SHORT COMMUNICATION

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WOOD LITTER STOCKS IN TROPICAL MOIST FOREST IN CENTRAL AMAZONIA

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Key words: Amazonia, biomass, litter layer, rainforest, standing stocks, wood litter.

Dead organic matter (DOM) is the starting point of the decomposer food chain. In forest ecosystems, a large fraction of DOM occurs in the form of wood. However, compared with leaf-litter, wood-litter (consisting of branches and logs) is often not adequately assessed, especially in tropical rainforests, and few data are available. Wood-litter data would provide an important input for the construction of forest carbon budgets. The activity of decomposers determines nutrient dynamics and the rate of carbon mineralization during the decay process (e.g., Schaefer 1990, Martius 1994). These processes are also affected by, among other factors, the amount and the spatial distribution of available wood.

We report on a quantitative assessment of wood-litter stocks, the distribution of size classes, and spatial distribution of wood in a central Amazonian rainforest. The study site was the "Reserva Florestal Adolfo Ducke" near the city of Manaus, Brazil, a rainforest reserve of the Instituto Nacional de Pesquisas da Amazônia (INPA). The area is dominated by dense, primary lowland ("terra firme") rainforest (for details cf. Prance 1990). The soil is a nutrient-poor yellow clayey oxisol (Chauvel *et al.* 1987). The climate is characterized by a short dry season (months with precipitation < 100 mm) from July to September. The 1911–1990 average annual rainfall of the Manaus region was 2107 mm (Ribeiro 1991); average minimum and maximum air temperatures were 20 and 26°C (Ribeiro 1976, Marques-Filho *et al.* 1981). Leaf-litter stocks of the study area have been determined by Höfer *et al.* (1996), leaf-litter production of nearby sites has been studied by Franken *et al.* (1979) and Luizão & Schubart (1987).

Our study was carried out in May 1993. Forty-five plots of 5x5 m were marked at random along three transects. The individual plots were at least 20 m apart and the distance between the three transects was about 500 m. One transect was situated on a small plateau, the other two were on adjacent lower terrain, though away from the valley bottom where a small creek flows. All dead wood on the floor of each plot was collected and sorted into two size groups (fine wood = 1–3 cm diameter; coarse wood > 3 cm diameter). The fresh mass (FM) of each size fraction was determined to 0.1 kg accuracy with a mechanical field balance. For the determination of the dry mass (DM), a representative sample of the wood (approx. 10% by volume) was taken to the laboratory, oven-dried 4 days at 105° C and weighed to obtain the DM:FM ratio. For 5 plots from where no such sample was taken, the mean DM:FM ratio of the respective size groups of the other plots was used to calculate dry mass. Fresh and dry mass values of both size classes of wood litter are not normally distributed, and non-parametric procedures were used for the statistical analyses. Here, arithmetic

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means [± 1 SD] are given instead of medians to make our study comparable with others.

An assessment of the standard error of the samples vs. cumulative sample average showed that for fine wood-litter, 15 sample units (plots of 25 m^2) would produce a standard error of about 15% of the average; with 31 sample units fine wood-litter would be assessed to 10% error ($P = 0.05$). The standard error for coarse wood-litter, which is much more unevenly distributed, was about 30% with 45 sample units.

The median fresh mass of fine wood-litter from all 45 plots was 5.5 kg per plot. The median mass of coarse wood-litter was approximately 3 times higher (18.9 kg per plot). The arithmetic means of the wood-litter from the transects were 6.2 ±3.4 and 43.7 ±80.6 kg per plot respectively. Median and average of fine wood did not differ very much. The means for coarse wood were much higher than the medians because some plots showed very large amounts of coarse wood (Table 1). Fine matter varied only between 1.6 and 17.0 kg per plot, whereas coarse wood ranged from 0.0 to 488.0 kg per plot.

The DM:FM ratio, which indicates moisture content of the wood, varied considerably between the plots (Table 1), probably due to the fact that dead wood originates from many species and has different decay histories. Also, the average ratios of both size classes (fine wood: 0.55, coarse wood: 0.46) were significantly different (normal distribution, t-Test, $P < 0.001$). On average, coarse wood contained more water than fine wood. It also showed a much higher variability. Water accounted for 1/3 to 3/4 of the fresh mass of the dead wood, depending on the degree of decay. Therefore, fresh mass is no reliable indicator of the importance of wood-litter. We calculated the dry masses from the original data using the DM:FM ratios. For all 45 plots, dry mass averaged 1.34 ±0.73 t ha^{-1} (fine matter) and 8.20 ±15.50 t ha^{-1} (coarse matter), giving 9.54 ±15.59 t ha^{-1} total dead wood.

Only for one transect (lowland 1) a weak positive relationship (linear regression) between the dry masses of fine and coarse wood-litter ($R = 0.62$, $P = 0.013$) was found, but for the other blocks no correlation between the two size fractions was detectable. The calculated dry masses of both size fractions, and of the total dead wood in the plots from the 3 transects (lowland 1, lowland 2, plateaú), did not differ significantly (Kruskal-Wallis one-way ANOVA on ranks; $P = 0.611$). The variation in the distribution of dead wood between the single plots prevailed over any differences between the locations in the study area.

In several studies in Amazonian rainforests, forest floor wood-litter ranged from 4.7 to 33.0 t ha^{-1} (Table 2). The value of 9.5 t ha^{-1} from Reserva Ducke is among the lower figures. We cannot assess at present to which extent stand-specific factors (stand biomass, site productivity, species composition) or seasonal effects determine the amount of wood-litter on the forest floor. This study was carried out at the end of the rainy season; wood-litter stocks may be lower then due to the higher decomposition rates in this season and because more dead wood is produced in the dry period of the year. Table 2 shows that two stands which are about 50 and 100 km distant from Reserva Ducke (EEST and Reserva Egler) exhibit the highest amounts of wood-litter. Wood mass in the EEST reserve, where only wood >10 cm diameter was considered, is thought to be even higher than the given value (Y. Biot, pers. comm.).

TABLE 1. Dead wood fresh mass in 25 m^2 plots and DM:FM ratios determined using subsamples from the plots in Reserva Florestal A. Ducke, Central Amazonia, Brazil.

	Fresh Mass (kg per plot)		DM:FM ratios	
	Fine Wood Matter (1–3 cm diameter)	Coarse Wood Matter (> 3 cm diameter)	Fine Wood	Coarse Wood
Samples (n)	45	44	44	35
Mean	6.2	43.7	0.551	0.463
SD	3.4	80.6	0.077	0.103
Normality of Distribution	no	no	yes	yes
Median	5.5	18.9		
Range	1.6–17.0	0.0–488.0	0.377–0.753	0.240–0.649

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TABLE 2. Mass of dead wood- and leaf-litter on the forest floor in Central Amazonian forests (t ha^{-1}). UHE = hydroeletric dam (usina hidrelétrica); these areas were assessed prior to the dam construction.

Site	Type	Litter on Forest Floor (t DW ha^{-1})			Wood as % of Total	Source
		Wood-Litter	Leaf-Litter	Total		
Reserva/Ducke	Rainforest	9.5[a]	13.8[b]	23.3	40.9	[a] this study [b] Höfer *et al.* (1996)
Reserva Egler	Rainforest	18.2	7.2	25.4	71.6	Klinge *et al.* (1975)
Reserva EEST	Rainforest	33.0[c]	10.0[d]	43.0	76.7	[c] Higuchi & Biot (1995) [d] Luizão (1989)
Ilha de Maracá	Rainforest	5.9	2.9*	8.8	67.0	Scott *et al.* (1992)
UHE Samuel (Roraima)	Rainforest	1.8	6.6	15.2	24.2	Revilla Cardenas (1986) (mean of 2 sites)
UHE Babaquara, Rio Xingú	Rainforest	8.9	12.3	21.2	41.9	Revilla Cardenas (1988)
UHE Samuel (Roraima)	Submontane Rainforest	27.0	10.0	37.0	73.0	Martinelli *et al.* (1988)**
UHE Kararão Xingú	River Fringe Forest	11.2	8.3	19.5	57.4	Revilla Cardenas (1987)
UHE Babaquara Xingú	River Fringe Forest	11.3	11.3	22.6	50.0	Revilla Cardenas (1988) (mean of 3 sites)
Ilha de Marchanaria	Floodplain	11.4–12.9	5.8	17.2–18.7	66.3–68.9	Martius (1997)

* corrected for fine wood
** cited from Fearnside (1994)

In the present study, dead wood accounts for about 41% of the total litter found on the forest floor, which is within the very wide range shown in other studies of 25–75% in rainforests, submontane forests and riparian and floodplain forests (Table 2). Here again, the highest percentage (75–77%) is found in the two other Central Amazonian sites. Leaf-litter mass in the three sites does not differ greatly.

We found fine litter dry mass to be about 14% of the total wood mass. Klinge *et al.* (1975) found the same proportion of 14% for fine to total matter. However, this is an average value and coarse matter mass was not a good predictor of fine matter in the present study. Wood decomposing organisms will find a much more evenly distributed resource in fine wood matter, which is only 1/7 or less of the total wood available.

Dead wood on the forest floor is only a fraction of the total dead wood in forest ecosystems. Standing dead wood (snags) was not assessed here, but added 11 to 30% to the total dead wood mass on the forest floor in two other studies in Central Amazonia (Klinge *et al.* 1975, Higuchi & Biot 1995), 0 to 80% in a lowland rainforest on Ilha de Maracá (Scott *et al.* 1992), and 80% (by volume) in a floodplain forest (Martius 1997). In addition to snags there are many dead branches of living trees, which have never been assessed in tropical forests. For temperate forests, dead branches were found to be about 100 to 600% of the mass of the snags (Ovington & Madgwick 1959, Christensen 1977). Thus, the dead wood on the forest floor assessed in the present study may be increased by 1.1–7.6 t ha^{-1} for snags, and an additional 1.1–45.6 t ha^{-1} for attached dead branches. This would result in a calculated range of 11.6–62.7 t ha^{-1} of total dead wood available in this forest (which would be in the normal range for Central Amazonian rain forests, cf. Table 2).

In view of the large variability of dead wood mass found at the sites studied and the uncertainties about the amount of standing dead wood, more detailed studies should be undertaken. A standardized sampling protocol would be required regarding the treatment of size fractions, snags, and attached dead wood, as well as seasonal effects, with the aim of finding reliable but easy-to-assess predictors of dead wood stocks and production rates in these forests.

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REFERENCES

Chauvel, A., Lucas, Y., & R. Boulet. 1987. On the genesis of the soil mantle of the region of Manaus, Central Amazonia, Brazil. Experientia 43: 234–241.

Christensen, O. 1977. Estimation of standing crop and turnover of dead wood in a Danish oak forest. Oikos 28: 177–196.

Fearnside, P.M. 1994. Biomassa das florestas amazônicas brasileiras. Pp. 95–124 *in* Companhia Vale do Rio Doce (ed.). Anais do Seminário: Emissão X Sequestro de CO_2 – uma nova oportunidade de negócios no Brasil. Rio de Janeiro, Brazil.

Franken, M., Irmler, U., & H. Klinge. 1979. Litterfall in inundation, riverine and terra firme forests of central Amazonia. Tropical Ecology 20: 225–235.

Higuchi, N., & Y. Biot. 1995. Convênio INPA/ODA: BIONTE. Biomassa Florestal e Nutrientes. Relatório Semestral (Janeiro a junho 1995), Volume 2. Unpublished report, Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus.

Höfer, H., Martius, C., & L. Beck. (1996). Decomposition in an Amazonian rain forest after experimental litter addition in small plots. Pedobiologia 40: 570–576.

Klinge, H., Rodriguez, W.A., Brünig, E., & E.J. Fittkau. 1975. Biomass and structure in a central Amazonian rain forest. Pp. 115–122 *in* Golley, F.B., & E. Medina (eds.). Tropical ecological systems. Berlin, Germany.

Luizão, F.J. 1989. Litter production and mineral element input to the forest floor in a central Amazonian forest. Geojournal 19: 407–417.

Luizão, F.J., & H.O.R. Schubart. 1987. Litter production and decomposition in a terra firme forest of central Amazonia. Experientia 43: 259–265.

Marques-Filho, A.O., Ribeiro, M.N.G., Santos, H.M., & J.M. Santos. 1981. Estudos climatológicos da reserva Florestal Ducke, Manaus-AM. IV. Precipitação. Acta Amazonica 11: 759–768.

Martinelli, L.A., Victoria, R.L., Moreira, M.Z., Arruda Jr., G., Brown, I.F., Ferreira, C.A.C., Coelho, L.F., Lima, R.P., & W.W. Thomas. 1988. Implantação de parcelas para monitoreamento de dinâmica florestal na área de proteção ambiental. UHE Samuel, Rondônia. Relatório Preliminar. Unpublished report, Centro de Energia Nuclear na Agricultura (CENA), Piracicaba.

Martius, C. 1994. Diversity and ecology of termites in Amazonian forests. Pedobiologia 38: 407–428.

Martius, C. 1997. Decomposition of wood. Pp. 267–276 *in* Junk, W.J. (ed.). The central Amazonian floodplain – ecology of a pulsing system. Ecological Studies 126. Berlin, Germany.

Ovington, J.D., & H.A.I. Madgwick. 1959. Distribution of organic matter and plant nutrients in a plantation of Scots Pine. Forest Science 5: 344–355.

Prance, G.T. 1990. The floristic composition of the forests of central Amazonian Brazil. Pp. 112–140 *in* Gentry, A.H. (Ed.) Four Neotropical rainforests. New Haven, U.S.A.

Revilla Cardenas, J.D. 1986. Estudos da ecologia e controle ambiental na região do reservatório da UHE de Samuel. Convênio: ELN-MCT-CNPq-INPA de 1.7.82, Relatório: setorial, Segmento: Estimativa da Fitomassa. Período julho-dezembro 1986. Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil.

Revilla Cardenas, J.D. 1987. Relatório: Levantamento e Análise da Fitomassa da UHE de Kararaô, Rio Xingú. Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil.

Revilla Cardenas, J.D. 1988. Relatório: Levantamento e Análise da Fitomassa da UHE de Babaquara, Rio Xingú. Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil.

Ribeiro, A. 1991. Análise das variações climáticas observadas na região de Manaus (AM). M.Sc. Thesis, Univ. of São Paulo, São Paulo, Brazil.

Ribeiro, M.N.G. 1976. Aspectos climatológicos de Manaus. Acta Amazonica 6: 229–233.

Schaefer, M. 1990. The soil fauna of a beech forest on limestone: trophic structure and energy budget. Oecologia 82: 128–136.

Scott, D.A., Proctor, J., & J. Thompson. 1992. Ecological studies on a lowland evergreen rain forest on Maracá Island, Roraima, Brazil. II. Litter and nutrient cycling. Journal of Ecology 80: 705–717.

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