

Modeling decay rates of dead wood in a neotropical forest

Bruno Hérault · Jacques Beauchêne · Félix Muller ·
Fabien Wagner · Christopher Baraloto · Lilian Blanc ·
Jean-Michel Martin

Received: 30 September 2009 / Accepted: 2 March 2010 / Published online: 31 March 2010
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Abstract Variation of dead wood decay rates among tropical trees remains one source of uncertainty in global models of the carbon cycle. Taking advantage of a broad forest plot network surveyed for tree mortality over a 23-year period, we measured the remaining fraction of boles from 367 dead trees from 26 neotropical species widely varying in wood density ($0.23\text{--}1.24\text{ g cm}^{-3}$) and tree circumference at death time ($31.5\text{--}272.0\text{ cm}$). We modeled decay rates within a Bayesian framework assuming a first order differential equation to model the decomposition process and tested for the effects of forest management (selective logging vs. unexploited), of mode of death (standing vs. downed) and of topographical levels (bottomlands vs. hillsides vs. hilltops) on wood decay rates. The general decay model predicts the observed remaining fraction of dead wood ($R^2 = 60\%$) with only two biological predictors: tree circumference at death time and wood specific density. Neither selective logging nor local topography had a differential effect on wood decay rates. Including the mode of death into the model revealed that

standing dead trees decomposed faster than downed dead trees, but the gain of model accuracy remains rather marginal. Overall, these results suggest that the release of carbon from tropical dead trees to the atmosphere can be simply estimated using tree circumference at death time and wood density.

Keywords Amazonia · Carbon cycle · Decomposition · Selective logging · Rainforest · Coarse woody debris

Introduction

Forests play a key role in the global carbon cycle accounting for 80% of terrestrial above-ground biomass (Dixon et al. 1994). Tropical forests alone are responsible for about 35% of the global net primary production (Melillo et al. 1993). Dead wood represents an important component in tropical forest carbon cycling, with up to 40% of the total biomass of trees $>10\text{ cm}$ in diameter (Brown et al. 1995; Rice et al. 2004; Pyle et al. 2008). Despite the importance of dead wood fluxes in determining the carbon balance of tropical forests, decay rate variation remains one of the major sources of uncertainty in models of global carbon cycle (Weedon et al. 2009).

Recent studies have elegantly demonstrated the importance of dead wood carbon dynamics in determining year-to-year variations in forest carbon balance (Chambers et al. 2004; Pyle et al. 2008), and this means that the accurate estimation of the dead wood decay rates is a key link for a quantitative understanding of forest carbon dynamics (Yin 1999). Given the international efforts aimed at reducing atmospheric concentrations of greenhouse gases, developing predictive models to estimate net carbon fluxes between the biosphere and atmosphere is a necessary step

Communicated by Christian Koerner.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-010-1602-8) contains supplementary material, which is available to authorized users.

B. Hérault (✉) · F. Wagner · J.-M. Martin
Université des Antilles et de la Guyane, UMR EcoFoG,
97387 Kourou, French Guiana
e-mail: bruno.herault@ecofog.gf

J. Beauchêne · F. Muller · F. Wagner · L. Blanc · J.-M. Martin
CIRAD, UMR EcoFoG, 97387 Kourou, French Guiana

C. Baraloto
INRA, UMR EcoFoG, 97387 Kourou, French Guiana

to quantify the degree to which forest ecosystems serve as a carbon sink or source. To date, the majority of studies on wood decay rates have been conducted in North American and European forests, and a recent review stressed the need to increase the geographical coverage, especially to obtain more data from subtropical and equatorial forests (Weedon et al. 2009). These gaps in our knowledge on carbon dynamic are evident in studies from Amazonian forests where carbon gain due to tree recruitment and growth were precisely estimated, whereas carbon losses from dead trees are often implicitly assumed to return directly after death to the atmosphere (Phillips et al. 2009).

Dead wood decay rates have been linked to a number of environmental variables, among which the most often recognized are the mode of death and the decomposition environment. Mode of death can be roughly split into two categories: standing and downed trees. Due to the absence of contact with soil and, consequently, insufficient moisture in wood tissues, it has been suggested that standing tree decomposition is slower than that of downed trees (e.g., Yatskov et al. 2003). Decomposition environment is more difficult to assess in situ but two local environmental factors may play a pivotal role in tropical forests. Firstly, topographical levels have been linked with soil fertility as well as forest dynamics. Indeed, it has been recently suggested that soil waterlogging and slope angle may be among the primary ecological drivers of forest dynamics in French Guiana with, for instance, treefall rates twice as high in bottomlands than in hilltops (Ferry et al. 2009). The changing rates of treefall mortality have important consequences on dead wood availability for decomposers. And, secondly, selective logging is the most widely employed management practice for timber wood production in Amazonia (Asner et al. 2004) and throughout the humid tropics (Okuda et al. 2003). Stocks of dead wood may be larger in logged than in unlogged forests (Palace et al. 2007), and conventional logging management can produce up to three times as much dead wood as reduced impact logging (Keller et al. 2004). Selective-logging creates canopy gaps that expose, at least for 1–5 years, these additional flux of dead wood from downed trees to more solar radiation that, in turn, increases soil temperature and lowers soil surface humidity through higher evaporation (Denslow 1987). It has been suggested that these changing conditions may boost wood decay rates in temperate forests, while they might be of negligible influence under wet and warm tropical climate (Rock et al. 2008). Given the importance of forest response to management in assessing regional and global-scale carbon budgets for the whole Amazonian region (Chambers et al. 2004), studies on the factors that affect decay rates of dead wood are important.

Inventories of dead wood are rather straightforward to perform and are already done for a number of neotropical

forests (Keller et al. 2001, 2004; Palace et al. 2007, 2008; Pyle et al. 2008), but directly measuring the decay rates is difficult due to the slow nature of the decomposition process. We took advantage of a unique dataset from a broad plot network (56 ha) and used a chronosequence approach to estimate decay rates. In other words, the biomass of the decomposed individual trees was related to the corresponding biomass of trees just before death as estimated from annual censuses. The specific goals of this study were (1) to measure the remaining fraction of wood for boles of dead trees representative of the variation of wood density and of diameter at breast height encountered in Amazonian forests (Table 1), on diverse forest topographical levels and from managed versus natural forests, (2) to model decay rates using biologically realistic mathematical functions leading to interpretable model parameters, and (3) to investigate the role of some environmental factors in controlling decay rate constants.

Materials and methods

Study site

The study was conducted at the Paracou experimental site (5°18'N, 52°55'W), a lowland tropical forest near Sinnamary, French Guiana (Gourlet-Fleury et al. 2004). The site receives nearly two-thirds of the annual 3,041 mm of precipitation between mid-March and mid-June, and less than 50 mm per month in September and October. The most common soils in Paracou are the shallow ferralitic soils limited in depth by a more or less transformed loamy saprolithe. Some very thick ferralitic soils, with free vertical drainage, are primarily encountered on the highest residual summits of the area (approximately 40 m above sea level). The forest is typical of Guianan rainforests (Ter Steege et al. 2003). More than 550 woody species attaining 2 cm DBH have been described at the site, with an estimated 160–180 species of trees ≥ 10 cm DBH per hectare. The dominant families at the site include Leguminosae, Chrysobalanaceae, Lecythidaceae, Sapotaceae, and Burseraceae.

In 1984, nine square 6.25-ha plots were established at the Paracou site for a complete annual inventory of all trees ≥ 10 cm DBH. Annual inventories of mortality and circumference were conducted, and we report data until the most recent inventory in 2008. Circumference measurements were made at positions of 1.3 m above the soil surface, and points of measurement were marked using permanent paint. From 1986 to 1988, six plots underwent logging treatments. Selected timbers were extracted, with an average of 30–45 trees ≥ 40 cm DBH removed per hectare. Subsequently, timber stand improvement (TSI) by

Table 1 Species summaries for modeling decay rates of coarse woody debris in a neotropical forest

Species name	Botanical family	<i>n</i>	Tree death (year) ^a	Circumference (cm) ^b	Wood density (g cm ⁻³) ^c	<i>T</i> _{0.50} (years) ^d	<i>T</i> _{0.90} (years) ^d
<i>Bocoa prouacensis</i>	Caesalpiniaceae	17	1991 (1985; 2004)	99.0 (33.0; 198.0)	1.241	14.0	46.3
<i>Brosimum rubescens</i>	Moraceae	9	1990 (1987; 2000)	60.0 (42.0; 94.5)	1.084	10.9	36.2
<i>Carapa procera</i>	Meliaceae	28	1992 (1985; 2006)	66.5 (35.5; 179.0)	0.709	5.0	16.7
<i>Cecropia obtusa</i>	Cecropiaceae	24	2000 (1991; 2008)	37.7 (32.0; 75.0)	0.230	0.6	2.1
<i>Cecropia sciadophylla</i>	Cecropiaceae	17	2004 (1994; 2006)	55.0 (34.0; 84.0)	0.405	1.8	6.0
<i>Chrysophyllum sanguinolentum</i>	Sapotaceae	15	1989 (1985; 2006)	118.5 (45.5; 212.0)	0.796	6.2	20.6
<i>Dicorynia guianensis</i>	Caesalpiniaceae	14	1991 (1985; 2004)	141.8 (35.0; 227.0)	0.807	6.4	21.2
<i>Eperua falcata</i>	Caesalpiniaceae	17	1991 (1985; 2004)	132.0 (31.5; 260.0)	0.818	6.5	21.7
<i>Eperua gradiflora</i>	Caesalpiniaceae	11	1994 (1992; 2006)	117.0 (40.5; 236.0)	0.895	7.7	25.6
<i>Goupia glabra</i>	Celastraceae	9	1993 (1985; 2006)	89.6 (33.5; 203.0)	0.856	7.1	23.6
<i>Iryanthera hostmanni</i>	Myristicaceae	11	1998 (1995; 2004)	62.0 (42.0; 73.5)	0.691	4.8	15.9
<i>Iryanthera sagotiana</i>	Myristicaceae	12	1997 (1995; 2002)	71.5 (39.5; 99.0)	0.685	4.7	15.7
<i>Jacaranda copaia</i>	Bignoniaceae	23	1993 (1985; 2004)	44.0 (32.0; 155.0)	0.458	2.3	7.5
<i>Lecythis persistens</i>	Lecythidaceae	7	2004 (1998; 2006)	53.5 (32.5; 64.5)	0.914	8.0	26.5
<i>Licania heteromorpha</i>	Chrysobalanaceae	11	2004 (1994; 2006)	61.0 (34.5; 97.5)	0.988	9.2	30.6
<i>Oxandra asbeckii</i>	Annonaceae	8	2003 (1998; 2006)	38.2 (33.0; 48.0)	0.964	8.8	29.3
<i>Pogonophora schomburgkiana</i>	Euphorbiaceae	9	2002 (1993; 2006)	40.0 (36.0; 57.5)	0.952	8.6	28.6
<i>Pradosia cochlearia</i>	Sapotaceae	15	1989 (1985; 2004)	165.0 (42.5; 259.0)	0.929	8.2	27.3
<i>Qualea rosea</i>	Vochysiaceae	7	1994 (1988; 2004)	52.0 (35.0; 203.0)	0.746	5.5	18.3
<i>Recordoxylon speciosum</i>	Caesalpiniaceae	11	1990 (1985; 2000)	87.5 (45.0; 151.0)	0.997	9.4	31.1
<i>Sextonia rubra</i>	Lauraceae	12	1991 (1985; 2006)	84.5 (35.5; 233.0)	0.588	3.6	11.9
<i>Sterculia pruriens</i>	Sterculiaceae	23	1993 (1985; 2006)	131.5 (32.0; 272.0)	0.619	3.9	13.0
<i>Symphonia globulifera</i>	Clusiaceae	14	1992 (1985; 2000)	69.1 (32.5; 148.5)	0.712	5.1	16.8
<i>Tachigali melinonii</i>	Caesalpiniaceae	17	1990 (1986; 1996)	133.5 (36.5; 216.0)	0.748	5.5	18.4
<i>Virola michelii</i>	Myristicaceae	12	1995 (1990; 2004)	101.5 (33.0; 147.5)	0.558	3.2	10.8
<i>Vouacapoua americana</i>	Caesalpiniaceae	18	1990 (1985; 2004)	118.0 (39.0; 240.0)	0.946	8.5	28.2

^a Distribution of the year of tree death: median (min; max)^b Circumference distribution at tree death: median (min; max)^c Wood density (g cm⁻³ at 12% humidity, measured at the Paracou experimental site)^d Predicted times to lose, respectively, 50 and 90% of initial biomass for a 150-cm DBH tree: $T_{0.50} = -\ln(0.5)/K$, $T_{0.90} = -\ln(0.1)/K$ (with K the species decay rate constant)

poison girdling was conducted on selected non-commercial species, removing an average of 53.4 m³ ha⁻¹. Logging operations at Paracou were typical of conventional logging systems, with no effort to implement any of the recommendations suggested for reduced-impact logging techniques. The surface areas damaged in the plots are among the highest values reported in the literature for similar extracted timber volumes (Blanc et al. 2009).

Sampling methods

Decay rates were studied for boles of 367 dead trees (>10 cm DBH) from 26 common species in the Paracou forest using a chronosequence approach (Harmon and Sexton 1996). Annual mortality data from the nine square 6.25-ha permanent inventory plots were used to select dead

trees for sampling in order to obtain representative samples (1) of the density and circumference distributions (see Table 1) and (2) in logged and unlogged forests. Mortality was also stratified by topographical levels (94 trees in bottomlands, 173 trees in hillsides, and 100 trees in hill-tops) and modes of death (145 standing, 222 downed) to test for these additional controls over decay rates. The distribution of wood densities and tree circumference (the two variables included in the final model) against the environmental factors tested may lead to critical biases in the model parameterization and, in turn, in our conclusions. In a preliminary phase, we carefully checked these distributions in order to choose the most balanced sampling strategy.

In order to account for the intra-individual variability of decomposition levels, three cross-sections for each tree

were cut with a chainsaw: at 130 cm height (CS1), in the middle of the entire bole, and just before the first bole division. Cross-sections diameter (two diameter measurements at 90°, D_{\min} and D_{\max}) were measured with calipers to the nearest 0.1 cm. Cross-sections were labeled, bagged, and transported to the CIRAD wood science laboratory in Kourou. Prior to oven drying, cross-section thickness was measured with calipers at six equidistant points around the circumference. Next, cross-section samples were sawn into smaller pieces, in order to standardize the time required for drying. Dry mass of each specimen was next determined after oven drying at 103°C to a constant mass. Initial surfaces (SURF0) of CS1 were approximated using:

$$\text{SURF0}_{\text{CS1}} = \frac{\text{CIRC}^2 * D_{\min}/D_{\max}}{\pi * \left(D_{\min}/D_{\max} + 1 \right)^2} \quad (1)$$

where CIRC represents tree circumference at the time of death. The initial surface of cross-sections 2 and 3 were derived from assuming constant ratios between the initial and the final surface (Melin et al. 2009). Details on these calculations are provided in Electronic Supplementary Material (ESM) 1. Cross-section initial volumes were obtained by multiplying initial surfaces and thicknesses. The original cross-section mass was next calculated as the product of the initial cross-section volume and the mean wood specific gravity ($0.872 \times \text{wood density at 12\% humidity}$; following Chave et al. 2006). Wood densities at 12% humidity were measured at the Paracou experimental site (Table 1) to avoid biases due to regional database compilation (Baraloto et al. 2010), and are now available in a large trait database for the Guiana shield (Ollivier et al. 2007). Finally, the remaining fraction was obtained by dividing the current anhydrous mass of each cross-section by the estimated initial anhydrous mass. We chose to model decay rates using mass loss rather than density loss as vole creation and bole fragmentation are not taken into account in density loss studies, leading to underestimated decay rates (Yin 1999). All modeling work was performed on the level of the entire dead tree by weight-averaging the remaining fractions by individual tree.

In numerous cases, dead trees were not found in the field. Given that the death of each tree was annually recorded and that each tree was precisely mapped, we are confident that a tree that was recorded as ‘absent’ in the forest was at least broken into very small fragments if not completely decomposed. We included all these ‘absent’ trees in the sampling population. If these completely decomposed trees were not included in the sampling population, it was likely that results had been biased against soft- and fast-decomposing trees (Chambers et al. 2000). Indeed, not including completely decomposed trees is akin to equating the average speed of all runners to the speed of

those still on the track running without adjusting for those who have already crossed the finish line (Yin 1999).

Modeling decay rates

To model the basic decay process over time, a first order differential equation (Olson 1963) was chosen:

$$\frac{d_x}{d_t} = -kx(t) \quad (2)$$

The quantity of decomposed wood is the product of the decay rate k and the amount of wood x at time t . This means that the decomposition rate is proportional to the remaining fraction of wood. The solution of this differential equation is the exponential function:

$$M_t = M_0 e^{-kt} \quad (3)$$

where M is the oven dry mass (kg) of the tree at time t (years) after death, M_0 the initial oven dry mass, and k the decay rate. By factoring the initial value M_0 to the left side of the equation, we obtain $M_t/M_0 = R_t$ as a measure of the remaining fraction of deadwood at time t (Zell et al. 2009). The decay rate k depends on other co-variables which were often incorporated in a multiple linear regression (Chambers et al. 2000). Preliminary analyses convinced us to use biologically-realistic functions to link k to wood density and individual circumference (see ESM 3):

$$k = \frac{\alpha}{\text{WSG}^\beta * \text{CIRC}^\gamma} \quad (4)$$

where WSG is species wood specific gravity, CIRC is tree circumference at death time, and α , β , γ the parameters of the model. We chose to use power-law functions because they have several mathematical properties that are biologically more realistic than polynomial models. Indeed, k naturally tends toward infinity as WSG or CIRC tends toward zero, and k naturally tends toward zero as WSG or CIRC tends toward infinity. Second, the parameters β and γ control the shape of the function itself (i.e. the form of the decay rate through wood density or tree circumference) while α controls the speed of the decay rate.

Next, we wanted to test for an effect on decay rates of three factors: forest management (FM), local topography (LT), and mode of death (DT). We first assumed that these three factors did not change the shape of the relationship between WSG and CIRC on the one hand and k on the other. This implies that these factors did not affect β and γ but did probably affect α , i.e. the rhythm of the decay rate. We constructed the final models in a Bayesian framework (Clark 2005), and we quantified the effect of the three factors (and of their interactions) using the Deviance Information Criterion (DIC), a generalization of Akaike Information Criterion (AIC). The model with the smallest

DIC is estimated to be the model that would best predict a replicate dataset which has the same structure as that currently observed (Spiegelhalter et al. 2002). The model parameters, for which we used the mean of the posterior densities, and the parameter uncertainties, for which we used the distribution of the posterior densities, were estimated as follow:

$$R_{(t,FM,LT,DT)} = e^{-\left[\frac{\alpha(FM,LT,DT)}{WSG^{\beta} \cdot CIRC^{\gamma}}\right]t} + \varepsilon \quad (5)$$

$$\varepsilon \sim \text{LogN}\left(1, 1/\tau\right) \quad (6)$$

$$\tau \sim \text{Gamma}(0.01, 0.0_1) \quad (7)$$

$$\alpha \sim N(0, 0.00_1) \quad (8)$$

$$\beta \text{ and } \gamma \sim \text{LogN}(1, 0.00_1) \quad (9)$$

where R is the remaining fraction of deadwood at time t , WSG is the species wood specific gravity, CIRC is the tree circumference at death time, α , β , γ the parameters of the model, and ε the fitted-model residuals. Parameter prior distributions were chosen to be non-informative, so that parameter estimations were driven much by the data and less by the specified prior distributions. Markov chain Monte Carlo simulations were performed and Gibbs sampling (Geman and Geman 1984) was completed in Winbugs 1.4 (Lunn et al. 2000). For each model, the

parameter posterior densities were obtained with 200,000 iterations after a burning step (10,000 iterations). The coefficient of determination R^2 was compute with the following formula (Gelman et al. 2004):

$$R^2 = 1 - [\text{Var}_{\text{model}}/\text{Var}_{\text{data}}] \quad (10)$$

where $\text{Var}_{\text{model}}$ is the mean of the posterior density of the model variance and Var_{data} the variance of the data.

Complete datasets as well as Winbugs codes are available in ESM 2.

Results

Wood density (12% moisture) of the 367 individual trees sampled for this study varied from 0.23 g cm^{-3} for *Cecropia obtusa* (Urticaceae) to 1.24 g cm^{-3} for *Bocoa prouacensis* (Fabaceae) with a mean value of $0.75 \pm 0.24 \text{ g cm}^{-3}$. Tree circumference varied from 31.5 to 272.0 cm with a mean value of $91.7 \pm 55.6 \text{ cm}$. Among the 367 sampled trees, 211 individuals had completely decomposed and 156 were still present, resulting in 458 tree cross-sections sampled. Mean time after death was 13.7 ± 6.5 years with the oldest trees having died 23.5 years before sampling and the most recent 0.5 years earlier.

Five alternative models were tested (Table 2). In general, the parameters were well estimated, as shown by the

Table 2 Modeling decay rates in a neotropical forest in function of forest management (FM), local topography (LT), and mode of death (DT)

Models		Parameters estimates \pm SD			DIC	R^2
		α	β	γ		
1	$R_{(t)} = e^{-\left[\frac{\alpha}{WSG^{\beta} \cdot CIRC^{\gamma}}\right]t}$	4.01 ± 1.15	1.82 ± 0.13	0.85 ± 0.06	-379.1	0.60 ± 0.03
2	$R_{(t,FM)} = e^{-\left[\frac{\alpha(FM)}{WSG^{\beta} \cdot CIRC^{\gamma}}\right]t}$	3.98 ± 1.15 (logged) 4.08 ± 1.17 (unlogged)	1.82 ± 0.13	0.85 ± 0.06	-377.1	0.60 ± 0.03
3	$R_{(t,DT)} = e^{-\left[\frac{\alpha(DT)}{WSG^{\beta} \cdot CIRC^{\gamma}}\right]t}$	4.39 ± 1.29 (downed) 6.76 ± 2.15 (standing)	1.71 ± 0.14	0.88 ± 0.06	-402.6	0.63 ± 0.03
4	$R_{(t,LT)} = e^{-\left[\frac{\alpha(LT)}{WSG^{\beta} \cdot CIRC^{\gamma}}\right]t}$	3.15 ± 0.96 (bottomlands) 3.10 ± 0.92 (hillsides) 3.97 ± 1.11 (hilltops)	1.82 ± 0.14	0.81 ± 0.06	-383.8	0.61 ± 0.03
5	$R_{(t,LT,DT)} = e^{-\left[\frac{\alpha(LT,DT)}{WSG^{\beta} \cdot CIRC^{\gamma}}\right]t}$	6.35 ± 2.14 (bottomlands, downed) 11.47 ± 4.75 (bottomlands, standing) 6.34 ± 2.03 (hillsides, downed) 9.42 ± 3.28 (hillsides, standing) 7.47 ± 2.26 (hilltops, downed) 16.07 ± 9.94 (hilltops, standing)	1.70 ± 0.16	0.97 ± 0.06	-401.7	0.63 ± 0.03

DIC Deviance Information Criterion, R remaining fraction of deadwood at time t , WSG species wood specific gravity, CIRC tree circumference at death time

very small values of the parameter standard deviations. Moreover, the high R^2 (always above 0.60) indicate that the five models fitted the data well. Wood density as well as tree circumference were both very important variables of the model, as shown respectively by the thin confidence intervals of beta and gamma. The comparison of the DIC indicated that the best model is model 3, i.e. the model that includes the mode of death only. The effect of logging (model 2) on alpha was clearly not significant with a DIC superior to the most parsimonious general model. The effect of local topography (model 4) also remains rather low, with a decrease of the 5 points of DIC compared to 23 points of decrease for the model 3. However, it should be noted that the gain of R^2 in model 3 remains marginal, i.e. of about 0.03 (see Figs. 1 and 2 for a graphical comparison of the predictions made by models 1 and 3), and that the general community model 1 already performed very well. With this model, light-wooded species such as *Cecropia obtusa* were predicted to completely disappear in less than 10 years for the biggest trees, whereas the largest trees of dense-wooded species such as *Bocoa prouacensis* had lost only half of their mass to decomposition after 25 years. The estimated times to lose 50% (from 0.6 to 14 years) and 90% (from 2.1 to 46.3 years) of initial biomass for each studied species, adjusted to a standardized circumference of 150 cm, are shown in Table 1. This standardized measure was chosen because large trees gather a disproportional part of the forest biomass (Rutishauser et al. 2010). Decay rates of large trees are thus of primary importance.

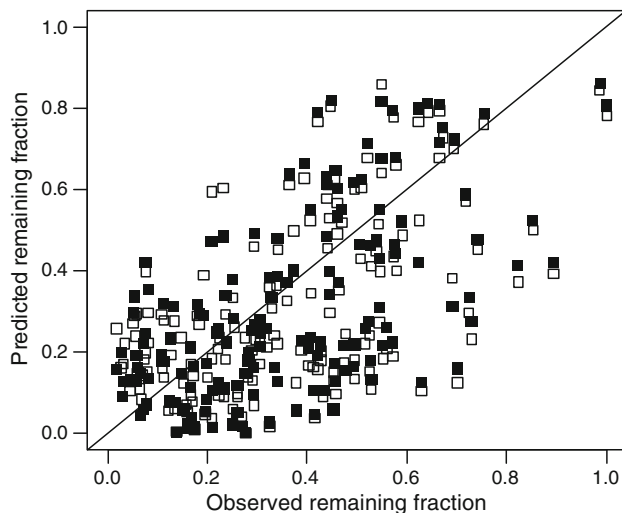


Fig. 1 Quality of the fit of the decay rate model of dead wood in a neotropical forest, predicted versus observed remaining fraction of dead wood for observed fraction superior to 0. Shown are the model predictions using the global model (*open squares* $R^2 = 0.60 \pm 0.03$), or the model predictions using the model parameterized using mode of death information (*black squares* the best model according to the DIC selection criterion, $R^2 = 0.63 \pm 0.03$)

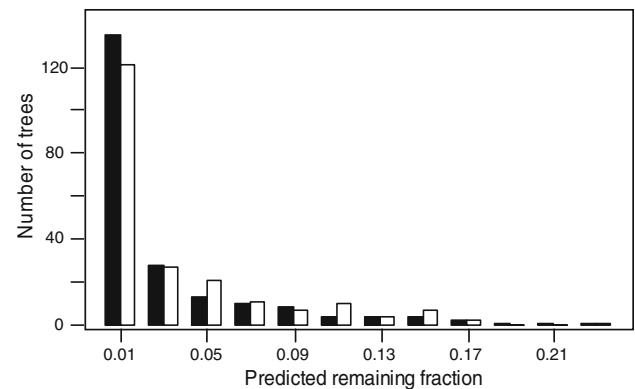


Fig. 2 Quality of the fit of the decay rate model of dead wood in a neotropical forest, predicted remaining fraction of dead wood for observed fraction equal to 0. The model predictions use the global model (*white*), or the model predictions use the model parameterized using mode of death information (*black* the best model according to the DIC selection criterion)

Discussion

The single-exponential model (Olson 1963) does not always adequately describe the dead wood decomposition process (Harmon et al. 2000) as some species decompose slowly during the first years because of high moisture content, high decay-resistant heartwood, or the time lag required for decomposers to become established (Harmon et al. 2000). However, our data did not suggest such a decomposition behavior, as we did not systematically under-predict the individuals having a large remaining fraction (see Fig. 1). Moreover, the residuals plotted against year since death did not indicate the need for including a lag phase in our model. Single-exponential models may also be problematic because a tree bole is composed of at least two wood types with different decomposition rates (i.e., sapwood and heartwood). This problem is often solved in single-species decay rate modeling by multi-exponential functions (Mackensen et al. 2003). However, when modeling multiple species, a model with more than one decay rate leads to highly instable k_1 and k_2 and strong difficulties in convergence given the numerous studied species (Zell et al. 2009). These problems were the main reason behind the use of a simple exponential decay model in the present study, which still resulted in 60% of explained variance. Nevertheless, there remains a significant proportion of unexplained residual variance, suggesting that factors we did not study also contribute to wood decomposition rates. For example, wood traits such as nitrogen, phosphorus, C:N ratio, and other chemical constituents, and climatic variables such as mean temperature or sum of precipitation per year (Zell et al. 2009), are all known to affect wood decomposition rates (Weedon et al. 2009). And we finally need to

acknowledge that termites exert strong effects on decomposition rates in these neotropical forests even if their effects are difficult to properly quantify as their distribution is highly localized in space (Torres and Gonzalez 2005).

Wood decomposition is a complex process consisting of several biological phenomena: respiration, biological transformation, fragmentation, leaching, and weathering (Mackensen et al. 2003). But the main biological mechanism explaining the loss of C from dead wood is respiration (Chambers et al. 2001). This explains why wood density and tree circumference explained so well the variability of decay rate constants. First, among species, wood density is highly correlated with wood moisture (Nogueira et al. 2008), which ultimately controls dead wood respiration rates (Weedon et al. 2009). This explains why low density woods show low respiration rates in dry environments, but when moistened by rainfall, respiration rates of low density woods rapidly increase (Chambers et al. 2001). Second, within species, our results are consistent with the fact that the decay rate of dead wood seldom shows a clear trend along a circumference gradient, a finding in contrast with other Amazonian studies (see ESM 3). The main reason behind this phenomenon is the ratio of surface:volume (S:V). Large trees have low S:V ratios leading to reduced access to decomposers and increasing barriers for gas and water exchange processes in proportion to volume of a bole (Zell et al. 2009). The S:V ratio is also consistent with a higher proportion of slow-decomposing heartwood being found in larger trees (Harmon et al. 1986). All in all, the extremely-wide variation in wood densities as well as in tree circumferences in our sampling explains why we found an extremely large range of decay rate constants compared to the other main study conducted in Amazonia (Chambers et al. 2000). This difference is mainly explained by the very high decay rate values obtained by low-density small-diameter trees such as the *Cecropia* (Fig. 3) that completely disappeared in less than 1 year in the field.

Neither selective logging nor local topography had an effect on wood decay rates (Table 2). Selective logging results in both a higher input of dead wood (Keller et al. 2004) and a greater canopy aperture due to logging gaps. An increasing input could be expected to favor multiplication of wood decomposers that, in turn, should increase the decay rates. On the other hand, a greater canopy aperture could be expected to increase the level of solar irradiation and to decrease the soil humidity that, in turn, should decrease the decay rates. Our results revealed neither effect, but we cannot rule out that both processes are active and counteract each other. Topographical levels had surprisingly no clear effect on the decay rates. This result was not really expected as moisture has been observed to have a profound nonlinear effect on decay rates (Yatskov et al. 2003). At low humidity levels, decay rates are

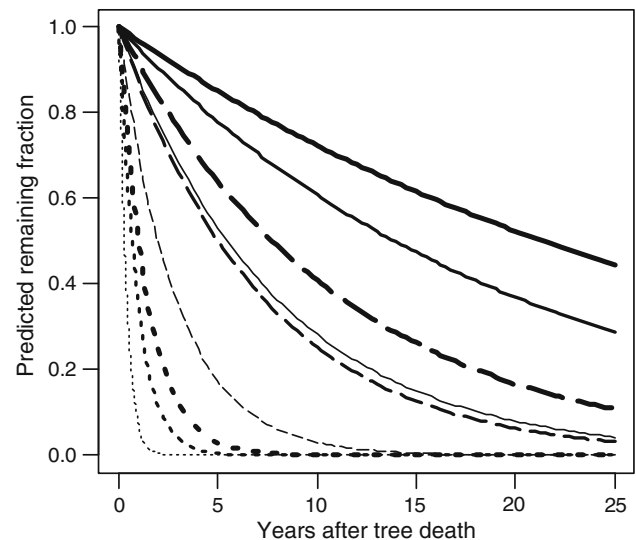


Fig. 3 Comparison of the decay rates for three contrasting species: *Cecropia obtusa* (dotted 0.23 g cm^{-3}), *Carapa procera* (dashed 0.71 g cm^{-3}), *Bocoa prouacensis* (plain 1.24 g cm^{-3}) at three circumference values (50 cm: thin curves; 150 cm: medium curves; 250 cm: bold curves) using the general decay model

expected to be low, whereas when moisture reaches the point of saturation (such as in bottomlands), most decomposers are unable to respire because of a lack in oxygen. In fact, there may be no decrease in decay rates at low soil moisture in tropical forests because the relative air humidity is always high (more than 80% in French Guiana). And the bottomland areas may not be flooded for long enough periods to reduce decomposer activities (Ferry et al. 2009).

The differences in decay rates between standing and downed trees observed in this study did not match with the hypothesis that standing tree decomposition is slower than that of downed trees because of insufficient moisture in snag wood tissues due to the absence of contact with soil (e.g., Yatskov et al. 2003). Again, this hypothesis is less true in tropical forests where the relative air humidity is always high, and it is likely that wood decay rates in tropical humid environments are higher in standing trees (Mackensen et al. 2003). Our results also suggest that death of tree while standing (and not falling by another tree, wind storm, etc.) affected mainly old trees for which decomposition was underway while the tree was still alive in the canopy. Such differential behavior between standing and felled dead trees could be tested in a larger dataset using a more flexible modeling of the overall decay process, assuming a time lag. In this way, the model would allow the start of the decay process before death time (Zell et al. 2009) for standing dead trees. Such a time-lag is clearly species-dependent (as some species always showed hollow boles and others never) and is probably linked to the

presence of particular secondary compounds toxic to microbiota and invertebrates. With the present dataset (comprising 26 species with very different biological properties), it was not possible to estimate a species-specific parameter without strong difficulties of convergence.

Conclusions

Decay rate constants of the 26 neotropical tree species investigated in this study were found to be significantly different among species. This indicates that the decay process for some species of the tropical forests can be as slow as in temperate ecosystems. The wide variation in decay rates was nevertheless well predicted by only two biological factors, i.e. tree circumference at death time and wood specific density, both factors having clear physiological interpretations. No strong effect of forest management (selective logging vs. unexploited), of mode of death (standing vs. downed) and of topographical levels (bottomlands vs. hillsides vs. hilltops) was found on wood decay rates. This suggests that the decay process in this neotropical forest was more driven by intrinsic biological factors than by extrinsic environmental variables. The decay rate model we report here, together with an estimation of the amount of deadwood in tropical forests, can thus be fruitfully used to estimate the release of carbon from dead wood to the atmosphere in a wide range of tropical forest situations.

Acknowledgments The project received financial support from the PO-FEDER program Guyafor. The authors gratefully acknowledge O. N'Gwete, R. Sante, F. Korysko and C. Nieder for their contribution in data collection. The authors thank the three anonymous reviewers for valuable comments.

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