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Influence of soil, topography and substrates on differences in wood decomposition between one-hectare plots in lowland tropical moist forest in Central Amazonia

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Abstract: Understanding how wood decomposition varies spatially at the mesoscale (between 1-ha plots) may improve carbon flux estimates in Amazonian forests. An experiment was carried out to test the influence of soil, slope, above-ground tree live biomass (biomass), fine-litter mass and characteristics of neighbouring trees on the variation of wood decomposition between 1-ha plots in four species of tropical trees that vary in wood density (*Manilkara huberi* – 0.86 g cm^{-3}, *Couratari guianensis* – 0.54 g cm^{-3}, *Hura crepitans* – 0.32 g cm^{-3} and *Parkia pendula* – 0.29 g cm^{-3}). A wood sample from each species (30 × 5 × 2.5 cm) was placed in each of 71 plots within 64 km^2 of terra firme tropical moist forest in Reserva Florestal Adolpho Ducke. One year later, samples were collected and weighed. The effects of specificity of decomposers was measured by the association of decomposition with the wood density and with the taxonomic group of the nearest tree with dbh $\geq$30 cm. Wood decomposition was independent of soil (texture and nutrients), slope, biomass and fine-litter mass at the mesoscale, except for *C. guianensis*, which showed greater decomposition in locations with greater biomass. Decomposition was also independent of wood density and taxonomic group of nearby large trees. In general, none of the variables was useful as a predictor of wood decomposition at the scale larger than 1 ha. Thus, the use of models that include soil and topography to improve estimates of carbon flux are limited because wood decomposition does not follow similar mesoscale patterns to that of biomass and fine-litter decomposition. Also, the results indicate that wood decomposition is more likely to be associated with generalist decomposers than with specialists associated with neighbouring trees.

Key Words: Brazil, density, fertility, mesoscale, neighbouring tree, slope, spatial variation, specificity, terra firme, texture

INTRODUCTION

Estimates of carbon flux depend on determination of carbon released by decomposition as well as its absorption and stocks in biomass (Chambers *et al.* 2004, Fearnside 2000). Although wood material ($\geq$2.5 cm in diameter) may comprise 82% of the total litter stock (Nascimento & Laurance 2002) and may generate 22% of the annual carbon emissions from heterotrophic respiration (Chambers *et al.* 2000, 2001, 2004), most of the studies that estimated carbon flux in Amazonia have not considered the spatial variation in wood decomposition (Baker *et al.* 2004; Phillips *et al.* 1998, 2009).

Soil characteristics are associated with topography in Central Amazonia (Chauvel *et al.* 1987, Luizão *et al.* 2004). While soil maps are imprecise for Amazonia, topographic variables (altitude and slope), can be obtained from images of digital elevation models derived from SRTM radar (Shuttle radio topographic mission). Such images can reach a horizontal resolution of 0.8 ha (Rennó *et al.* 2008), which allows extrapolation of results from 1-ha plots to larger areas. If soil and topography were related to wood decomposition at 1-ha resolution, they could be included in models to predict carbon release from wood decomposition over large areas.

In Central Amazonia, characteristics of soil and topography influence the mesoscale spatial distribution of above-ground live biomass of trees (Castilho *et al.* 2006, Laurance *et al.* 1999) and lianas (Nogueira 2006),

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as well as species composition of understorey plants, palms and fungi (Braga-Neto *et al.* 2008, Costa *et al.* 2005, 2009; Kinupp & Magnusson 2005). Fine-litter production (leaves, fruits and wood material ≤2.5 cm in diameter) is greatest in forests with clayey soils (Luizão 1989) and its decomposition as well as nutrient cycling are faster on clay than sandy soils (Luizão *et al.* 2004, 2007). However, the mesoscale spatial variation in wood decomposition is not well understood, and only density, moisture and trunk dimensions have been related to wood-decay rates in tropical forests (Chambers *et al.* 2000, 2001; Harmon *et al.* 1995, Martius 1997); few studies analysed the effects of topography and microclimatic variation on this process (Beard *et al.* 2005, Genet *et al.* 2001).

Fungal specificity for fine litter of particular tree species influences decomposition (Lodge 1997, Santana *et al.* 2005). Fungi involved in wood decomposition are usually generalists (Gilbert *et al.* 2002, Lindblad 2000, Lodge 1997), but there is evidence that some may be quite species-specific in tropical forests (Ferrer & Gilbert 2003, Gilbert & Sousa 2002, Lodge & Laessøe 1995). Such specificity may be due to physical and chemical characteristics of the wood, such as shape and size, xylem architecture, density, moisture, contents of carbon, nutrients, cellulose, hemicellulose, lignin and the presence of polyphenolics (Chambers *et al.* 2000, 2001; Weedon *et al.* 2009). Thus, it is possible that the species of tree near to where decomposition occurs may influence fungus species composition because its fallen branches may determine the quality of the wood litter (Ferrer & Gilbert 2003).

We carried out an experiment to evaluate the influence of soil, topography (slope), above-ground tree live biomass and fine-litter mass on the variation of wood decomposition between 1-ha plots in a terra firme forest in Central Amazonia. We hypothesized that wood decomposition may be faster on clayey soils and places with greater biomass due to the maintenance of suitable conditions for decomposers (Martius *et al.* 2004, Sariyildiz 2008, Weedon *et al.* 2009, Zhang & Zak 1995). Wood decomposition may also be faster on fertile soils because a large proportion of nutrients is available for decomposers (Crews *et al.* 1995, Takyu *et al.* 2003, Wang *et al.* 2008). However, we expected wood-decay rates to be inversely related to slope and fine-litter mass due to low soil moisture and fertility on slopes (Luizão *et al.* 2004, Takyu *et al.* 2003) and due to slow activity of decomposers expected for places with large quantities of litter (Olson 1963).

We also investigated the effects of specificity of decomposers by associating wood density and taxonomic group of the nearest large trees with wood decomposition. Since the characteristics of the litter-producing trees probably shape the species composition of fungi, we hypothesized that wood decomposition may be faster when the nearest tree has similar characteristics to the wood in decomposition.

METHODS

Study area

The experiment was carried out in Reserva Florestal Adolpho Ducke, which is managed by the Instituto Nacional de Pesquisas da Amazônia (INPA). The reserve (10 000 ha) is covered by humid tropical forest and it is located at the periphery of the city of Manaus, in the state of Amazonas, Brazil (2°55′S, 59°59′W). The forest has a closed canopy of 30–37 m, with occasional emergent trees reaching 45 m (Ribeiro *et al.* 1999). Annual average temperature is 26 °C (Ribeiro & Villa-Nova 1979) and the average annual rainfall from 1979 to 2008 was 2524 mm, with a dry season from July to September during which monthly rainfall is often around 100 mm (Coordenação de Pesquisas em Clima e Recursos Hídricos – INPA, unpubl. data). Topography is hilly with elevation varying from 40–140 m (Ribeiro *et al.* 1999). Soil type depends on topography, especially with respect to clay which is greatest in the higher parts of the relief (Castilho *et al.* 2006, Chauvel *et al.* 1987). Oxisols (allic yellow latosols in the Brazilian classification system) predominate in the plateaux, ultisols (yellowish red podzols) are more common on the slopes, and spodosols (sandy podzols) predominate in the valleys, usually near water (Chauvel *et al.* 1987). These soils are acidic and poor in phosphorus, calcium, sodium and potassium, while often high in aluminium (Chauvel *et al.* 1987, Fearnside & Leal-Filho 2001).

A grid of 9 × 9 trails, each separated by 1 km and 8 km in length, covers the reserve, encompassing 64 km^2. Plots ($n = 72$) were established along the east–west trails at least 1 km from one another. These plots are narrow and long (40 × 250 m) and follow the contours of the land, thereby maintaining a constant elevation, minimizing variation in soil type and depth to the water table along the plot (Magnusson *et al.* 2005).

Data collection and analysis

Four species of commercially available wood were used: *Manilkara huberi* (Ducke) Standl., *Couratari guianensis* Aubl., *Hura crepitans* L. and *Parkia pendula* Bth. ex Walp. Species identification was based on comparisons with wood samples in the Wood Anatomy Laboratory at INPA. Pieces of wood, approximately 5 × 3 × 2.5 cm, were used to determine specific gravity (density). Since wood was originally somewhat dry, we allowed the pieces to reabsorb water for 2 wk (Nogueira *et al.* 2005). The volume of each sample was determined based on the Archimedes principle by displacement of water. Each sample was immersed in water in a container resting on a digital balance. The dry weight was determined in an oven at 105 °C. Final wood densities were estimated to be 0.86 ± 0.01 g cm^{-3} (mean ± SD, $n = 4$) for *M. huberi*, 0.54 ± 0.02 g cm^{-3} (4) for *C. guianensis*, 0.32 ± 0.09 g cm^{-3} (12) for *H. crepitans* and 0.29 ± 0.09 g cm^{-3} (4) for *P. pendula*. We could not confirm whether the samples were only from heartwood or sapwood, but a comparison of our estimates of wood density with the averages calculated from Chave *et al.* (2006) indicates that the wood of *M. huberi*, *C. guianensis* and *P. pendula* was mostly from heartwood as the averages (0.93 g cm^{-3}, 0.51 g cm^{-3} and 0.37 g cm^{-3}, respectively) from Chave *et al.* (2006) were similar to our estimates. However, for *P. pendula*, most of the wood was possibly from sapwood as the average (0.53 g cm^{-3}) from Chave *et al.* (2006) was almost twice denser than our estimate. For each species, 72 samples (30 × 5 × 2.5 cm) were dried at 105 °C until weight was constant. A sample from each species was placed 10 m from the beginning of each of the 72 plots in March and April 2007. After 1 y (360–370 d) wood samples were collected, dried, and the percentage of the original dry weight lost to decomposition was calculated. Samples in one plot were not found. To test the overall importance of the environmental variables, we used a mean of wood decomposition of all species weighted by the wood density of each species.

Along the centre of each plot, six superficial soil subsamples (0–5 cm deep) were collected at 50-m intervals, and these were mixed to form a composite sample per plot. Soil samples were dried at 105 °C, then sieved (2 mm mesh size). A total of 23 soil parameters were estimated (Castilho *et al.* 2006, Mertens 2004). Soil texture and pH were measured at the Soil Laboratory of the INPA Agronomy Department and soil chemical measurements were carried out at the EMBRAPA (Brazilian Agriculture Research Company) soil chemistry laboratory in Manaus. We used 14 soil variables: clay and silt (particles < 0.002 and 0.002–0.05 mm, respectively), pH, available phosphorus (P), K^+, Ca^{2+}, Mg^{2+}, Na^+, Cu^+, Fe^{2+}, Mn^{2+}, Zn^{2+}, exchangeable aluminium (Al^{3+}) and potential acidity ($Al^{3+} + H^+$). More detailed description of these variables is given in Castilho *et al.* (2006).

Slope was estimated with a clinometer at five points along the plot and the average slope was used for each plot (Castilho *et al.* 2006). Altitude (height above sea level), another topographical variable measured, was not included in the analyses because of its strong correlation with clay content of the soil. Above-ground live biomass of trees and palms was taken from Castilho *et al.* (2006) as estimated in 2001 and 2002 following the protocol described in Magnusson *et al.* (2005). The data described here are available online through the Biodiversity Research Program (*Programa de Pesquisa em Biodiversidade* – PPBio) at http://ppbio.inpa.gov.br/Eng/inventarios/ducke/pterrestre. Fine-litter mass samples of 0.25 m^2 were collected every 50 m along the centre of each plot ($n = 5$) by Aguiar *et al.* (2006). The samples were dried at 45 °C until constant weight. Average dry weight was used to characterize each plot. Two plots were sampled during the dry season (September 2001) and the remainder during the rainy season (December 2001–May 2002).

The tree or palm with diameter at breast height ≥ 30 cm that was nearest to the wood sample was identified and the distance to the sample was estimated. The mapping of the trees and palms was done by C.V. Castilho (unpubl. data). Wood density of the nearest tree neighbours was taken from Chave *et al.* (2006). When information at species level was unavailable, we estimated average wood density for the genus or family.

We reduced the number of soil variables using Principal Components Analysis (PCA). The resultant components were used in subsequent analysis to test for their importance in decomposition. Multiple regression analysis was used to test for the combined effects of the first two components (PCA1 and PCA2), slope, fine-litter mass and biomass on decomposition. We tested the relationship between wood density of the nearest tree and decomposition with simple linear regression analysis. Also, the local influence of nearby trees (family) on decomposition was tested by analysis of variance (ANOVA). In this analysis, we used only those tree families that occurred in at least three plots. A sample from *M. huberi* which was an outlier was not included in the analysis. All analyses were performed in the R 2.6.1 statistical program (Crawley 2007).

RESULTS

The densest species, *M. huberi*, had the lowest per cent decomposition (mean ± SD, range, 5.6% ± 1.0%, 3.5%–8.2%). The decomposition of the medium- to low-density species *C. guianensis* was 24.7% ± 11.9% (5.6%–64.1%), and the two low-density species, *H. crepitans* and *P. pendula* had the highest decomposition (28.3% ± 20.7% (6.6%–87.9%) and 39.5% ± 23.7% (9.3%–100%), respectively). The weighted mean decomposition was 19.2% ± 6.6% (8.6%–37.3%).

The exclusion of one plot from the ordination did not generate different loadings from those presented in Castilho *et al.* (2006), who analysed soil results from all plots. Two principal components were generated. The first axis (PCA1) explained 34% of the variation of the original variables and described a textural gradient

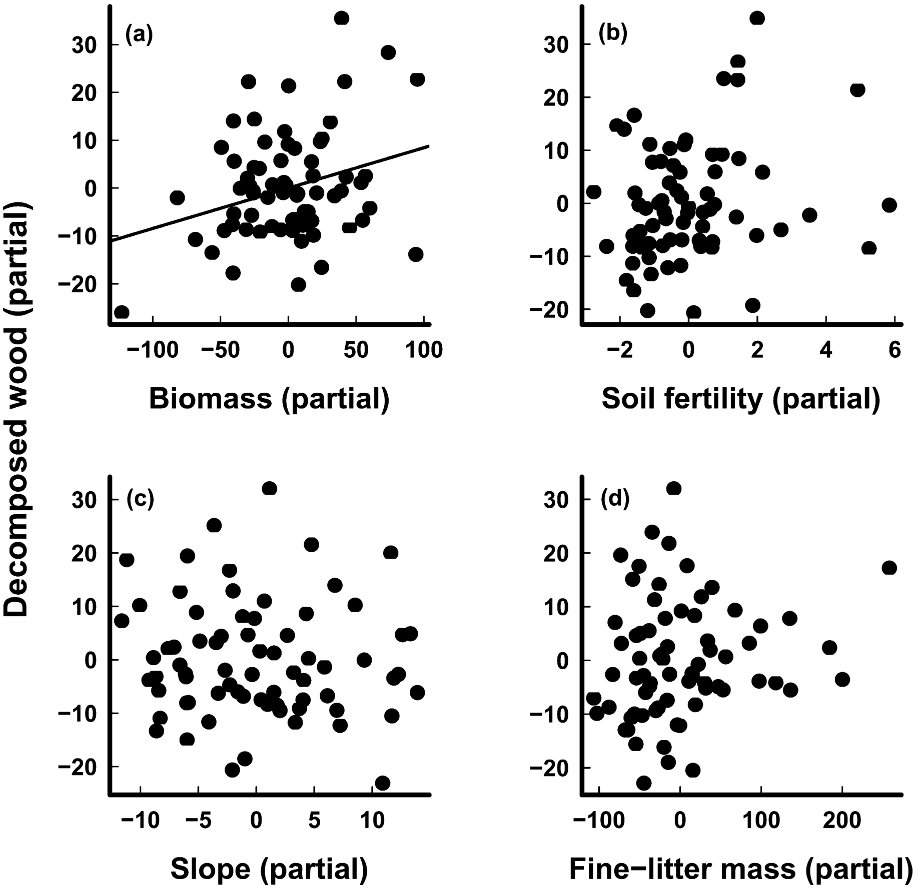

Figure 1. Partial regressions testing the effect of above-ground tree live biomass (a), soil fertility gradient (PCA2) (b), slope (c) and fine-litter mass (d) on the percentage of mass loss (decomposed wood) of wood blocks of *Couratari guianensis* after 1 y in 71 plots in a lowland tropical moist forest in Central Amazonia. The line in (a) denotes a significant partial regression.

between plots with greater clay content (and also high K^+, Na^+, Mg^{2+}, Al^{3+}, $Al^{3+} + H^+$, Fe^{2+} and $Mn^{2+}$and low pH) and those with greater sand content. The second axis (PCA2), which explained 23% of the variation, was positively associated with P, K^+, Ca^{2+}, Mg^{2+}, Zn^{2+}, Mn^{2+} and pH, and negatively with Fe^{2+} concentration. Above-ground tree live biomass and soil texture (PCA1) were not independent ($r = 0.43$, $P < 0.001$) and so these variables were not included in the same analysis.

Decomposition of *M. huberi* ($F_{4,65} = 0.97$, $P = 0.43$), *C. guianensis* ($F_{4,66} = 1.98$, $P = 0.11$), *H. crepitans* ($F_{4,66} = 0.39$, $P = 0.81$), *P. pendula* ($F_{4,66} = 0.08$, $P = 0.99$) and the weighted mean ($F_{4,65} = 0.19$, $P = 0.94$) were independent of the soil gradients of texture and fertility (as measured by PCA1 and PCA2), slope and fine-litter mass. Substituting PCA1 for above-ground tree live biomass resulted in a significant regression model ($F_{4,66} = 3.63$, $P = 0.01$) that explained 18% of the variance in decomposition for *C. guianensis*. Decomposition increased in *C. guianensis* ($t = 2.44$, $P = 0.02$) with increasing above-ground tree live biomass (Figure1a). Alone, above-ground tree live biomass explained 11% of the variance in *C. guianensis* decomposition (decomposed wood $= -6.88 + 0.097 \times$ above-ground tree live biomass, $F_{1,69} = 8.39$, $P = 0.005$). Decomposition was independent of PCA2, slope and fine-litter mass for *C. guianensis* (Figure 1b–d). The model, with above-ground tree live biomass replacing PCA1, was not significant for *M. huberi* ($F_{4,65} = 0.76$, $P = 0.56$), *H. crepitans* ($F_{4,66} = 0.25$, $P = 0.91$), *P. pendula* ($F_{4,66} = 0.14$, $P = 0.97$) or the weighted mean ($F_{4,65} = 0.62$, $P = 0.65$).

The average distance from a sample to the nearest tree or palm was 6.2 ± 5.4 m (1.2–37.5 m) and mean diameter at breast height was 42.2 ± 11.9 cm (30.0–87.6 cm). These neighbours comprised 24 families, in which 61 were identified to species, six to genus and four to family. Wood density was estimated for 41 individual plants that were identified to species, 25 plants identified to genus, and five individuals identified to family. Mean nearest-neighbour tree wood density was 0.71 ± 0.14 g cm^{-3} (0.33–0.96 g cm^{-3}). Families found in three or more plots were Chrysobalanaceae ($n = 4$), Fabaceae (10), Goupiaceae (3), Lauraceae (3), Lecythidaceae (11), Malvaceae (4), Myristicaceae (3) and Sapotaceae (14).

Wood decomposition was independent of wood density of the nearest tree neighbour for all species: *M. huberi* ($F_{1,68} = 0.29$, $P = 0.59$), *C. guianensis* ($F_{1,69} = 0.11$, $P = 0.74$), *H. crepitans* ($F_{1,69} = 0.02$, $P = 0.9$) and *P. pendula* ($F_{1,69} = 0.004$, $P = 0.95$). However, decomposition was associated with the taxonomic group of the nearest neighbour for *M. huberi* ($F_{7,43} = 2.25$, $P = 0.05$). The smallest (4.2%) and largest (6.7%) average decomposition were near trees of the families Goupiaceae and Malvaceae, respectively. However, the sample size for these families was low (Goupiaceae = 3, Malvaceae = 4) in comparison with the family of *M. huberi*, Sapotaceae (n = 14). Mean per cent decomposition under Sapotaceae (5.5%) was the same as that for all families (5.6%) and, excluding Malvaceae and Goupiaceae, the mean under all the other families were similar (ANOVA, $F_{5,38} = 1.05$, $P = 0.4$). Decomposition of *C. guianensis* ($F_{7,44} = 1.07$, $P = 0.4$), *H. crepitans* ($F_{7,44} = 0.73$, $P = 0.65$) and *P. pendula* ($F_{7,44} = 0.49$, $P = 0.84$) was independent of the taxonomic group of the nearest tree neighbour.

DISCUSSION

The instability of humidity probably contributed to the lack of a soil-texture influence on decomposition at the scale larger than 1 ha. As water-content influences wood decomposition (Chambers *et al.* 2001, Martius 1997, Weedon *et al.* 2009), this process may vary greatly through time in locations with large variation in humidity. In Reserva Ducke, the clayey soils on plateaux may suffer water deficits during the dry season and this possibly results in decreasing decomposer activity; fewer fungi species reproduce in clayey soils under little rainfall (Braga-Neto *et al.* 2008). Forests in valleys show higher tree mortality than on plateaux (J. J. Toledo, unpubl. data); hence valleys probably have more gaps, which can generate diverse microclimatic conditions regardless of the humidity provided by creeks and streams. Thus, decomposition possibly is limited by dry intervals on the plateaux and by canopy openness in the valleys. Beard *et al.* (2005) obtained slower wood-decay rates in streams than terrestrial areas, but the causes of such difference were not investigated.

Litter decomposition is usually more rapid on more fertile soils (Crews *et al.* 1995, Takyu *et al.* 2003, Wang *et al.* 2008). The lack of relationship between the nutrient gradient and wood decomposition may have been due to the small variation in soil fertility as well as temporal variability in nutrients in tropical soils (Sollins 1998). Another factor that might weaken this relationship is the activity of cord- or rhizomorph-forming fungi (Boddy *et al.* 2009). Such fungi can form extensive hyphal systems capable of interconnecting resources (wood or fine litter) on the forest floor and translocate nutrients from soil to wood and between wood resources (Boddy *et al.* 2009, Wells & Boddy 1990, Wells *et al.* 1999). Nutrients stored in earlier colonized wood may supply the mycelial growth and metabolic processes for decomposition of the recently attacked woods. As these fungi are not dependent on soil nutrient pools to grow and start decomposition, this process may be constant across the gradient of soil fertility.

The absence of a mesoscale relationship between wood decomposition and slope is possibly due to the low microclimatic variation through the slope gradient driven by low differences of soil (Luizão *et al.* 2004) and canopy openness regardless of the high gap frequency on slopes (Gale 2000, Poorter *et al.* 1994).

The litter mass is regulated by litter productivity and decomposition (Olson 1963). As accumulation of litter may be a result of slow initial rates of decomposition, we expected an inverse relationship between wood decomposition and fine-litter mass. The lack of such a relationship suggests that fine-litter decomposition and characteristics of soil and topography are weakly associated. The studies that attempted to relate fine-litter decomposition or productivity with soil and topography used few plots, which may restrict their conclusions (Luizão 1989, Luizão *et al.* 2004, 2007). Another limitation is related to changes in the spatial distribution of the litter over time since fine-litter data used in this study were collected a few years earlier.

The positive mesoscale relationship between aboveground tree live biomass and decomposition rate for *C. guianensis* wood may be due to a favourable microclimate created for decomposers in forest patches with higher biomass. Such patches usually have a closed canopy that limits the penetration of solar radiation and could maintain high humidity and constant temperature in the litter layer (Martius *et al.* 2004, Sariyildiz 2008, Weedon *et al.* 2009, Zhang & Zak 1995). Nonetheless, there was only a weak relationship between biomass and wood decomposition for one tree species, which is not sufficient to predict general patterns of decomposition.

Decomposition was independent of both wood density and taxonomic group of the nearest tree neighbour. Fungi that are involved in wood decomposition possibly are influenced by more than one species of neighbouring tree. Also, fungi that decompose wood are usually generalists (Gilbert *et al.* 2002, Lindblad 2000, Lodge 1997), which could make decomposition independent of the species of fungus. Other experiments with wood of the same species as the tree neighbour may help to determine whether substrate specificity influences wood decomposition in tropical forests.

The wood decomposition in *H. crepitans* and *P. pendula* was very variable, perhaps due to heterogeneity in the wood blocks that could have been partly heartwood and partly sapwood. However, the relationships between wood decomposition and the predictive variables were similar for all the species. Another source of variation in wood decomposition may be the fine-scale variation of the predictor variables. Soil texture and fertility may vary as a consequence of invertebrate activity, such as nest-building by termites which agglomerates organic matter and nutrients. Tree mortality also results in microclimatic variability through changes in canopy openness (light), humidity, temperature, soil pH and microbial activity (Martius *et al.* 2004, Sariyildiz 2008, Zhang & Zak 1995). Such micro-environmental variation can occur within a scale smaller than 1 ha; hence the effects of this variation cannot be tested on wood decomposition using our data and, even if it occurs, information on these processes will not allow extrapolation of results from 1-ha plots.

Soil and topography explain nearly one third of the variation in above-ground tree live biomass in Central Amazonia (Castilho *et al.* 2006, Laurance *et al.* 1999). As soil and topography are closely related (Chauvel *et al.* 1987, Luizão *et al.* 2004), topography alone may be used to predict spatial distribution of biomass over large areas using images from SRTM radar. However, the factors that affect wood decomposition appear to be more complex than we expected, and our results indicate that information on soils and topography at the scale of 1 ha will add little to models of wood decomposition in sites similar to those in Reserva Ducke. The lack of a mesoscale relationship between wood decomposition and the variables that influence above-ground tree live biomass and fine-litter decomposition indicates an asymmetry between productivity and decomposition. If wood-litter production follows a similar pattern to that of fine-litter, then places with similar soils, topography and biomass should accumulate wood litter at different rates since wood decomposition is unrelated to soil and topography. As litter does not accumulate indefinitely (Luizão 1989) decomposition losses must tend to equal rates of production in the long term. However, initial rates of decomposition affect the amount of carbon stored in dead biomass. Also, if conditions change rapidly, as expected under most models of climate change (Cox *et al.* 2008, Marengo *et al.* 2009), production may be out of balance with decomposition for some time.

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LITERATURE CITED

AGUIAR, N. O., GUALBERTO, T. L. & FRANKLIN, E. 2006. A medium-spatial scale distribution pattern of Pseudoscorpionida (Arachnida) in a gradient of topography (altitude and inclination), soil factors, and litter in a Central Amazonia forest reserve, Brazil. *Brazilian Journal of Biology* 66:791–802.

BAKER, T. R., PHILLIPS, O. L., MALHI, Y., ALMEIDA, S., ARROYO, L., DI FIORE, A., ERWIN, T., HIGUCHI, N., KILLEEN, T. J., LAURANCE, S. G., LAURANCE, W. F., LEWIS, S. L., MONTEAGUDO, A., NEILL, D. A., VARGAS, P. N., PITMAN, N. C. A., SILVA, J. N. M. & MARTINEZ, R. V. 2004. Increasing biomass in Amazonian forest plots. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* 359:353–365.

BEARD, K. H., VOGT, K. A., VOGT, D. J., SCATENA, F. N., COVICH, A. P., SIGURDARDOTTIR, R., SICCAMA, T. G. & CROWL, T. A. 2005. Structural and functional responses of a subtropical forest to 10 years of hurricanes and droughts. *Ecological Monographs* 75:345–361.

BODDY, L., HYNES, J., BEBBER, D. P. & FRICKER, M. D. 2009. Saprotrophic cord systems: dispersal mechanisms in space and time. *Mycoscience* 50:9–19.

BRAGA-NETO, R., LUIZÃO, R. C. C., MAGNUSSON, W. E., ZUQUIM, G. & CASTILHO, C. V. 2008. Leaf litter fungi in a Central Amazonian forest: the influence of rainfall, soil and topography on the distribution of fruiting bodies. *Biodiversity and Conservation* 17:2701–2712.

CASTILHO, C. V., MAGNUSSON, W. E., ARAÚJO, R. N. O., LUIZÃO, R. C. C., LUIZÃO, F. J., LIMA, A. P. & HIGUCHI, N. 2006. Variation in aboveground tree live biomass in a Central Amazonian forest: effects of soil and topography. *Forest Ecology and Management* 234:85–96.

CHAMBERS, J. Q., HIGUCHI, N., SCHIMEL, J. P., FERREIRA, L. V. & MELACK, J. M. 2000. Decomposition and carbon cycling of dead trees in tropical forests of the Central Amazon. *Oecologia* 122:380–388.

CHAMBERS, J. Q., SCHIMEL, J. P. & NOBRE, A. D. 2001. Respiration from coarse wood litter in Central Amazon forests. *Biogeochemistry* 52:115–131.

CHAMBERS, J. Q., TRIBUZY, E. S., TOLEDO, L. C., CRISPIM, B. F., HIGUCHI, N., SANTOS, J., ARAÚJO, A. C., KRUIJT, B., NOBRE, A. D. & TRUMBORE, S. E. 2004. Respiration from a tropical forest ecosystem: partitioning of sources and low carbon use efficiency. *Ecological Applications* 14:S72–S88.

CHAUVEL, A., LUCAS, Y. & BOULET, R. 1987. On the genesis of the soil mantle of the region of Manaus, Central Amazonia, Brazil. *Experientia* 43:234–241.

CHAVE, J., MULLER-LANDAU, H. C., BAKER, T. R., EASDALE, T. A., TER STEEGE, H. & WEBB, C. O. 2006. Regional and phylogenetic variation of wood density across 2456 neotropical tree species. *Ecological Applications* 16:2356–2367.

COSTA, F. R. C., MAGNUSSON, W. E. & LUIZÃO, R. C. 2005. Mesoscale distribution patterns of Amazonian understorey herbs in relation to topography, soil and watersheds. *Journal of Ecology* 93:863–878.

COSTA, F. R. C., GUILLAUMET, J. L., LIMA, A. P. & PEREIRA, O. S. 2009. Gradients within gradients: the mesoscale distribution patterns of palms in a Central Amazonian forest. *Journal of Vegetation Science* 20:69–78.

COX, P. M., HARRIS, P. P., HUNTINGFORD, C., BETTS, R. A., COLLINS, M., JONES, C. D., JUPP, T. E., MARENGO, J. A. & NOBRE, C. A. 2008. Increasing risk of Amazonian drought due to decreasing aerosol pollution. *Nature* 453:212–215.

CRAWLEY, M. J. 2007. *The R book*. John Wiley & Sons, Chichester. 942 pp.

CREWS, T. E., KITAYAMA, K., FOWNES, J. H., RILEY, R. H., HERBERT, D. A., MUELLER-DOMBOIS, D. & VITOUSEK, P. M. 1995. Changes in soil phosphorus fractions and ecosystem dynamics across a long chronosequence in Hawaii. *Ecology* 76:1407–1424.

FEARNSIDE, P. M. 2000. Global warming and tropical land-use change: greenhouse gas emissions from biomass burning, decomposition and soils in forest conversion, shifting cultivation and secondary vegetation. *Climatic Change* 46:115–158.

FEARNSIDE, P. M. & LEAL-FILHO, N. 2001. Soil and development in Amazonia. Pp. 291–312 in Bierregaard, R. O., Gascon, C., Lovejoy, T. E. & Mesquita, R. C. G. (eds.). *Lessons from Amazonia: the ecology and conservation of a fragmented forest.* Yale University Press, New Haven.

FERRER, A. & GILBERT, G. S. 2003. Effect of tree host species on fungal community composition in a tropical rain forest in Panama. *Diversity and Distributions* 9:455–468.

GALE, N. 2000. The relationship between canopy gaps and topography in a western Ecuadorian rain forest. *Biotropica* 32:653–661.

GENET, J. A., GENET, K. S., BURTON, T. M., MURPHY, P. G. & LUGO, A. E. 2001. Response of termite community and wood decomposition rates to habitat fragmentation in a subtropical dry forest. *Tropical Ecology* 42:35–49.

GILBERT, G. S. & SOUSA, W. P. 2002. Host specialization among wood-decay polypore fungi in a Caribbean mangrove forest. *Biotropica* 34:396–404.

GILBERT, G. S., FERRER, A. & CARRANZA, J. 2002. Polypore fungal diversity and host density in a moist tropical forest. *Biodiversity and Conservation* 11:947–957.

HARMON, M. E., WHIGHAM, D. F., SEXTON, J. & OLMSTED, I. 1995. Decomposition and mass of woody detritus in the dry tropical forests of the northeastern Yucatan Peninsula, Mexico. *Biotropica* 27:305–316.

KINUPP, V. F. & MAGNUSSON, W. E. 2005. Spatial patterns in the understory shrub genus *Psychotria* in Central Amazonia: effects of distance and topography. *Journal of Tropical Ecology* 21:1–12.

LAURANCE, W. F., FEARNSIDE, P. M., LAURANCE, S. G., DELAMONICA, P., LOVEJOY, T. E., RANKIN-DE-MERONA, J., CHAMBERS, J. Q. & GASCON, C. 1999. Relationship between soils and Amazon forest biomass: a landscape-scale study. *Forest Ecology and Management* 118:127–138.

LINDBLAD, I. 2000. Host specificity of some wood-inhabiting fungi in a tropical forest. *Mycologia* 92:399–405.

LODGE, D. J. 1997. Factors related to diversity of decomposer fungi in tropical forests. *Biodiversity and Conservation* 6:681–688.

LODGE, D. J. & LAESSØE, T. 1995. Host preference in *Camillea verruculospora*. *Mycologist* 9:152–153.

LUIZÃO, F. J. 1989. Litter production and mineral element input to the forest floor in a Central Amazonian forest. *GeoJournal* 19:407–417.

LUIZÃO, R. C. C., LUIZÃO, F. J., PAIVA, R. Q., MONTEIRO, T. F., SOUSA, L. S. & KRUIJT, B. 2004. Variation of carbon and nitrogen cycling processes along a topographic gradient in a Central Amazonian forest. *Global Change Biology* 10:592–600.

LUIZÃO, R. C. C., LUIZÃO, F. J. & PROCTOR, J. 2007. Fine root growth and nutrient release in decomposing leaf litter in three contrasting vegetation types in Central Amazonia. *Plant Ecology* 192:225–236.

MAGNUSSON, W. E., LIMA, A. P., LUIZÃO, R. C. C., LUIZÃO, F. J., COSTA, F. R. C., CASTILHO, C. V. & KINUPP, V. F. 2005. RAPELD: a modification of the Gentry method for biodiversity surveys in long-term ecological research sites. *Biota Neotropica* 5:19–24.

MARENGO, J. A., JONES, R., ALVES, L. M. & VALVERDE, M. C. 2009. Future change of temperature and precipitation extremes in South America as derived from the PRECIS regional climate modeling system. *International Journal of Climatology* 29: Early View. Available at: http://www3.interscience.wiley.com/cgi-bin/fulltext/122211831/PDFSTART

MARTIUS, C. 1997. Decomposition of wood. Pp. 267–276 in Junk, W. J. (ed.). *The Central Amazon floodplain: ecology of a pulsing system*. Springer-Verlag, Berlin.

MARTIUS, C., HOFER, H., GARCIA, M. V. B., ROMBKE, J., FORSTER, B. & HANAGARTH, W. 2004. Microclimate in agroforestry systems in Central Amazonia: does canopy closure matter to soil organisms? *Agroforestry Systems* 60:291–304.

MERTENS, J. 2004. *The characterization of selected physical and chemical soil properties of the surface soil layer in the "Reserva Ducke", Manaus, Brazil with emphasis on their spatial distribution.* B.Sc. Thesis. Humboldt Universität zu Berlin, Berlin. Available at: http://www.agrar.hu-berlin.de/struktur/institute/pfb/struktur/bodenkstandortl/mitarbeiter/Mertens_BSc_thesis.pdf

NASCIMENTO, H. E. M. & LAURANCE, W. F. 2002. Total aboveground biomass in Central Amazonian rainforests: a landscape-scale study. *Forest Ecology and Management* 168:311–321.

NOGUEIRA, A. 2006. Variação da densidade, área basal e biomassa de lianas em 64 km^2 de floresta de terra firme na Amazônia Central. Master Thesis. INPA/UFAM, Manaus. Available at: http://ppbio.inpa.gov.br/Port/public/d/dissertanselmo.pdf

NOGUEIRA, E. M., NELSON, B. W. & FEARNSIDE, P. M. 2005. Wood density in dense forest in Central Amazonia, Brazil. *Forest Ecology and Management* 208:261–286.

OLSON, J. S. 1963. Energy storage and balance of producers and decomposers in ecological systems. *Ecology* 44:322–331.

PHILLIPS, O. L., MALHI, Y., HIGUCHI, N., LAURANCE, W. F., NUNEZ, P. V., VASQUEZ, R. M., LAURANCE, S. G., FERREIRA, L. V., STERN, M., BROWN, S. & GRACE, J. 1998. Changes in the carbon balance of tropical forests: evidence from long-term plots. *Science* 282:439–442.

PHILLIPS, O. L., ARAGAO, L. E. O. C., LEWIS, S. L., FISHER, J. B., LLOYD, J., LOPEZ-GONZALEZ, G., MALHI, Y., MONTEAGUDO, A., PEACOCK, J., QUESADA, C. A., VAN DER HEIJDEN, G., ALMEIDA, S., AMARAL, I., ARROYO, L., AYMARD, G., BAKER, T. R., BANKI, O., BLANC, L., BONAL, D., BRANDO, P., CHAVE, J., DE OLIVEIRA, A. C. A., CARDOZO, N. D., CZIMCZIK, C. I., FELDPAUSCH, T. R., FREITAS, M. A., GLOOR, E., HIGUCHI, N., JIMENEZ, E., LLOYD, G., MEIR, P., MENDOZA, C., MOREL, A., NEILL, D. A., NEPSTAD, D., PATINO, S., PENUELA, M. C., PRIETO, A., RAMIREZ, F., SCHWARZ, M., SILVA, J., SILVEIRA, M., THOMAS, A. S., TER STEEGE, H., STROPP, J., VASQUEZ, R., ZELAZOWSKI, P., DAVILA, E. A., ANDELMAN, S., ANDRADE, A., CHAO, K. J., ERWIN, T., DI FIORE, A., HONORIO, E., KEELING, H., KILLEEN, T. J., LAURANCE, W. F., CRUZ, A. P., PITMAN, N. C. A., VARGAS, P. N., RAMIREZ-ANGULO, H., RUDAS, A., SALAMAO, R., SILVA, N., TERBORGH, J. & TORRES-LEZAMA, A. 2009. Drought sensitivity of the Amazon rainforest. *Science* 323:1344–1347.

POORTER, L., JANS, L., BONGERS, E. & VAN ROMPAEY, R. S. A. R. 1994. Spatial distribution of gaps along three catenas in the moist forest of Taï National Park, Ivory Coast. *Journal of Tropical Ecology* 10:385–398.

RENNÓ, C. D., NOBRE, A. D., CUARTAS, L. A., SOARES, J. V., HODNETT, M. G., TOMASELLA, J. & WATERLOO, M. J. 2008. HAND, a new terrain descriptor using SRTM-DEM: mapping terra-firme rainforest environments in Amazonia. *Remote Sensing of Environment* 112:3469–3481.

RIBEIRO, J. E. L. S., HOPKINS, M. G., VICENTINI, A., SOTHERS, C. A., COSTA, M. A. S., BRITO, J. M., SOUZA, M. A. D., MARTINS, L. H. P., LOHMANN, L. G., ASSUNÇÃO, P. A. C. L., PEREIRA, E. C., SILVA, C. F., MESQUITA, M. R. & PROCÓPIO, L. 1999. *Flora da Reserva Ducke: guia de identificação das plantas vasculares de uma floresta de terra firme na Amazônia Central*. INPA-UFAM, Manaus. 779 pp.

RIBEIRO, M. N. G. & VILLA-NOVA, N. A. 1979. Estudos climatológicos da Reserva Florestal Ducke, Manaus, AM. III Evapotranspiração. *Acta Amazônica* 9:305–309.

SANTANA, M. E., LODGE, D. J. & LEBOW, P. 2005. Relationship of host recurrence in fungi to rates of tropical leaf decomposition. *Pedobiologia* 49:549–564.

SARIYILDIZ, T. 2008. Effects of gap-size classes on long-term litter decomposition rates of beech, oak and chest nut species at high elevations in northeast Turkey. *Ecosystems* 11:841–853.

SOLLINS, P. 1998. Factors influencing species composition in tropical lowland rain forest: does soil matter? *Ecology* 79:23–30.

TAKYU, M., AIBA, S. I. & KITAYAMA, K. 2003. Changes in biomass, productivity and decomposition along topographical gradients under different geological conditions in tropical lower montane forests on Mount Kinabalu, Borneo. *Oecologia* 134:397–404.

WANG, Q. K., WANG, S. L. & HUANG, Y. 2008. Comparisons of litterfall, litter decomposition and nutrient return in a monoculture *Cunninghamia lanceolata* and a mixed stand in southern China. *Forest Ecology and Management* 255:1210–1218.

WEEDON, J. T., CORNWELL, W. K., CORNELISSEN, J. H. C., ZANNE, A. E., WIRTH, C. & COOMES, D. A. 2009. Global meta-analysis of wood decomposition rates: a role for trait variation among tree species? *Ecology Letters* 12:45–56.

WELLS, J. M. & BODDY, L. 1990. Wood decay, and phosphorus and fungal biomass allocation, in mycelial cord systems. *New Phytologist* 116:285–295.

WELLS, J. M., HARRIS, M. J. & BODDY, L. 1999. Dynamics of mycelial growth and phosphorus partitioning in developing mycelial cord systems of *Phanerochaete velutina*: dependence on carbon availability. *New Phytologist* 142:325–334.

ZHANG, Q. H. & ZAK, J. C. 1995. Effects of gap size on litter decomposition and microbial activity in a subtropical forest. *Ecology* 76:2196–2204.