the vastness of the region and the huge range of forest types determined by different environmental conditions and land uses (Chambers et al., 2000; Hérault et al., 2010; Fearnside, 2016). Most studies in undisturbed forests in Amazonia have assumed a steady-state between production and CWD decomposition in order to estimate residence time, stocks and input of carbon through dead tree biomass (Chao et al., 2008; Silva et al., 2016). However, this steady-state has been altered by direct human activity (e.g., selective logging: Keller et al., 2004; Palace et al., 2008), and indirect effects (e.g., increased frequency of surface fires: Alencar et al., 2015; Barni et al., 2015). In both cases, prolonged droughts associated with extreme weather events can maximize the imbalance (Phillips et al., 2009; Vasconcelos et al., 2013).

Selective logging and deforestation provide an increased stock of residual wood pieces and non-commercial trees that are killed as a result of logging (Fearnside, 2000; Aguiar et al., 2016). In this case, the decomposition rates associated with carbon emissions are highly dependent on the replacement landscape (e.g., pastures and secondary forest), with most CWD being considered missing after the first years following deforestation (Buschbacher, 1984; Barbosa and Fearnside, 1996; Fearnside, 2008). In contrast, prolonged drought and surface fires increase tree mortality, reducing standing biomass and dramatically increasing the amount of CWD in undisturbed ecosystems (Brando et al., 2014; Doughty et al., 2015). This imbalance has a direct influence on the residence time of carbon fixed in the living biomass and its subsequent emission from CWD decomposition in undisturbed forests, and it can become part of a positive feedback process with global climate change (Galbraith et al., 2013). Because the Amazon supports forest formations with high species diversity and large carbon reservoirs (Nogueira et al., 2015), it is crucial to estimate CWD decomposition taking into account specific wood attributes (e.g., wood density) associated with the environmental conditions, and the community structure and species composition of the different forest types (Toledo et al., 2009). This provides a weighted calculation of CWD decomposition rates in terms of forest type, avoiding the use of simple averages that do not represent the ecosystem as a whole.

The Rio Negro-Rio Branco Basin ($\sim$600,000 km^2; Montero and Latrubesse, 2013) lacks information on CWD stocks and carbon flows (Barbosa and Ferreira, 2004; Chao et al., 2009; Silva et al., 2016). This region is characterized by a remarkably variable hydrological regime (different hydro-edaphic restrictions) that shapes vegetation mosaics among seasonally flooded and unflooded forest formations (Junk et al., 2011; Targhetta et al., 2015; Barni et al., 2016). Flooded and unflooded forest types are distinct in community structure and species composition (Hawes et al., 2012), as well as in abiotic characteristics. The present study offers an opportunity to determine the relative importance of taxonomic groups and wood-density classes on CWD decomposition rates in different forests in the Amazon. This approach will improve our understanding of CWD decomposition in undisturbed Amazon forests, especially in ecosystems where distinct hydro-edaphic restrictions can determine differences in the natural decomposition rates.

This study aims to investigate the CWD decomposition rates of different species that occur in undisturbed oligotrophic forests in the Rio Negro-Rio Branco Basin in the Northern Amazon. Our goal was to estimate CWD decomposition rates in two forest formations (seasonally flooded and unflooded) that naturally occur in this region, based on observations made on species in different wood-density classes over two time periods (12 and 24 months). It is expected that CWD decomposition rates in seasonally flooded formations are lower because this type of environment supports tree species with higher wood density and resistance to natural processes of fragmentation (Parolin and Worbes, 2000; Wittmann et al., 2006). The specific objectives of the study were (i) to estimate annual CWD decomposition rates of different taxonomic groups and wood-density classes, (ii) to estimate decomposition rate for each forest formation considering taxonomic groups and wood-density classes weighted by the dominance of individuals (structure) and species (composition) of each formation, and (iii) to estimate the residence time (decay time = number of years for the wood piece to completely lose its physical integrity) and carbon emissions to the atmosphere associated with the annual CWD production in each forest formation. The decomposition rates given here are the first for the oligotrophic forests of the northern Brazilian Amazon.

2. Materials and methods

2.1. Study area

Sampling for CWD decomposition rates was performed in the PPBio (Biodiversity Research Program) research grid in Viruá National Park (1°36′N, 61°13′W); a federal protected area (215.917 ha) located in the state of Roraima (Fig. 1). Viruá is part of the Rio Negro-Rio Branco basin, an ecoregion of the Amazon where the vegetation structure is directly related to the hydro-edaphic restrictions determined by different topographical features, soils and flooding levels (Cordeiro et al., 2016). Viruá is set

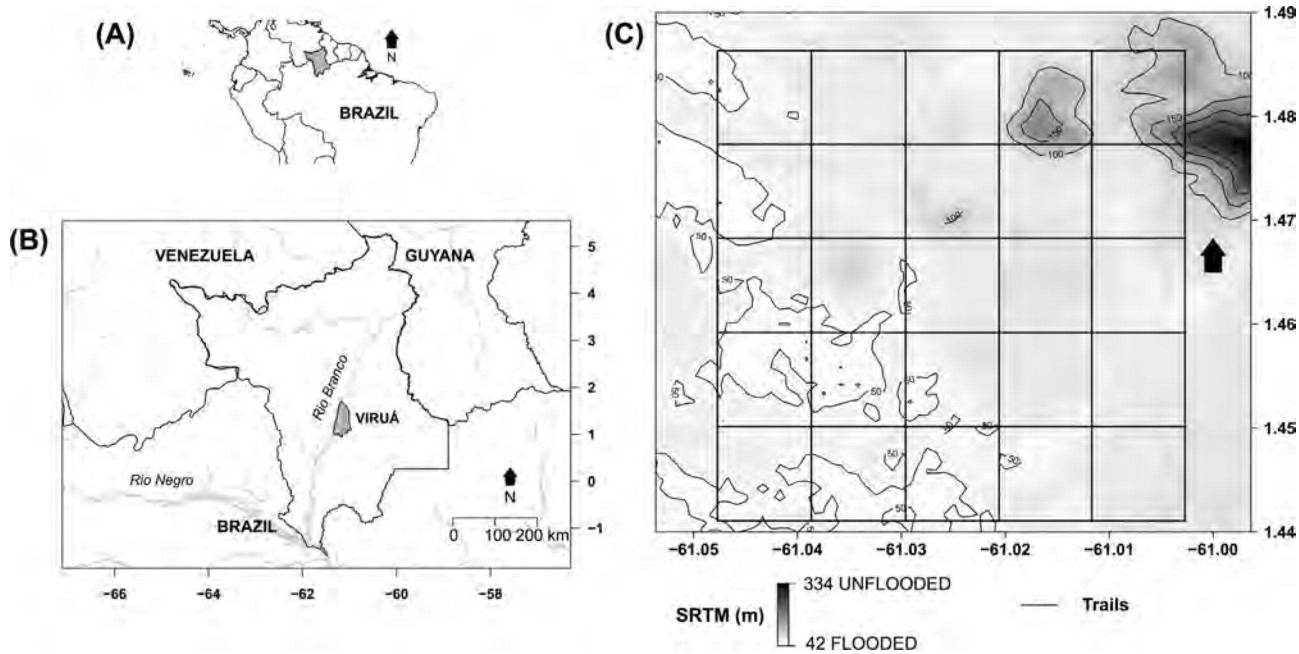

Fig. 1. Study area: (A) North of South America; state of Roraima highlighted, (B) Rio Negro-Rio Branco basin (Viruá National Park highlighted) and (C) PPBio grid system installed in Viruá – SRTM image provided by Brazilian Biodiversity Research Program (PPBio, 2014).

in a climatic transition zone (Aw-Am under the Köppen classification system) with a dry season lasting from January to March and a wet season between May and August (Schaefer et al., 2008). Annual rainfall ranges from 1750 to 2000 mm (Barbosa, 1997). In general, the PPBio grid in Viruá can be divided into two major forest formations: (i) seasonally flooded forests characterized by white-sand hydromorphic soils (also called "*campinas*" *and* "*campinaranas*") and alluvial forests occurring along major watercourses, and (ii) unflooded forests (upland ombrophilous forests) scattered among isolated mountain ranges and ecotone zones, occurring on relatively shallow soils with rocky outcrops (Damasco et al., 2013; Mendonça et al., 2014; Vale Jr. et al., 2016).

2.2. Sampling design

CWD samples to estimate annual decomposition rates were selected from dead arboreal individuals (Trees and Palms) detected by monthly inspections carried out on the PPBio trail grid between December 2011 and March 2012 (t_0 = initial time). The samples were selected based on the following criteria: (i) Trees and Palms with known mortality history (<30 days) determined by the falling of other trees (i.e., living individuals that died due to mechanical action of the wind or from other individuals) and (ii) general bole appearance (bark, heartwood and sapwood) with no trace of fragmentation by decomposition. These criteria were used in order to avoid bias in sampling, ensuring the same initial physical condition and that the date of death is known (the tree falling does not necessarily represent its death or the beginning of decomposition).

We sampled 20 individuals (Trees = 15 individuals in 11 species; Palms = 5 individuals in 3 species) (Appendix A, Table A1). All of these samples were collected in unflooded forest. Taxonomic identification was done in the field for species that could be easily recognized; we did not collect voucher specimens of these species. For individuals for which vouchers were collected, we made the taxonomic determinations by comparison with herbarium specimens housed at MIRR, INPA, RB and UFRR (acronyms following *Index Herbariorum* (Thiers, 2016 [continuously updated])). The families followed the APG-IV (2016) system; collected specimens were deposited in the UFRR herbarium.

The bole of each selected individual was segmented into 25 discs using a chainsaw, taking into account the distance between the approximate DBH position and the first significant branch (tree canopy base). In total, 500 discs were numbered and the biometric attributes of each piece were measured using calipers (disc width and bark thickness) and a measuring tape (circumference of each disc). The central disc of each individual was taken to the laboratory where it served as a control sample for estimating moisture (water content; %) and basic wood density (ratio between dry weight and saturated volume in the field; g cm^{-3}) at the initial time of observation (t_0). The initial dry weight (initial biomass) of each piece was estimated from the relationship among volume, wet weight and dry weight calculated for each control sample. This was done because it was not possible to remove all discs from the field, dry them in the laboratory and return them back to the field. The basic wood density of each control sample served as the basis for associating the sample with the categories adopted by the Brazilian Institute of the Environment and Renewable Natural Resources (IBAMA) (Sternadt, 2001): very-soft wood species ($\leq$0.350 g cm^{-3}), soft (0.351–0.500 g cm^{-3}), medium-soft (0.501–0.650 g cm^{-3}), medium-hard 0.651–0.800 g cm^{-3}), hard (0.801–0.950 g cm^{-3}) and very-hard ($\geq$0.951 g cm^{-3}).

All of the discs that were not controls (i.e., 24 discs per individual) were left at the site where the individual had fallen. These discs were divided into two groups: 12 discs were placed on the ground with the broad (cross-sectional) face in contact with the soil (denominated "*latitudinal*" discs) and the other 12 discs were placed standing on edge (denominated "*longitudinal*" discs). The positioning of the discs can be seen in the Appendix A (Fig. A1, panel D). This equitable distribution was adopted to represent different positions of CWD pieces in relation to contact with the soil in the same way as occurs in natural environments. After the initial field experiment had been installed (t_0), two observations were made (t_1 and t_2, after 12 and 24 months, respectively). Each observation was based on a random collection of four discs from the sampled individual (two *latitudinal* discs and two *longitudinal*).

The remaining sampling discs were discarded. The collected discs were dried in an oven at 100 ± 2 °C until constant weight (kg) and were not returned to the field.

2.3. Data analysis

2.3.1. Annual decomposition rate

The annual decomposition rate (k; yr^{-1}; ±SD [standard deviation]) of each individual was estimated as a function of the temporal variation between the initial (t_0) and final (t_1 and t_2) biomasses based on the average of the collected discs (latitudinal + longitudinal) in each observation period, following the model of Olson (1963):

$$k = \frac{-\ln\left(\frac{X_{tn}}{X_o}\right)}{t}$$

where k = annual decomposition rate (fraction per year) of CWD for each individual; X_{tn} = residual biomass (kg) based on the average of four pieces sampled at time t_n (two longitudinal + two latitudinal); X_0 = initial biomass (kg) based on the average of four parts at the initial time (t_0); t = time period (in years) between t_0 and t_n.

The estimate of decomposition rate by wood-density class was calculated as a proportional representation of the velocity of fragmentation of each species group (Trees and Palms), and was analyzed by ANOVA followed by Tukey's test ($\alpha = 0.05$). Regression analysis was performed in order to generate the relational model between wood density (independent) and annual decomposition rate (dependent), taking into account the mean values obtained for each individual of the two taxonomic groups in the two sampling periods (t_1 and t_2).

2.3.2. Decomposition rate by forest formation

To calculate the decomposition rate in terms of forest formation (unflooded and seasonally flooded), we assumed that the annual CWD production is a proportional representation of the aboveground live biomass (DBH ≥ 10 cm), as suggested by Silva et al. (2016) for the same study area. This was done because the use of a simple average of the decomposition rate does not represent the whole forest formation due to individual intrinsic factors (e.g., wood density, degree of lignification) that are not incorporated proportionately in the final decomposition rate.

We therefore took into account the results of a forest inventory conducted in the Viruá grid by C.V. de Castilho and collaborators (29 plots of 1 ha: 17 seasonally flooded and 12 unflooded) and produced a database where each individual with DBH ≥ 10 cm (Trees and Palms) was associated with its basic wood density based on published databases (Chave et al., 2006; Wittmann et al., 2006; Nogueira et al., 2007; Zanne et al., 2009). After completing this step, the biomass of each individual in the Trees group was estimated using the "moist-forest" model (Chave et al., 2005) taking into account the wood density values associated with the species. The biomasses of individuals without taxonomic identification were calculated using the default value of 0.642 g cm^{-3} for basic wood density (Nogueira et al., 2007). Palm biomass (Arecaceae) was calculated using the Goodman model (Goodman et al., 2013). All biomass calculated from the forest inventory was distributed within its respective wood-density class, being distinguished among taxonomic groups (Trees and Palms) and forest formation (seasonally flooded and unflooded). The biomass of unidentified individuals for trees (5–10% of the total) was proportionally distributed across all wood-density classes described by IBAMA (Sternadt, 2001) in order to preserve the total biomass estimated for the forest formation and to maintain the initial balance among the wood-density classes.

The decomposition rate for each forest formation was estimated by weighting the individual rates of each wood-density class, taking into account the proportional tree biomass distribution of each taxonomic group within each forest formation by observation period. For calculation purposes, the decomposition rate of the Hard and Very-hard classes in the Trees group was estimated by regression based on the values of the other categories. For comparison between the two forest formations, we assume that the decomposition rate obtained in each wood-density class in unflooded forest holds for both forest formations, and the formations were distinguished by their respective proportions of taxonomic groups and wood-density categories. We also assumed no effect in relation to diameter of the sample pieces because the mean diameter of the samples (22.4 ± 6.7 cm; Appendix A, Table A1) was an approximate representation of the mean diameter in the forest inventory (18.2 ± 9.7 cm) conducted in the Viruá grid by C.V. de Castilho and collaborators.

2.3.3. Decay time and CWD carbon flux

Estimates of CWD decay time (± SE [standard error]) were based on decomposition rates calculated for each forest formation. For this purpose, the hypothetical CWD decay curve was adopted taking into account the time (independent variable) and the constant of decomposition to 5%, 10%, 25%, 50%, 75% and 95% of the material remaining (dependent variable) as indicated by Olson (1963). Regression analysis was adopted in the hypothetical models for CWD decay time of the two forest formations using a 95% confidence interval (CI). To estimate the long-term annual carbon emissions to the atmosphere (respiration) derived from CWD decomposition, we assumed a predictor interval (range of 95%) of 65–88% of all carbon produced by annual CWD decomposition as indicated by Chambers et al. (2001). The calculations were based on the annual CWD carbon production range (seasonally flooded = 0.04–0.27 MgC ha^{-1} yr^{-1}; unflooded = 0.49–0.58 MgC ha^{-1} yr^{-1}) estimated by Silva et al. (2016) for the PPBio grid in Viruá. All graphics were performed with R software (R Core Team, 2016).

3. Results

3.1. Annual decomposition rate

The annual decomposition rate for all samples varied between 0.044 and 0.963 yr^{-1}, considering the individual average of the latitudinal and longitudinal pieces weighted by the two observation periods (12 and 24 months) (Appendix A, Table A2). On average, decomposition rate of the latitudinal pieces was −18.7% (t_1) and −4.6% (t_2) lower than the rate of the longitudinal pieces. The effect of wood density on the decomposition rates was significant ($ANOVA_{0.05}$, F = 15.01, p < 0.00001), indicating that very-soft woods (in low density classes) have higher decomposition rates (Palms = 0.732 ± 0.206 [SD] yr^{-1}; Trees = 0.630 ± 0.263 yr^{-1}) as compared to the rates for the higher-density classes (Palms = 0.158 ± 0.083 yr^{-1}; Trees = 0.119 ± 0.101 yr^{-1}) (Table 1). The correlation between wood density and decomposition rate in both periods (t_1 and t_2) was negative and significant ($r_p = -0.567$; p < 0.0001), and it is best explained by a simple exponential model, especially for the Trees group (Fig. 2).

3.2. Decomposition rate by forest formation

CWD decomposition rate was estimated at 0.152 ± 0.072 [SE] yr^{-1} (CI = 0.081–0.224 yr^{-1}) for seasonally flooded forests and 0.181 ± 0.083 yr^{-1} (CI = 0.098–0.264 yr^{-1}) for unflooded habitat (Table 2). These results express the structural and floristic differ-

Table 1
Decomposition rate (±SD) defined by sampling periods, taxonomic group, wood-density classes and orientation of contact with the soil (CWD, diameter ≥ 10 cm). Different uppercase letters (columns) indicate significant differences between the means of wood-density classes by taxonomic group (ANOVA, Tukey, α = 0.05).

Taxonomic group	Wood-density class[a]	n ($t_1 + t_2$)	Latitudinal		Longitudinal		Mean		Weighted mean[b]
			t_1	t_2	t_1	t_2	t_1	t_2	
Trees	Very-soft	8	0.612	0.643	0.630	0.627	0.624 ± 0.274	0.632 ± 0.271	0.630 ± 0.263[A]
	Soft	6	0.202	0.375	0.219	0.412	0.213 ± 0.091	0.400 ± 0.169	0.338 ± 0.161[B]
	Medium-soft	8	0.087	0.237	0.238	0.314	0.188 ± 0.160	0.289 ± 0.083	0.256 ± 0.136[B]
	Medium-hard	8	0.109	0.141	0.120	0.110	0.116 ± 0.091	0.121 ± 0.117	0.119 ± 0.101[B]
Palms	Very-soft	2	0.893	0.621	1.024	0.606	0.981 ± 0.093	0.611 ± 0.010	0.732 ± 0.206[A]
	Soft	4	0.225	0.473	0.314	0.439	0.284 ± 0.126	0.450 ± 0.056	0.395 ± 0.135[B]
	Medium-soft	4	0.070	0.114	0.138	0.211	0.115 ± 0.043	0.179 ± 0.109	0.158 ± 0.083[B]

[a] The decomposition rates (±SD) of the Hard (0.076 ± 0.073 yr^{-1}) and Very-hard (0.045 ± 0.054 yr^{-1}) classes of the Trees group were estimated by regression based on the values of other categories: $Y = 2.141 \times EXP(-3.514 \times X)$, $R^2 = 0.972$, where Y = annual decomposition rate estimated and X is the upper limit of the each wood-density class described by IBAMA (Sternadt, 2001) (from $X_{very\text{-}soft} = 0.350\ g\ cm^{-3}$ to $X_{very\text{-}hard} = 1.100\ g\ cm^{-3}$).
[b] Considering the average number of days in each period of time ($t_1 = 365$, $t_2 = 743$) for all pieces sampled in the field.

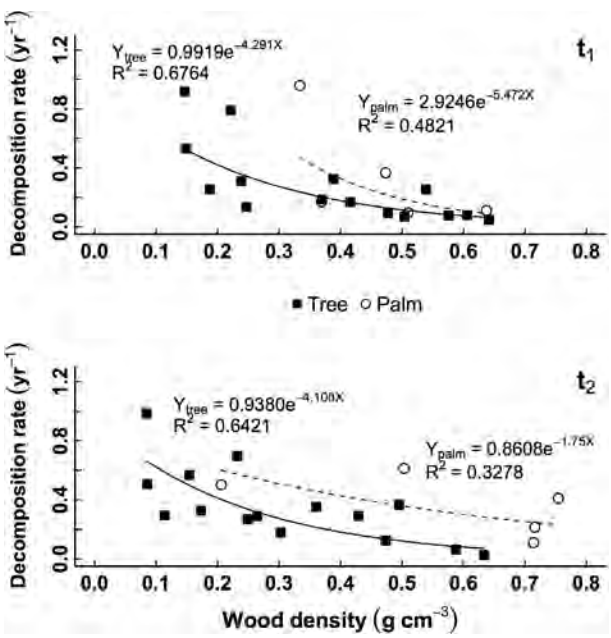

Fig. 2. Relation between wood density and CWD decomposition rate (simple exponential model) in each period of time (t_1 and t_2) considering the two taxonomic groups (Palms and Trees) sampled in Viruá National Park, Roraima, Brazil.

ences for formations with different hydro-edaphic restrictions in Viruá, where ~40% of the biomass forming the CWD of the seasonally flooded formation is derived from the higher wood-density classes (Very-hard and Hard) (Appendix A, Tables A3 and A4).

3.3. Decay time and CWD carbon flux

Based on the decomposition rate calculated for each forest formation we estimated that the hypothetical mean time for decomposition of 95% of the CWD produced per year in Viruá is ~20 years (CI = 13–37) for the seasonally flooded formation and ~17 years (CI = 11–30) for the unflooded formation (Fig. 3). The annual carbon flow to the atmosphere was estimated at 0.002–0.010 MgC ha^{-1} yr^{-1} (flooded) and 0.022–0.026 MgC ha^{-1} yr^{-1} (unflooded) considering the CWD carbon production and the respective decay times of the two forest formations. In this scenario, the maximum residence time (upper limit) of estimated CWD carbon is just under 40 years, when it is estimated that 95% of the total necromass will disappear in both formations.

4. Discussion

Our study indicates a considerable variation in annual decomposition rates (range 0.044–0.963 yr^{-1}) in Viruá. The rates varied according to the taxonomic group and the wood-density class, indicating that the diversity of tree species with different degrees of resistance has a direct impact on the decomposition rates in the study region. The interspecific variation found in Viruá is common in tropical forests, but differs from values found in temperate forests (e.g. Russell et al., 2014; Herrmann et al., 2015) or boreal forests (e.g. Krankina and Harmon, 1995; Freschet et al., 2012), which are ecosystems with lower diversity of species associated with low temperatures and lower CWD decomposition rates.

The high variability in the decomposition rates determined in Viruá was also observed by Martius (1997) in estimates made from wood pieces exposed in a lowland floodplain ecosystem in the central Amazon (range 0.049–1.000 yr^{-1}). Both cases differ from the higher values found by Chambers et al. (2000) (0.015–0.670 yr^{-1}) obtained from estimates derived from tree mortality monitoring in an undisturbed *terra firme* (unflooded upland) forest area in the central Amazon. This difference in upper values is expected for forest formations with different restrictions on the CWD stock (Eaton and Lawrence, 2006). However, distinctions between methods for obtaining the decomposition coefficients also suggest that methodology influences these differences. For example, although there is no firm consensus on the effects of exposure to soil in decomposition rates (e.g. van Geffen et al., 2010), the use of sample pieces in direct contact with the soil in our study influenced the range of values due to increased exposure and the easier access of decomposers to the samples. On the other hand, use of observations derived from monitoring can further reduce the range because most of the samples are derived from large standing dead trees where decomposition rates are initially lower (Palace et al., 2007; Palace et al., 2008).

Regardless of the methods, the most visible implication of our study is the recognition that wood classes with low resistance (Very-soft; k > 0.600 yr^{-1}) represent trees with rapid decomposition (<10 years), contrasting with groups with higher resistance (k < 0.150 yr^{-1}), which contain species with longterm decay attributes. This inverse relationship between decomposition rate and wood density in Viruá was supported by a simple exponential model, as was also observed by Summers (1998) and Chambers et al. (2000) in the central Amazon. While this relationship may be the subject of controversy due to distinct patterns of decomposition among species (Harmon et al., 2000), exponential models have been consistent for Amazonian forests, indicating that they are significant predictors depending on the observed numbers of species and individuals.

Table 2
Decomposition rate (IC; $\alpha = 0.05$) weighted by the average composition of arboreal biomass (diameter $\geq$ 10 cm; Trees + Palms) of seasonally flooded and unflooded forest formations in Viruá National Park, Roraima, Brazil.

Taxonomic group	Wood-density Class	Flooded		Unflooded	
		Mg ha^{-1}	k (yr^{-1})	Mg ha^{-1}	k (yr^{-1})
Trees	Very-soft	0.29	0.150 (0.079–0.222)	0.57	0.171 (0.092–0.250)
	Soft	9.41		22.08	
	Medium-soft	29.17		40.69	
	Medium-hard	38.26		81.17	
	Hard	48.61		32.20	
	Very-hard	1.84		0.97	
	Sub-total	127.58		177.68	
Palms	Very-soft	0.00	0.195 (0.106–0.284)	3.24	0.386 (0.226–0.546)
	Soft	0.81		0.61	
	Medium-soft	4.36		4.94	
	Medium-hard	0.00		0.00	
	Hard	0.00		0.00	
	Very-hard	0.00		0.00	
	Sub-total	5.16		8.79	
Total	Very-soft	0.29	0.152 (0.081–0.225)	3.81	0.181 (0.098–0.264)
	Soft	10.22		22.69	
	Medium-soft	33.53		45.63	
	Medium-hard	38.26		81.17	
	Hard	48.61		32.20	
	Very-hard	1.84		0.97	
	Total	132.74		186.47	

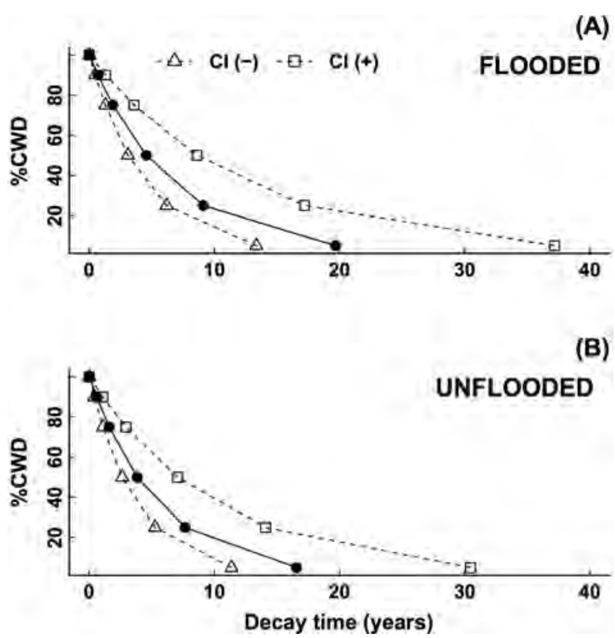

Fig. 3. Hypothetical time for decomposition of 95% of CWD produced in a year in (A) flooded and (B) unflooded forest formations in Viruá National Park, Roraima, Brazil; CI = confidence interval.

Taxonomic and structural differences between the two forest types (Table 2) are the likely explanation of the ~19% lower decomposition rate for seasonally flooded forests (0.152 yr^{-1}) as compared to that estimated for unflooded forests (0.181 yr^{-1}). Because CWD composition (necromass quality) depends on the forest type and its respective live biomass (Schlegel and Donoso, 2008; Silva et al., 2016), different decomposition rates are expected in distinct regions of the Amazon (Baker et al., 2007), and decomposition rate was best explained in Viruá by the lower abundance of species with high wood density in unflooded forests. The largest weight in the construction of the coefficients was credited to the Trees group (which has greater representation), although the Palms group has higher decomposition rates. The two taxonomic groups differ in their form of fragmentation, with the center of the Palm samples decomposing more quickly than the outer parts, while the sapwood was lost faster than the heartwood in Trees, in a process similar to that observed by Chao et al. (2008). In any case, the values estimated here were representative of the two formations because the estimates incorporate proportionally the decomposition rates of the different wood-density classes and taxonomic groups. This proportional association generates a proxy for annual CWD production and allows construction of a representative metric and a realistic decay time in order to estimate the carbon flow derived from CWD in each forest formation.

Our estimates for these forests are compatible with the values obtained by Chambers et al. (2000) (0.190 yr^{-1}; monitoring tree mortality in the central Amazon), and Palace et al. (2008) (0.170 yr^{-1}; using the steady-state model for large necromass observed in the eastern Amazon). The difference in methods of obtaining decomposition rates indicated no significant effects between the values for the unflooded forests, but there were distinctions in rates for ecosystems with hydro-edaphic restrictions, where forest soils are nutrient-poor (predominantly sandy) and are seasonally flooded.

The highest abundance of high-wood density species partly explain the lower decomposition rate calculated in our study (0.152 yr^{-1}) for seasonally flooded formations, even without considering the effect of the natural deceleration of the decomposition process as a result of seasonal anoxia. Because the decompostion rate of each wood-density class in the flooded forest is based on measurements made in the unflooded forest, these estimates do not include the effect of greatly reduced decompostion rate during the months that the floor of the flooded forest is submerged. If the flooded period were considered, the seasonally flooded forests would tend to be characterized by even lower decomposition rates, as pointed out by Martius (1997), indicating that residence times for CWD carbon in these formations could be even longer than the values estimated here. In this condition, Amazonian seasonally flooded forests can play a important role in the region due their greater proportional capacity for storage of CWD carbon as compared to unflooded forests.

The mean values determined for CWD carbon residence times (17–20 years) in the two formations are within the expected range for terrestrial forest biomes (12–54 years; Yizhao et al., 2015), but they differ when compared to the studies carried out in the laboratory (e.g. Australian tree species; 6–375 years; Mackensen et al., 2003) or studies on specific groups of trees (e.g. North American hardwoods; 46–71 years; Russell et al., 2014). Although similar to other studies conducted in South American upland rain forests (2–46 years; Hérault et al., 2010), our values are considerably greater than both the default value suggested by the Intergovernmental Panel on Climate Change (IPCC, 1997) (10 years) and the 5–10 years expected for all forest formations in Viruá, when estimated based on the steady-state assumption between stock and annual CWD production (Silva et al., 2016). The assumption of a steady state is commonly used in regional models (Palace et al., 2008), but this method can produce CWD decay times that are unrepresentative when associated with longterm climate change, thereby generating unrealistic estimates for carbon stocks and flows derived from necromass.

Under increasing tree mortality due to forecasted global warming, Amazon forests ($\sim$4 milhões km^2: Brazil-INPE, 2013) will tend to become in a huge source of carbon emissions to the atmosphere (Brienen et al., 2015; Bonal et al., 2016). In this case, the tendency is for an increase in mortality of larger (non-pioneer) trees that represent substantial amounts of carbon per unit area (Phillips et al., 2010; Lindenmayer et al., 2012), suggesting that undisturbed forests will produce significant amounts of CWD with higher wood density. Within this configuration, the carbon emissions derived from respiration by CWD decomposition in both oligotrophic forest formations in Viruá (flooded = 0.002–0.010 MgC ha^{-1} yr^{-1} and unflooded = 0.022–0.026 MgC ha^{-1} yr^{-1}) will tend to rise due to increasing accumulation of necromass. The magnitude of emissions would be directly related to reducing the carbon sequestration capacity, particularly in seasonally flooded formations due to higher accumulation of CWD with greater resistance to decay as a function of hydro-edaphic characteristics. These differences reflect distinctions in the future CWD carbon stock among the studied formations, directly affecting the disappearance time and the CWD decomposition rate.

This difference in decomposition rates affects the assumptions in Brazil's national inventories of greenhouse gas emissions. The CWD stock and its decomposition are implicitly constant in the third (most recent) inventory (Brazil-MCTI, 2014; Bustamante et al., 2015). However, these stocks are not in equilibrium today, and under a scenario with continued global warming it is expected that tree mortality will increase in undisturbed forests, thereby increasing the stock of CWD and, consequently, emission from decomposition (Barros and Fearnside, 2016). This extra carbon source to the atmosphere is not yet considered by the Brazilian inventory (see Brandão Jr. et al., 2015). Under these conditions, the current net removal rate of carbon estimated for the Amazonia biome (0.43 MgC ha yr^{-1}; Bustamante et al., 2015) will be reduced due to the impoverishment of larger individuals and of species with higher wood density in the forest formations, causing uncertainties in global models and reducing the mitigating role of the region in the global carbon budget.

5. Conclusions

The decomposition rate of coarse woody debris (CWD) in the Viruá area is slower in forests over nutrient-poor and seasonally flooded soils (higher hydro-edaphic restrictions), where the structure and species composition represent $\sim$40% of the aboveground biomass in tree species with high wood density. This means that CWD in seasonally flooded forest formations has a longer residence time and slower carbon release by decomposition (respiration) than in unflooded forests. These results improve our ability to model carbon stocks and fluxes derived from decomposition of dead wood in undisturbed oligotrophic forests in the Rio Negro-Rio Branco Basin, northern Brazilian Amazon.

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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.2017.04.026.

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Appendix A - Supplementary Material

Decomposition rates of coarse woody debris in undisturbed Amazonian seasonally flooded and unflooded forests in the Rio Negro-Rio Branco Basin in Roraima, Brazil

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Appendix A. Supplementary Table A1 - Taxonomic identification of the species, biometric aspects and wood density of the sampling disks used to estimate the CWD decomposition rates in forests in Viruá National Park, Roraima, northern Brazilian Amazonia.

Sample (number)	Family	Species	Biometric aspects, sampling disks (cm)			% Bark	Wood Density (g cm^{-3}) (1)		
			Diameter	Width	Bark thickness		t_0	t_1	t_2
1	Arecaceae	*Attalea maripa* (Aubl.) Mart.	28.5±1.1	4.1±0.4	-	-	0.554	0.369	0.206
2	Bixaceae	*Cochlospermum orinocense* (Kunth) Steud.	37.2±1.7	4.3±0.2	1.55±0.48	2.69	0.341	0.146	0.084
3	Araliaceae	*Schefflera morototoni* (Aubl.) Maguire, Steyerm. & Frodin	28.6+4.5	4.8±0.4	0.58±0.15	1.35	0.318	0.247	0.086
4	Fabaceae	*Inga* sp.	24.3±1.1	3.8±0.1	0.35±0.06	0.81	0.601	0.504	0.249
5	Urticaceae	*Cecropia palmata* Willd.	23.8±2.7	4.5±0.1	0.58±0.05	0.63	0.288	0.187	0.114
6	Fabaceae	*Centrolobium paraense* Tul.	30.8±3.0	4.9±0.2	0.53±0.05	1.11	0.665	0.606	0.473
7	Chrysobalanaceae	*Licania heteromorpha* Benth.	22.2±0.9	4.9±0.2	0.55±0.17	1.55	0.717	0.641	0.588
8	Bignoniaceae	*Jacaranda copaia* (Aubl.) D.Don	15.8±0.5	4.2±0.1	0.30±0.14	1.21	0.349	0.239	0.173
9	Arecaceae	*Attalea maripa* (Aubl.) Mart.	27.9±1.0	4.7±0.1	-	-	0.473	0.473	0.754
10	Arecaceae	*Oenocarpus bacaba* Mart.	13.5±0.8	4.0±0.1	-	-	0.628	0.510	0.714
11	Annonaceae	*Onychopetalum amazonicum* R.E.Fr.	20.4±0.4	4.5±0.2	0.95±0.10	2.96	0.563	0.416	0.303
12	Araliaceae	*Schefflera morototoni* (Aubl.) Maguire, Steyerm. & Frodin	16.8±0.5	5.2±0.1	0.58±0.05	2.19	0.540	0.370	0.361
13	Bixaceae	*Cochlospermum orinocense* (Kunth) Steud.	23.3±1.9	5.7±0.1	1.50±0.39	4.05	0.297	0.221	0.232
14	Urticaceae	*Cecropia palmata* Willd.	23.4±2.5	4.3±0.1	0.43±0.13	0.93	0.275	0.149	0.154
15	Arecaceae	*Oenocarpus bacaba* Mart.	14.5±1.6	3.3±0.2	-	-	0.587	0.637	0.716
16	Fabaceae	*Bowdichia nitida* Spruce ex Benth	31.1±1.3	3.5±0.5	0.70±0.08	1.43	0.704	0.576	0.633
17	Burseraceae	*Protium unifoliolatum* Engl.	16.5±0.4	3.3±0.2	0.53±0.10	2.02	0.654	0.539	0.429
18	Arecaceae	*Oenocarpus bataua* Mart.	13.9±0.8	3.7±0.1	-	-	0.315	0.334	0.503
19	Burseraceae	*Protium crassipetalum* Cuatrec.	16.9±0.7	3.4±0.2	0.45±0.06	1.68	0.583	0.477	0.264
20	Burseraceae	*Protium crassipetalum* Cuatrec.	18.0±0.9	3.6±0.2	0.45±0.13	1.60	0.509	0.388	0.495
	Mean±SD		22.4±6.7	4.2±0.2	0.61±0.14	1.60±0.91	0.498±0.153	0.401±0.163	0.377±0.222

(1) t_0 refers to control pieces, while t_1 and t_2 are averages of the disks collected in the field with latitudinal and longitudinal orientation, respectively.

Appendix A. Supplementary Table A2 - Decomposition rate (yr^{-1}) arranged by species, wood-density class assumed, orientation of soil contact and sample period, Viruá National Park, Roraima, Brazil. Weighted decomposition rate (yr^{-1}) was calculated using the simple means obtained in each latitudinal and longitudinal piece standardized by the number of days in each sample period.

Family	Species	Wood density class	t_1 (days)	Orientation		t_2 (days)	Orientation		Decomposition rate (weighted)
				Latitudinal	Longitudinal		Latitudinal	Longitudinal	
Annonaceae	*Onychopetalum amazonicum*	Medium-soft	368	0.103	0.236	740	0.138	0.217	0.175
Araliaceae	*Schefflera morototoni*	Soft	363	0.114	0.154	729	0.648	0.364	0.383
	Schefflera morototoni	Soft	368	0.228	0.144	740	0.172	0.530	0.296
Arecaceae	*Attalea maripa*	Soft	363	0.142	0.198	729	0.516	0.488	0.392
	Attalea maripa	Soft	368	0.306	0.427	740	0.430	0.391	0.396
	Oenocarpus bacaba	Medium-soft	368	0.049	0.145	740	0.124	0.096	0.106
	Oenocarpus bacaba	Medium-soft	364	0.092	0.130	747	0.105	0.325	0.181
	Oenocarpus bataua	Medium-soft	364	0.893	1.024	747	0.621	0.606	0.727
Bignoniaceae	*Jacaranda copaia*	Soft	368	0.262	0.357	740	0.310	0.340	0.320
Bixaceae	*Cochlospermum orinocense*	Very-soft	363	0.939	0.899	729	0.984	0.985	0.963
	Cochlospermum orinocense	Very-soft	349	0.759	0.823	721	0.644	0.749	0.727
Burseraceae	*Protium unifoliolatum*	Medium-hard	364	0.221	0.289	747	0.365	0.216	0.279
	Protium crassipetalum	Medium-soft	364	0.057	0.130	747	0.260	0.322	0.226
	Protium crassipetalum	Medium-soft	344	0.116	0.534	727	0.313	0.418	0.353
Chrysobalanaceae	*Licania heteromorpha*	Medium-hard	368	0.033	0.064	740	0.036	0.089	0.058
Fabaceae	*Inga* sp.	Medium-soft	363	0.072	0.068	729	0.239	0.301	0.203
	Centrolobium paraense	Medium-hard	372	0.073	0.086	735	0.145	0.100	0.108
	Bowdichia nitida	Medium-hard	364	0.110	0.044	747	0.018	0.036	0.044
Urticaceae	*Cecropia palmata*	Very-soft	372	0.211	0.302	735	0.293	0.296	0.282
	Cecropia palmata	Very-soft	348	0.553	0.507	720	0.652	0.482	0.555

Appendix A. Supplementary Table A3 – Estimates of the distribution (%) of biomasses of Trees and Palms (DBH ≥ 10 cm) by wood-density class and forest formation (flooded and unflooded) in Viruá National Park, Roraima, Brazil.

Taxonomic group	Wood density class	Biomass (%)	
		Flooded	Unflooded
Palms	Very-soft	0.0	36.9
	Soft	15.6	6.9
	Medium-soft	84.4	56.2
Trees	Very-soft	0.2	0.3
	Soft	7.4	12.4
	Medium-soft	22.9	22.9
	Medium-hard	30.0	45.7
	Hard	38.1	18.1
	Very-hard	1.4	0.5

Appendix A. Supplementary Table A4 – Wood-density classes of species (DBH ≥ 10 cm) with high biomass concentration (%) determined by forest formation (flooded and unflooded) in Viruá National Park, Roraima, Brazil. Forest inventory and taxonomy of species were performed by C. V. de Castilho (Castilho, 2011), C. V. de Castilho and R. Perdiz (Castilho and Perdiz, 2013) and G. Damasco (Damasco *et al.*, 2012).

Forest Formation	Family	Species	Wood-density class (IBAMA)	% Biomass on the total of forest formation
Flooded	Chrysobalanaceae	*Licania micrantha* Miq.	Very-hard	8.68%
	Lecythidaceae	*Eschweilera parvifolia* Mart. ex DC.	Very-hard	7.67%
	Phyllanthaceae	*Amanoa guianensis* Aubl.	Very-hard	5.79%
	Vochysiaceae	*Ruizterania retusa* (Spruce ex Warm.) Marc.-Berti	Hard	5.50%
	Chrysobalanaceae	*Exellodendron barbatum* (Ducke) Prance	Very-hard	4.43%
Unflooded	Vochysiaceae	*Ruizterania retusa* (Spruce ex Warm.) Marc.-Berti	Hard	9.28%
	Goupiaceae	*Goupia glabra* Aubl.	Hard	8.34%
	Chrysobalanaceae	*Licania heteromorpha* Benth.	Very-hard	6.86%
	Lauraceae	*Ocotea canaliculata* (Rich.) Mez	Soft	4.32%
	Burseraceae	*Tetragastris panamensis* (Engl.) Kuntze	Hard	4.30%

Appendix A. Supplementary Figure A1 – (A) Selection and collection of botanical material, (B) cutting the bole in 25 sample disks (C) biometry and numbering of disks and (D) positioning of the discs in the field: "*longitudinal*" discs are standing on edge in the center of the photograph, and "*latitudinal*" discs are lying flat on the ground in the lower right.

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