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The trait contribution to wood decomposition rates of 15 Neotropical tree species

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Abstract. The decomposition of dead wood is a critical uncertainty in models of the global carbon cycle. Despite this, relatively few studies have focused on dead wood decomposition, with a strong bias to higher latitudes. Especially the effect of interspecific variation in species traits on differences in wood decomposition rates remains unknown. In order to fill these gaps, we applied a novel method to study long-term wood decomposition of 15 tree species in a Bolivian semi-evergreen tropical moist forest. We hypothesized that interspecific differences in species traits are important drivers of variation in wood decomposition rates. Wood decomposition rates (fractional mass loss) varied between 0.01 and 0.31 yr^{-1}. We measured 10 different chemical, anatomical, and morphological traits for all species. The species' average traits were useful predictors of wood decomposition rates, particularly the average diameter (dbh) of the tree species ($R^2 = 0.41$). Lignin concentration further increased the proportion of explained inter-specific variation in wood decomposition (both negative relations, cumulative $R^2 = 0.55$), although it did not significantly explain variation in wood decomposition rates if considered alone. When dbh values of the actual dead trees sampled for decomposition rate determination were used as a predictor variable, the final model (including dead tree dbh and lignin concentration) explained even more variation in wood decomposition rates ($R^2 = 0.71$), underlining the importance of dbh in wood decomposition. Other traits, including wood density, wood anatomical traits, macronutrient concentrations, and the amount of phenolic extractives could not significantly explain the variation in wood decomposition rates. The surprising results of this multi-species study, in which for the first time a large set of traits is explicitly linked to wood decomposition rates, merits further testing in other forest ecosystems.

Key words: *Bolivia; carbon cycling; traits; tropical forest; wood decomposition.*

Introduction

Understanding ecosystem processes that are involved in the global carbon cycle is essential for predicting vegetation responses and biosphere feedbacks to climate change (Cao and Woodward 1998, Chapin et al. 2008). Approximately 360 Pg (1 Pg = 10^{15} g) of carbon is fixed in plant biomass in forests (Dixon et al. 1994). Therefore, forests present a crucial component of the global carbon cycle (Bonan 2008). A significant fraction, up to 22%, of the forest carbon is found in dead wood (Delaney et al. 1998, Eaton and Lawrence 2006, Chao et al. 2009). During decomposition, the carbon fraction of dead wood is either redistributed in the ecosystem (e.g., streams, soil) or respired to the atmosphere as carbon dioxide as a consequence of microbial decomposition. The latter pathway can account for approximately 76% of carbon loss from decomposing tropical wood (Chambers et al. 2001). Decomposition of dead wood is, therefore, one of the driving processes in the global carbon cycle.

During the past decades, much research has been devoted to the decomposition of leaf litter (Aerts 1997, Cadisch and Giller 1997, Berg 2000, Parton et al. 2007), whereas the decomposition of wood has received far less attention. Moreover, there is a striking knowledge gap for wood decomposition rates and processes in tropical forests (Chambers et al. 2000, Chao et al. 2009, Weedon et al. 2009). This is surprising, as tropical forest vegetation contains more than 210 Pg C, i.e., almost 60% of the total carbon stored in total forest plant biomass (Dixon et al. 1994). Although there have been a

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substantial number of studies on in situ decomposition of wood particularly in temperate and boreal ecosystems (Harmon et al. 1986, Alban and Pastor 1993, Schowalter et al. 1998, Yatskov et al. 2003), the factors controlling wood decomposition rates, and their interactions, are still poorly understood (Cornwell et al. 2009). Consequently, wood decomposition is incorporated in global carbon models in highly generalized forms (Cramer et al. 2001, Cornwell et al. 2009), contributing to large variations in future climate predictions (IPCC 2007) and uncertainties in ecosystem responses to climate change (Cramer et al. 2001, IPCC 2007). Whether forests are a global source or sink for atmospheric carbon remains debated (Houghton 2003, 2005) and is obviously highly dependent on decomposition processes of dead wood (Houghton 2003, Chave et al. 2009). More empirical studies on the abiotic and biotic determinants of wood decomposition rates are needed to reduce uncertainties in global carbon cycling models. In this study we focus on biotic determinants of wood decomposition rates by studying the effects of interspecific variation in trait values on wood decomposition rates, which can be quantified most conveniently within sites with a common climate regime (Weedon et al. 2009).

Two recent studies (a review and meta-analysis) have indicated that species traits exert a strong control over wood decomposition rates (Cornwell et al. 2009, Weedon et al. 2009) in a way analogous to what has commonly been found for leaves (Cornelissen and Thompson 1997, Cornelissen et al. 1999, Santiago 2007, Cornwell et al. 2008). Cornwell et al. (2009) indicated that both chemical and anatomical wood traits are likely to be useful in predicting the decomposition rate of woody species. In addition, a preliminary global meta-analysis revealed that wood decomposition rates were related to several chemical wood traits such as N and P concentrations (Weedon et al. 2009), but this analysis was strongly limited by the very few species included in each of the individual study sites. Macronutrient concentrations, the concentration of secondary compounds, and wood anatomical traits that determine microbial accessibility such as vessel size and number, were identified as potentially important determinants of wood decomposition rates. However, further evidence is required from site-based multi-species field studies to single out the species trait contribution to wood decomposition more robustly. More specifically, insight in controls over decomposition rates from tropical regions, which were under-represented in the recent global meta-analysis (Weedon et al. 2009), is needed to expand the meta-analysis findings from northern temperate forests to the tropics.

Therefore, the aims of this study are (1) to compare decomposition rates of 15 different tropical tree species that have been decomposing under a common climatic regime, and (2) to link these decomposition rates to chemical, anatomical and morphological traits in order to determine which set of traits can be used as predictors of wood decomposition rates. To our knowledge, this will be the first study to link multi-species wood decomposition rates to species traits in an empirical and standardized way. We hypothesize that large interspecific differences in wood decomposition rates occur as a result of trait variation between species, and, more specifically, that low macronutrient (N, P) concentrations and high lignin concentrations will have a negative effect on wood decomposition rates (Scheffer and Cowling 1966, Cornwell et al. 2009, Weedon et al. 2009) whereas large and/or numerous vessels (i.e., large vessel cross-sectional area; Cornwell et al. 2009) and a small stem size (diameter; Harmon et al. 1986, Chambers et al. 2000) will positively affect wood decomposition rates. We test our hypotheses on 15 tree species representing contrasting functional groups in a Bolivian tropical moist forest.

Materials and Methods

Study site

Fieldwork was conducted in the 100 000-ha forestry concession of Agroindustria Forestal La Chonta, approximately 30 km east of Ascención de Guarayos, Bolivia (15°47′ S, 62°55′ W). This area is covered by semi-evergreen tropical forests, with an average annual rainfall of 1580 mm and a distinct dry period (monthly precipitation $<$ 100 mm) from May to September, and potential evapotranspiration exceeding average rainfall in July. The study area is a 200–300 year old secondary forest (based on the presence of anthropogenic black soils), it has an average canopy height of 27 m, tree basal area of 19.3 m^2/ha, tree density of 367 tress/ha, and species richness of 59 species/ha (all data for trees $>$10 cm diameter at breast height; Peña-Claros et al. 2008*a*). Commercial timber species are selectively logged, after which canopy gaps regenerate naturally. In this concession, Instituto Boliviano de Investigación Forestal (IBIF) maintains 12 experimental plots nested within three 27-ha blocks. Four different silvicultural treatments of varying intensity are applied to the plots in order to investigate the effect of the different silvicultural treatments on tree growth, vegetation structure and forest regeneration (Peña-Claros et al. 2008*a*). For this aim, all trees in the plots with a diameter at breast height (1.3 m, dbh) $>$ 10 cm have been tagged in 2000 or 2001. The trees are monitored every one to two years for their survival and growth. All data is gathered in a database (henceforth, IBIF database), which also includes information on logged and naturally fallen trees (species identification, date of logging/death, exact location of stems based on x,y coordinates).

Species selection

We determined wood decomposition rates of 15 tree species from 12 different families (for nomenclature, see Table 1) for which sufficient dead individuals were available in the research area. The species belonged to

TABLE 1. The 15 selected tree species, ordered by the functional group (FG) to which they belong (following Poorter et al. [2006]): ST, shade tolerant; PST, partly shade tolerant; LLP, long-lived pioneer; P, short-lived pioneer. The table reports the mode of death (MOD: L, logged; N, naturally fallen) of the trees that were sampled for decomposition rate determination, number of stems sampled (*n*) for decomposition rate determination, the time range (*t*; in years) these stems had been decomposing, and the species' average trait values and standard deviations (in parentheses).

Species	Family	FG	MOD	*n*	*t*	WD
Pseudolmedia laevis (Ruiz & Pavón) J. F. Macbr.	Moraceae	ST	L	10	8.75	0.61 (0.05)
Hura crepitans L.	Euphorbiaceae	PST	L	10	8.67–8.75	0.40 (0.06)
Ocotea sp.	Lauraceae	PST	N	9	1.83–6.42	0.46 (0.04)
Pourouma cecropiifolia C. Martius	Cecropiaceae	PST	N	8	1.83–3.83	0.33 (0.02)
Pouteria nemorosa Baehni	Sapotaceae	PST	L	8	8.25–8.75	0.61 (0.03)
Sapindus saponaria L.	Sapindaceae	PST	N	8	1.83–6.42	0.62 (0.03)
Terminalia oblonga (Ruiz & Pavón) Steudel	Combretaceae	PST	L	10	8.67–8.75	0.58 (0.03)
Acacia bonariensis Gillies ex. Hook. & Arn.	Mimosaceae	LLP	N	8	1.83–6.75	0.69 (0.03)
Cariniana estrellensis (Raddi) Kuntze	Lecythidaceae	LLP	L	9	8.25–8.75	0.63 (0.08)
Ficus boliviana C. C. Berg	Moraceae	LLP	L	10	8.67–8.75	0.37 (0.03)
Ocotea guianensis	Lauraceae	LLP	N	8	1.83–3.83	0.54 (0.02)
Schizolobium parahyba (Vell. Conc.) S. F. Blake	Caesalpinaceae	LLP	L	8	8.25–8.67	0.33 (0.07)
Cecropia concolor Willd.	Cecropiaceae	P	N	8	1.83–4.33	0.32 (0.05)
Heliocarpus americanus L.	Tiliaceae	P	N	8	1.00–4.33	0.22 (0.02)
Trema micrantha (L.) Blume	Ulmaceae	P	N	8	3.83–6.75	0.30 (0.04)

Notes: Key to abbreviations: WD, wood density (g/cm^3); dbh, diameter at breast height (cm); VA, vessel area (%); FA, fiber area (%); PA, parenchyma area (%); CN, C:N ratio; N, nitrogen concentration (mg N/g dry mass [DM]); P, phosphorus concentration (mg P/g DM); L, lignin concentration (mg lignin/g DM); PE, phenolic extractives concentration (mg phenolic extractives/g DM). Values of vessel area, fiber area, and parenchyma area are adapted from Poorter et al. (2010); no standard deviations are shown for these traits because they are based on only one measurement.

four different functional groups of trees (i.e., long- and short-lived pioneers and [partial] shade-tolerant species; Poorter et al. 2006, Peña-Claros et al. 2008*b*) that possess different wood characteristics (van Gelder et al. 2006, Poorter 2008, Poorter et al. 2010). For this study, we used the stem residuals of logged trees for seven tree species and naturally fallen trees for eight species.

Trait selection and measurement

A total of 10 traits (Table 1) were selected based on literature pointing to their likely influence on wood decomposition rates (Scheffer and Cowling 1966, Chave et al. 2009, Cornwell et al. 2009, Weedon et al. 2009). These traits were measured on living trees of the 15 studied species. Wood density and chemical traits were determined from 30 cm long increment cores (diameter 0.5 cm), containing both sapwood and heartwood, which were sampled from five living adult trees per species (two cores per individual tree to ensure enough and representative material for analysis). These living trees were selected based on the average diameter that adult individuals of a certain species reached (information from IBIF database). Cores were dried to constant mass at 70°C for export to the Netherlands. For wood density determination, one subset of the cores was rewetted in the Netherlands until their moisture content was above the fiber-saturation point, after which we determined the green volume using the water displacement method (Chave et al. 2006). After 96 hours at 40°C, the dry mass of these wood cores was recorded. Another subset was manually filed using a medium-coarse iron file prior to mechanical grinding using a MM200 ball mixer (Retsch, Haan, Germany). Total carbon and nitrogen of this ground wood were determined by dry combustion with a Flash EA1112 elemental analyzer (Thermo Scientific, Rodana, Italy). After digestion in a 1:4 mixture of 37% (by volume) HCl and 65% (by volume) HNO_3, phosphorus was measured colorimetrically (Murphy and Riley 1962). Lignin was determined following Poorter and Villar (1997): in short, after several extraction steps to ensure that only cellulose and lignin made up the composition of the residue of the sample, the C and N concentrations of this residue were used to calculate the lignin concentration, based upon the difference in carbon content between cellulose and lignin. Furthermore, after extraction in 50% MeOH, the amount of phenolic extractives was determined using the Folin Ciocalteu method, using tannic acid (Merck, Darmstadt, Germany) as a standard. The percentages of cross-sectional area occupied by vessels (henceforth vessel area), fibers (henceforth fiber area), and parenchyma (henceforth parenchyma area) have previously been determined on small sapwood samples (one replicate per species) that were collected in the La Chonta concession (Poorter et al. 2010). For more details on methods of vessel area, fiber area and parenchyma area measurements, see Poorter et al. (2010). Diameter at breast height (dbh) was measured on the trees from which the wood cores were taken.

Determination of decomposition rates and sampling method

In the field, we looked for 8–10 decomposing stems for each species (Table 1). We selected those dead trees that approached that species' average dbh as much as possible, so that the use of dbh as a predictor trait would be justified. Furthermore, we only selected those naturally fallen trees for which information in the IBIF

TABLE 1. Extended.

dbh	VA	FA	PA	CN	N	P	L	PE
47.6 (4.2)	18.89	29.73	51.02	182.9 (21.3)	2.45 (0.28)	0.93 (0.50)	213.8 (6.8)	15.81 (2.70)
99.0 (24.1)	4.91	65.55	24.86	238.7 (63.9)	2.06 (0.73)	0.14 (0.10)	197.3 (12.5)	8.92 (7.65)
39.6 (5.6)	17.69	53.56	28.75	137.5 (17.7)	3.37 (0.40)	0.18 (0.10)	194.0 (14.3)	18.52 (5.53)
35.0 (3.8)	13.79	32.31	53.64	308.4 (24.2)	1.52 (0.12)	0.09 (0.02)	209.6 (6.2)	2.63 (0.88)
60.8 (9.1)	13.75	31.36	53.85	336.1 (18.1)	1.33 (0.09)	1.31 (0.55)	152.1 (9.8)	20.91 (1.73)
29.4 (4.5)	5.95	41.06	52.40	156.7 (15.4)	2.80 (0.28)	0.54 (0.37)	161.6 (5.4)	5.28 (4.02)
42.6 (4.7)	9.47	38.07	51.54	191.5 (10.9)	2.31 (0.22)	0.23 (0.11)	200.9 (28.0)	34.09 (7.62)
42.6 (14.6)	11.80	42.08	46.12	222.3 (18.1)	2.03 (0.15)	0.68 (0.16)	192.9 (14.7)	14.26 (8.98)
55.2 (6.6)	7.31	48.90	43.78	258.1 (50.4)	1.80 (0.38)	0.58 (0.33)	203.2 (14.0)	21.84 (5.56)
146.0 (11.4)	5.37	53.65	40.98	236.1 (31.8)	1.91 (0.27)	0.63 (0.71)	210.3 (7.7)	9.07 (1.62)
25.2 (4.1)	15.83	61.26	22.90	205.9 (34.5)	2.35 (0.48)	0.13 (0.04)	204.5 (8.6)	13.74 (1.59)
45.8 (9.4)	6.18	67.82	25.99	274.5 (11.2)	1.66 (0.07)	0.18 (0.06)	199.9 (6.4)	5.54 (0.77)
31.6 (3.8)	6.22	61.13	31.95	333.0 (33.6)	1.36 (0.14)	0.18 (0.03)	178.2 (7.7)	4.18 (0.62)
33.6 (3.0)	11.04	40.42	47.68	237.9 (64.0)	1.94 (0.55)	0.89 (0.67)	132.2 (7.9)	6.12 (2.70)
38.2 (7.4)	11.05	66.04	22.40	339.9 (40.3)	1.35 (0.16)	0.14 (0.06)	203.3 (8.8)	16.75 (2.96)

database indicated that they were healthy, standing upright, had not been infested by fungi or attacked by insects prior to death, and had fallen immediately after death. Only the stems which were in immediate contact with the soil were selected and we assumed tentatively that they had been in soil contact throughout the decomposition period. For sample collection of the logged trees, we were restricted to the upper stem part that remained after logging (boles were extracted for timber production). However, for standardization, we were able to collect our samples below the first major branch. Considering height-related variation in wood properties within trees (Gartner 1995), and to allow for comparisons between logged and naturally fallen trees, we also sampled the naturally fallen trees within 1 m below the first major branch. Using a chainsaw, we cut an approximately 5 cm thick disk of the stem or stem residue of each dead tree within 1 m below the first major branch. With a machete, three approximately 5-cm^3 subsamples were extracted from different parts of each disks, encompassing (1) sapwood from the lower part of the disk which had been in direct contact with the soil (SSC), (2) sapwood from the upper part of the disk which had not been in contact with the soil (SNSC), and (3) heartwood near the center of the stem disk (HW), but avoiding the pith of the stems (see Plate 1).

We determined wood decomposition rates by applying the chronosequence method (Harmon et al. 1986), in which decomposition time is determined, and the change in wood density after this time period is examined. For this aim, wood density (g/cm^3) of each partly decomposed subsample was determined by measuring dry mass and fresh volume using the water-displacement method (Chave et al. 2006). Furthermore, because the initial wood density of the sampled stems was not available, species-specific average wood densities were calculated based on the wood density measurements on the cores from five living trees of each species (see *Trait selection and measurements*). The duration of decomposition differed per sampled tree and was obtained from the IBIF database. For logged trees, the exact felling date was available, whereas for naturally fallen trees, the date of the first monitoring census when the tree was found dead was used for determining decomposition time. Consequently, the time resolution for logged trees was one day, and for naturally fallen trees one or two years, i.e., the interval of two monitoring census occasions.

Decomposition rate constants (k values; fractional mass loss per year) were calculated for each subsample using a single exponential decay model (Olson 1963):

$$k = \frac{-\ln\left(\frac{X_t}{X_0}\right)}{t} \quad (1)$$

in which t represents the duration of decomposition, X_t is the wood density of the partly decomposed wood, and X_0 the initial wood density. We tried to test whether the decomposition process of the study species followed an exponential decrease in mass loss through time (as is required for the application of the decay model of Olson [1963]) by plotting mass loss of the sampled trees against decomposition time. However, due to small ranges in t (Table 1) and low sample sizes, we were only able to verify a decrease in mass loss through time, and had to assume that this decrease followed an exponential pattern, as was done in other wood decomposition studies (e.g., Chambers et al. 2000, Beets et al. 2009).

For each individual tree, we calculated k values for all three subsamples of the disk. We used these subsample k values to calculate a weighted average decomposition rate for the complete stem disk of each individual tree, representative for the decomposition rate of the whole stem. For this aim, we assumed a heartwood : sapwood ratio of 3:1, and 30% of the sapwood being in direct contact with the soil (K. G. van Geffen, *personal observations*; we tested whether possible artifacts in

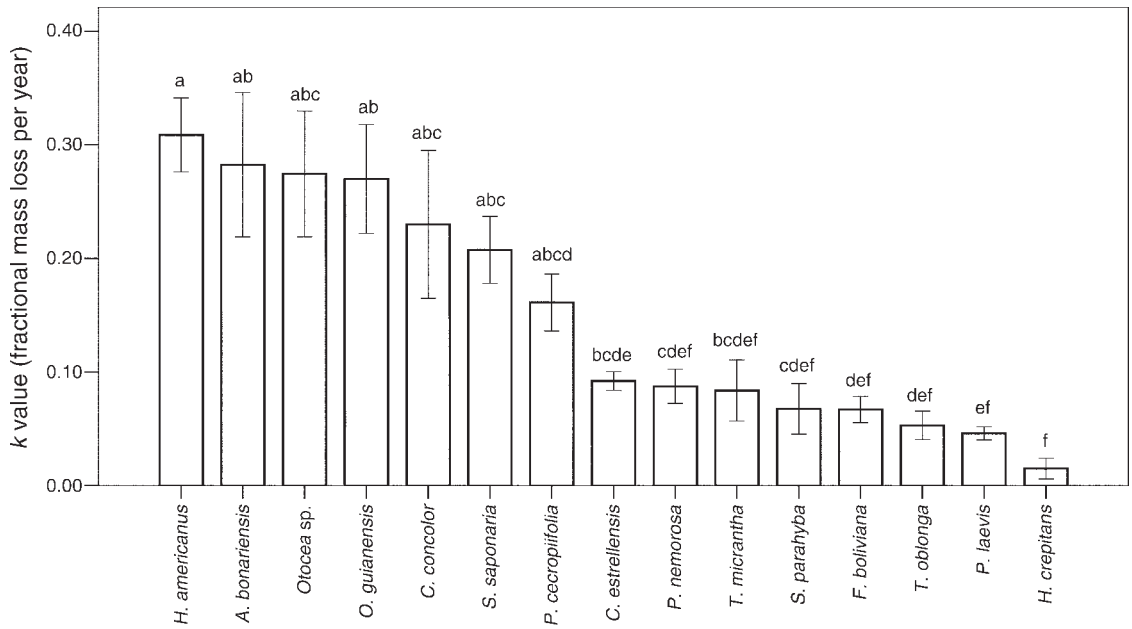

FIG. 1. Average exponential decomposition rates (k) for the 15 tree species. Bars indicate one standard error of the mean. Species that do not share any letters are significantly different at $P < 0.05$ (Tukey's hsd test). Species are listed in Table 1. The sample size varies from 8 to 10 (Table 1).

these assumptions had consequences for decomposition rates and the trait-contribution to wood decomposition, and concluded that our assumptions were robust [Appendix A]). We used k values from the individual stem disks to determine species average k values for all 15 tree species which were used for further statistical analyses.

Statistical analyses

All statistical analyses were performed in SPSS 15.0 (SPSS, Chicago, Illinois, USA). In order to meet the assumptions of normality and homogeneity of variances, k values, P concentration, N concentration, and phenolic extractives were ln-transformed; dbh was $\log_{10}$-transformed; and lignin concentration was power-transformed (x^2) prior to analyses.

One-way ANOVA and Tukey hsd post-hoc tests were applied to test for interspecific differences in decomposition rates. A principal component analysis (PCA) was used to visualize the wood economics spectrum (Chave et al. 2009) of the species incorporated in our study. We performed linear regression analyses with the first two PCA components as predictor variables and k as dependent variable to see whether the position of tree species within the wood economics spectrum reflects differences in wood decomposition rates. Furthermore, to assess the influence of different traits on wood decomposition rates, trait values of single trees were averaged into species-specific traits before performing linear regression analyses for each trait (predictor variables) separately. An additional linear regression analysis was performed using the dbh of the dead trees that we sampled for decomposition rate determination (henceforth dead tree dbh) as a predictor variable. Data on the dead tree dbh was obtained from the IBIF database and was $\log_{10}$-transformed prior to analysis. The dependent variables for the regression analyses were the species' average original (non-transformed) k values, since k values met assumptions for regression when averaged. Based on the linear regression analyses with single traits, we selected the traits with significant and nearly significant ($P < 0.1$) predictive power and used these in multiple regression analyses to test whether the combined predictive power of traits was higher than the single trait predictive power.

RESULTS

Wood decomposition rates

Species differ significantly in decomposition rates (one-way ANOVA, $F = 9.529$, df = 14, 108, $P < 0.001$). The decomposition rates varied 30-fold, with fractional mass losses ranging from 0.01 yr^{-1} for *Hura crepitans* to 0.31 yr^{-1} for *Heliocarpus americanus* (Fig. 1). Logged tree species had, on average, a four times lower decomposition rate than naturally fallen tree species (average k values 0.23 and 0.06 yr^{-1}, respectively; t test, $t = -5.445$, df = 13, $P < 0.001$). The decomposition time estimates for naturally fallen tree species are approximations, but given the large interspecific variation in decomposition rates, potential intraspecific deviations in decomposition rates due to uncertainties in decomposition time estimates would not disturb the overall pattern. We tested whether wood decomposition rates were related to regeneration light

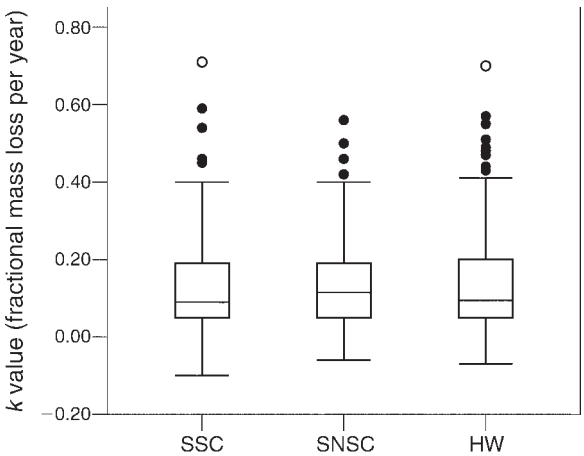

FIG. 2. Decomposition rates (k) of SSC (sapwood in direct soil contact), SNSC (sapwood without direct soil contact), and HW (heartwood) when all species are considered together. $N = 130$ stems sampled for all three wood types. Negative k values occur when the wood density of the sampled tree is higher than the species' average wood density (intraspecific variation in wood density), combined with a short decomposition period (i.e., a minor decrease in wood density due to decomposition). Boxes represent the inter-quartile range (IQR), of which the bottom and top represent the 25th and 75th percentile, respectively. The band in the IQR is the median. Lower ends of the bars represent minimum values; upper ends of the bars represent the maximum values that are not outliers. Filled dots are outliers (>1.5 IQR); open dots are extreme outliers (>3 IQR).

requirements (i.e., the inverse of shade tolerance) using a linear regression analysis with juvenile crown exposure (CE_{juv}, data from Poorter et al. 2006) as independent variables representative of regeneration light requirements. CE_{juv} appeared to be a poor predictor of wood decomposition rates ($R^2 = 0.018$, $P = 0.948$).

Surprisingly, no significant differences were detected between decomposition rates of HW, SSC, and SNSC; neither when all species were pooled (Fig. 2; t tests: SSC–SNSC $t = -0.632$, df = 237, $P = 0.528$; SSC–HW $t = -0.126$, df = 236, $P = 0.900$; SNSC–HW $t = -0.740$, df = 235, $P = 0.460$), nor when this was tested for each species separately. The only exception was *Pseudolmedia laevis*, for which a significant higher decomposition rate was found for SNSC compared to HW (Tukey's hsd, $P < 0.05$; Appendix B).

Traits as predictors of decomposition rates

All species-average trait values and associated standard deviations for the 15 species are presented in Table 1. Large interspecific variation in trait values were found for P concentration and phenolic extractives (14.5- and 13-fold, respectively), whereas interspecific variation in lignin concentration, N concentration and C:N ratio was low (1.6-, 2.5-, and 2.5-fold, respectively).

The correlations and trade-offs among wood traits, i.e., the wood economics spectrum (cf. Chave et al. 2009), of the tree species employed in our study is visualized in Fig. 3. There were significant (Pearson's) correlations between wood density and ln-transformed phenolic extractives ($r = 0.58$, $P < 0.01$), parenchyma area and fiber area ($r = -0.83$, $P < 0.01$), ln-transformed P concentration and parenchyma area ($r = 0.62$, $P < 0.05$), and ln-transformed N concentration and C:N ratio ($r = -0.99$, $P < 0.01$; Appendix C). The first axis of PCA graph (Fig. 3) shows a trade-off between storage (parenchyma, N, and P concentration) and safety (fibers, C:N ratio), similar to the findings of Poorter et al. (2010). However, this trade-off does not significantly explain variation in wood decomposition rates ($R^2 = 0.22$, $P = 0.082$). The second axis does not show clear distinguished strategies, and does not significantly explain decomposition rates either ($R^2 = 0.21$, $P = 0.088$).

The linear regression analyses indicate that dbh is the most important wood trait affecting wood decomposition rates, explaining 41% of the interspecific variation in wood decomposition rates ($P = 0.011$; Table 2, Fig. 4A) in a negative relationship ($\beta = -0.637$; see Table 2 for definition). The dbh also explains why, on average, logged tree species decomposed more slowly than naturally fallen tree species, with logged tree species having significantly larger average dbh than naturally fallen tree species (average dbh = 71.0 and 34.4 cm, respectively; t test, $t = 2.691$, df = 13, $P = 0.019$). For five out of 15 species, there were differences between average living tree dbh (measured on living trees from which we took our wood cores) and the average dbh of the dead trees that we sampled for decomposition rate determination (significant t test results for *Ficus boliviana* [$t = 2.773$, df = 13, $P = 0.016$], *Pouteria nemorosa* [$t = -2.903$, df = 11, $P = 0.014$], *Schyzolobium parahyba* [$t = -2.655$,

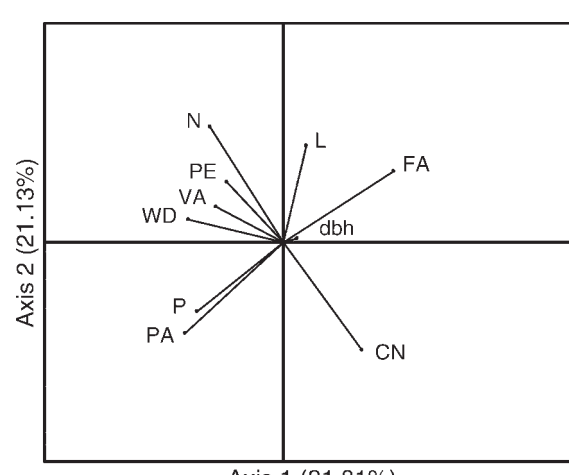

FIG. 3. PCA graph visualizing correlations among traits. Abbreviations are: WD, wood density; dbh, living tree diameter at breast height; VA, vessel area; FA, fiber area; PA, parenchyma area; CN, C:N ratio; N, N concentration; P, P concentration; L, lignin concentration; PE, concentration of phenolic extractives.

TABLE 2. Results of the single linear (SL) and multiple (M) regression analyses with species' traits as predictor variables for interspecific variation in wood decomposition rates.

Trait	β	R^2	P
Single linear			
WD	−0.050	0.00	0.861
VA	0.293	0.02	0.290
FA	−0.187	0.04	0.506
PA	−0.004	0.00	0.990
CN	−0.232	0.05	0.405
N‡	0.263	0.07	0.343
P‡	0.023	0.00	0.935
L§	−0.457	0.21	0.086
PE‡	−0.258	0.07	0.352
dbh†	−0.637	0.41	0.011
Dead dbh†	−0.789	0.62	<0.001
Multiple			
dbh†	−0.556	0.50	0.016
L§	−0.313		
Dead dbh†	−0.723	0.71	0.001
L§	−0.296		

Notes: "Dead dbh" is dead tree diameter at breast height; β values indicate the nature of relationship between trait and k values. Positive β values refer to a positive relationship, and vice versa. R^2 indicates the total variation in wood decomposition that is accounted for by each trait (SL) or combination of traits (M), and the P value shows the probability that the F values (not shown) are obtained by chance.

† Data $\log_{10}$-transformed prior to analysis.

‡ Data ln-transformed prior to analysis.

§ Data power-transformed (x^2) prior to analysis.

df = 11, $P = 0.022$], *Terminalia oblonga* [$t = -3.538$, df = 13, $P = 0.004$], and *Cariniana estrellensis* [$t = -4.458$, df = 12, $P = 0.001$]). As expected, in the additional regression analysis using dead tree dbh instead of living tree dbh, dead tree dbh explained more of the interspecific variation in k values (62%, $P < 0.001$) than living tree dbh (Table 2, Fig. 4A).

Surprisingly, wood decomposition rates were not significantly related to wood density (Fig. 4B), macronutrients, wood anatomical traits, lignin, and phenolic extractives (Table 2). However, the species average lignin concentrations ($R^2 = 0.21$, $P = 0.086$; Fig. 4C) might have been a significant predictor of interspecific variation in wood decomposition rates if more species would have been included in our study, including more low-lignin concentration species, which are poorly represented in this study (Fig. 4C).

The potential role of lignin is underlined by multiple regression analyses using dbh and power-transformed lignin as predictor variables. The combination of these two traits results in regression models that significantly explain 50% ($P = 0.016$; living tree dbh) and 71% ($P = 0.001$; dead tree dbh) of the interspecific variation in wood decomposition rates (Table 2).

DISCUSSION

Wood decomposition rates

Generally, decomposition rates in mesic tropical regions are higher than at higher latitudes (Swift et al. 1979). However, overlap in decomposition rates of dead plant material in tropical regions with those of higher latitude regions can occur (Aerts 1997). The decomposition rates we found are within the range reported in earlier studies on tropical wood decomposition rates (0.008–0.67 yr^{-1}; Harmon et al. 1995, Chambers et al. 2000, Eaton and Lawrence 2006). The lowest decomposition rates (i.e., 0.01 yr^{-1} for *H. crepitans*, 0.05 yr^{-1} for *P. laevis* and *T. oblonga*, and 0.07 yr^{-1} for *F. boliviana* and *S. parahyba*) are at the low end for wood decomposition in tropical regions. Here, indeed, we find an overlap in decomposition rate constants with wood in temperate and even boreal regions, where wood decomposition rates of these orders of magnitude are common (Harmon et al. 1986, Alban and Pastor 1993, Krankina and Harmon 1995, Schowalter et al. 1998, Yatskov et al. 2003). However, at the high end of the range, we might have underestimated decomposition rates of some logs that might have been reduced in volume owing to parts falling off or having been decomposed almost completely. Nevertheless, we believe that our data allows for ranking species according to their decomposition rates.

Soil contact usually improves the ability of fungal colonization due to a higher moisture content of the wood and increased accessibility, especially for fungal species that colonize by mycelial cords (Dix and Webster 1995). Consequently, significantly higher decomposition rates have been demonstrated for dead plant material in contact with soil compared to that not in soil contact (Alban and Pastor 1993, Henriksen and Breland 2002, Yatskov et al. 2003). Interestingly, we did not detect differences in decomposition rates of sapwood in direct soil contact (SSC) and sapwood non-soil contact (SNSC; Fig. 2). This could be a consequence of the generally favorable warm and moist climate conditions that may cause optimal wood-moisture conditions for decomposition which allows for rapid radial and tangential fungal dispersal through the stems (Dix and Webster 1995, Cornwell et al. 2009).

The trait contribution to wood decomposition

In this study, we determined wood decomposition rates of 15 tropical tree species within a relatively small area. By doing so, we were able to standardize the climatic regime for decomposition to a presumably acceptable degree, only allowing for inevitable variation in micro-climate and soil conditions, and to attribute variation in decomposition rates largely to variation in species traits (Weedon et al. 2009).

Traits that matter.—Tree dbh appeared to be the only significant predictor of wood decomposition rates. Living tree dbh alone explained 41% of the variation in wood decomposition rates between species, whereas the dbh of the dead trees that we used for decomposition rate determination explained 62% (Table 2, Fig. 4A). This size effect on wood decomposition (i.e., large-dbh trees decompose more slowly than small-dbh trees) has

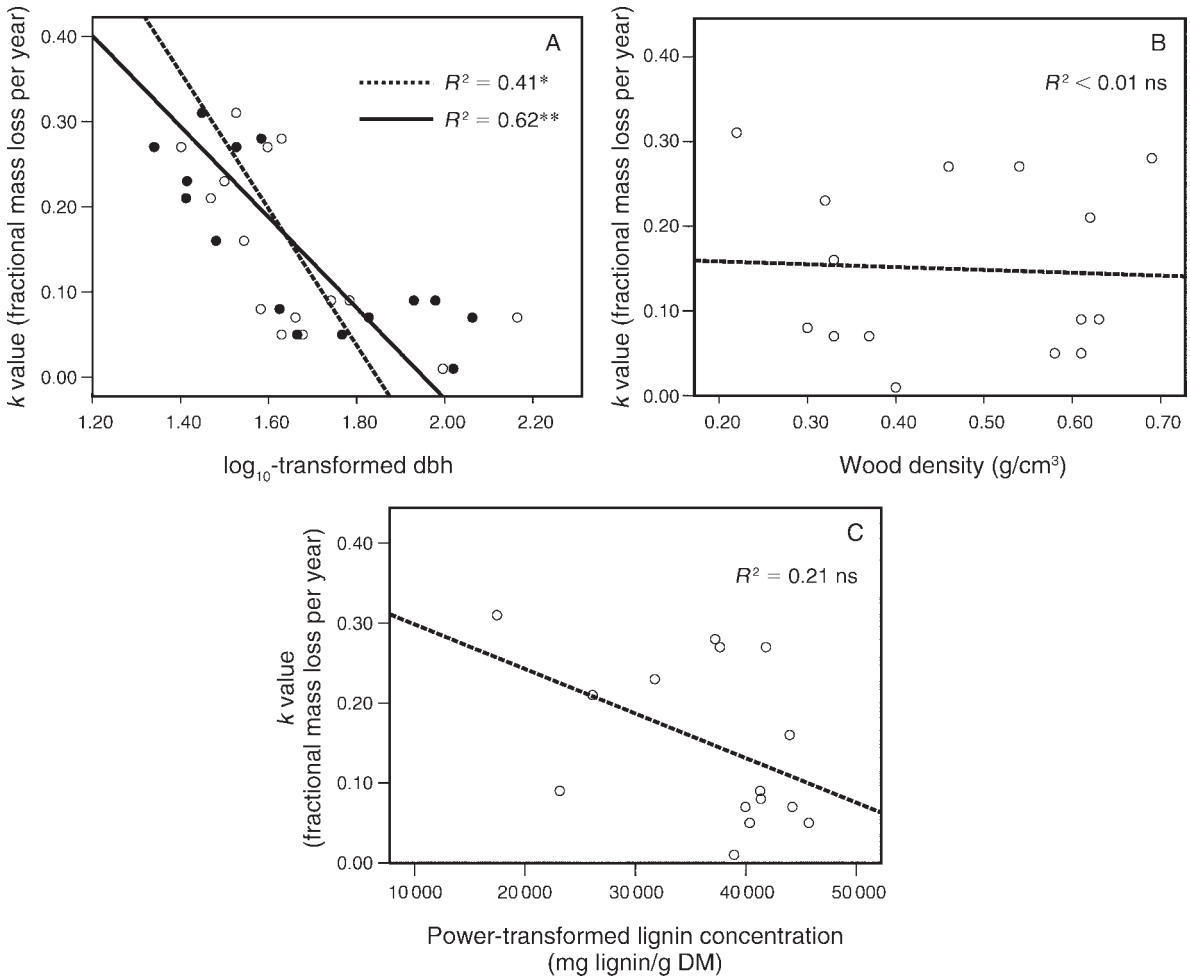

FIG. 4. Relationships between average wood decomposition rates and (A) average dbh of living trees (open circles, dashed line) and dead trees (filled circles, continuous line); (B) wood density; and (C) power (x^2)-transformed lignin concentration of 15 moist forest tree species. Regression lines and coefficients of determination are shown. DM stands for dry mass.
* $P < 0.05$; ** $P < 0$ .001; ns, nonsignificant.

been shown in many other studies on wood decomposition (Harmon et al. 1986, 1995, Chambers et al. 2000, Eaton and Lawrence 2006) and is a logical consequence of a decrease in surface area : volume ratio with an increase in diameter, which affects microbial and macrodecomposer accessibility to the substrate (Cornwell et al. 2009). The relative importance of dbh as compared to other traits has not been quantified before and it has not been shown previously how strongly this relationship is driven by consistent inter-specific variation among multiple tree species.

Most wood-degrading microorganisms are mainly decomposing cellulose. A high lignin content makes cellulose less accessible because lignified cell walls act as physical barriers to non-lignin degrading microbes (Scheffer and Cowling 1966). As a consequence of its recalcitrant nature, lignin has previously been shown to have a negative influence on decomposition of leaf litter (Aerts 1997, Cadisch and Giller 1997, Cusack et al. 2009) and wood (Scheffer and Cowling 1966, Cornwell et al. 2009). However, our results indicate that lignin alone does not significantly explain interspecific variation in wood decomposition rates. We believe that this is mainly the result of the small variation in lignin concentration (1.6-fold; Table 1) between species, and the negatively skewed distribution in lignin concentrations among tree species (Fig. 4C). The potential role of lignin is shown by the multiple regression analyses, in which the combined explanatory power of (both living and dead tree) dbh and lignin is 9% higher than when dbh alone is used (Table 2). Further studies, incorporating a wider and more representative range of wood lignin concentrations are obviously needed for stronger conclusions about the relative contribution of lignin in wood decomposition.

Traits that do not matter.—Wood density is a key wood trait, as it correlates to many crucial properties of stems such as mechanical support and water transport,

PLATE 1. (Top) A slice of a decaying log of *Sapindus saponaria* is cut for decomposition analysis. (Bottom) Don Wicho takes a wood core of *Hura crepitans*, the slowest decomposing species, for trait analysis. Photo credits: K. G. van Geffen.

both critical determinants of maximum height, as well as with vital rates such as growth and mortality (Chave et al. 2006, 2009, Swenson and Enquist 2007, Poorter et al. 2008). In addition, wood density is commonly believed to be (among) the primary control(s) over wood decomposition rates (Chao et al. 2009, Chave et al. 2009). This sounds intuitively appealing, and indeed, wood density was shown to exert the strongest control over decomposition of 155 boles in Manaus in the Brazilian Amazon (Chambers et al. 2000). The results of our study contradict this generally established idea; we found that wood density was an unimportant trait for predicting interspecific differences in wood decomposition (Table 2, Fig. 4B). This is, however, in line with the results of a global meta-analysis of 36 wood decomposition studies, which showed that wood density could not explain the difference in decomposition rates between gymnosperms (lower wood density, slower decomposition) and angiosperms (higher wood density, faster decomposition) decomposing in a common environment (Weedon et al. 2009). Our explanation for these results is that relative mass loss underlying k values is expressed per unit dry mass, not per unit of volume. So any lumen volume filled with air or water does not contribute directly to calculations of decomposition rates; dry mass amount per volume does not directly affect these calculations either. Any effect of wood density per se could be, for instance, through facilitation or inhibition of access by fungi or through effects on the wood moisture regime. Thus, the quantity of dry matter in a particular volume of wood should not exert a strong influence on wood decomposition rates.

Wood anatomical traits are of potential importance for wood decomposition (Chave et al. 2009), although direct evidence for this relationship is lacking (Cornwell et al. 2009). The size of conduits (mainly vessels in angiosperms) determines the permeability of the wood and influences access to wood for fungal hyphae. Therefore, a larger vessel cross-sectional area could, theoretically, increase decomposition rate. However, many vessels are plugged with tyloses and gum or resin-like substances, especially in the heartwood, which reduces the accessibility for microorganisms. For our 15 study species, vessel cross-sectional area was a poor predictor of variation in wood decomposition rates. Another wood anatomical trait that potentially affects wood decomposition is the parenchyma cross-sectional area (Cornwell et al. 2009). Parenchyma cells are living carbohydrate storage cells that are relatively rich in nitrogen compared to other wood cell types (Zabel and Morrell 1992, Dix and Webster 1995, Gartner 1995, Cornwell et al. 2009). High proportion of parenchyma cells attracts molds and insects that favor infection with wood-degrading fungi. However, a negative relation between mass loss of wood decomposed by two species of brown-rot fungi and the amount of axial parenchyma has previously been demonstrated, and was related to a high resistance of the cell-wall of parenchyma cells to degradation (Schwartze et al. 2003). Possibly as a consequence of this high decay resistance of parenchyma cell walls, we found no relation between the amount of parenchyma and decomposition (Table 2). A third wood anatomical trait that we included, fiber cross-sectional area, shows a strong trade-off with vessel and (mainly) parenchyma cross-sectional area (Fig. 3). It is considered important because fibers, as a tissue for mechanical strength, contain thick cell walls and comprise most of the decomposable material. But also this trait did not significantly explain variation in wood decomposition rates (Table 2). We do not have a clear explanation for this, but suspect that any underlying causal contribution to have been masked by the predominant effects of dbh and lignin, which showed very different interspecific rankings than that of fiber area (dbh showing a slight negative trend with fiber area).

We found no clear relationship between C:N ratio and wood decomposition (Table 2), which contrasts the broadly recognized conception that macronutrient content exerts an important stimulatory control over

decomposition (Swift et al. 1979, Aerts 1997, Cadisch and Giller 1997), including wood decomposition (Cornwell et al. 2009, Weedon et al. 2009). Indeed, the extremely high C:N ratios of wood (generally ranging between ~300 and 1000) result in constraints on the N availability to wood decaying fungi, which have C:N ratios of ~40–400 (Dix and Webster 1995). However, the C:N ratios of the trees in this study range between 137 and 340, and thus N availability may not have been an important constraining factor for fungal growth in dead wood of these trees. Further studies are needed to demonstrate whether this finding is a new rule or an exception, by incorporating tree species with higher C:N ratios.

There is large variation in the amount of secondary chemicals in wood, especially among angiosperms (Cornwell et al. 2009). The importance of phenolic extractives—non-structural secondary compounds—in decay resistance has been extensively reviewed (Scheffer and Cowling 1966) and earlier studies have also indicated their inhibiting effect on wood decomposition (Dix and Webster 1995, Cornwell et al. 2009). However, our results indicate that the inhibiting effect of phenolic extractives on wood decomposition rates of our 15 study species is absent; the amount of phenolic extractives cannot explain inter-specific variation in wood decomposition in our study (Table 2), possibly due to the detoxifying activities of enzymes (laccases, tyrosinases) that are known to be produced by some wood decomposing fungi (Lyr 1962).

Implications and applications

Climatic influences on decomposition in tropical regions are believed to be less extensive than in higher latitude regions, because of the generally favorable climate for microbial decay in the tropics (Coûteaux et al. 1995). In this respect, the trait contribution to wood decomposition should be especially important in tropical forests. Our results suggest that a large part (41%) of the variation in wood decomposition rates between species can be explained and predicted by one easily measurable trait: the species average dbh. That the relationship between species dbh and wood decomposition rate is directly causal, is indicated by the fact that the predictive power of dbh increases when it is directly measured on the actual dead stem used for decomposition rate determination, pushing the explanatory power of diameter up to 62%. Therefore, we conclude that traits, particularly tree dbh in this study, can be of significant importance in explaining variation in wood decomposition rates in certain tropical forests. Although the role of chemical and anatomical wood traits in predicting interspecific variation in decomposition rates was minor in our study, there was still a significant role for lignin in inhibiting wood decomposition, especially in combination with dbh. However, a recent large-scale study on leaf litter decomposition in the tropics indicated that the magnitude of the litter quality effect on decomposition varied between sites (Powers et al. 2009). Thus, it is likely that the trait contribution to wood decomposition also varies between different tropical forests.

The traits employed in our study left between 50% (living tree dbh) and 29% (dead tree dbh) of the interspecific variation in wood decomposition rates unexplained. This is likely to be the (combined) result of (1) differences between the average trait values that we used in the regression analysis (measured on living trees) and the actual trait values of the dead trees which we sampled for decomposition rate determination (as indicated by the difference in explained variation between living tree dbh and dead tree dbh), (2) variation in decomposer community, micro-climate and/or soil conditions (Toledo et al. 2009) between sites within the La Chonta concessions, or (3) interspecific variation in possible further relevant traits not covered in this study. Further site-specific studies linking species trait variation to tropical wood decomposition rate are obviously needed before more general conclusions are justified.

Conclusion

To our knowledge, this is the first empirical field-based, multi-species study to understand and quantify the wood decomposition–trait relationship using a large set of traits of potential importance. Our results contradict generally established ideas about the substrate quality influence on wood decomposition, with the possible exception of lignin (Chave et al. 2009, Cornwell et al. 2009, Weedon et al. 2009). However, the interspecific variation in mature stem diameter fulfils a key role in the trait–wood decomposition relationship. This indicates that, while trait–decomposition relationships are important both for leaf litter (Cornelissen and Thompson 1997, Santiago 2007, Cornwell et al. 2008), and for wood, the identity of the traits that matter differ between them. Trait–wood decomposition relationships, especially when tested further in other sites in the tropics and in other biomes, will allow for more precise incorporation of wood decomposition rates and accompanying carbon fluxes in carbon and vegetation modeling efforts, at the regional and eventually also at the global scale.

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APPENDIX A

Validating assumptions (*Ecological Archives* E091-259-A1).

APPENDIX B

Decomposition rates of different wood types (*Ecological Archives* E091-259-A2).

APPENDIX C

Correlations among traits (*Ecological Archives* E091-259-A3).