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Fine litter accumulation in Central Amazonian Tropical Rainforest canopy

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ABSTRACT

Fine litter dynamics within the canopy di er from litter dynamics on the forest oor for reasons such as di erences in microclimate, substrate, disturbance level, *stratum* in uence and decomposition rates. is study is the rst attempt to quantify the ne litter accumulated in the canopy of Central Amazonian forests. We compared the canopy litter accumulation to ne litter-layer on forest oor and to other forests and also investigated which were the mostly accumulated litter omponents. We found that Central Amazonian Rainforest intercepts greater ne litter in the canopy (294 $g.m^{-2}$) compared to other forest formations with higher winds speed as in a Costa Rican Cloud Forest (170 $g.m^{-2}$). e mean canopy ne litter accumulated at the end of the dry season was less than a half of that on soil surface (833 $g.m^{-2}$) and the ne wood component dominates the canopy samplings (174 $g.m^{-2}$) while leafy component predominate on soil surface litter (353 $g.m^{-2}$).

KEYWORDS: Canopy access; Canopy litter; Litterfall; Rope techniques; Soil litter layer.

Acúmulo de liteira fina no dossel de uma Floresta Tropical na Amazônia Central

RESUMO

A dinâmica da liteira na no dossel difere da dinâmica no chão da oresta por razões como diferenças no microclima, tipo de substrato, taxas de decomposição, distúrbios e in uência dos estratos. Esta é a primeira tentativa de quanti car a liteira na acumulada no dossel das orestas da Amazônia Central. Comparamos o acúmulo da liteira no dossel com a camada de liteira do chão da oresta e com outros tipos de orestas e investigamos quais componentes da liteira acumularam em maiores quantidades. A oresta estudada na Amazônia Central interceptou uma maior quantidade de liteira no dossel (294 $g.m^{-2}$) do que outras orestas com maior in uência dos ventos, como na Costa Rica (170 $g.m^{-2}$). A média de liteira no dossel no m da estação seca foi menos da metade da acumulada sobre o solo (833 $g.m^{-2}$). Os galhos nos dominaram nas amostras do dossel (174 $g.m^{-2}$) enquanto as folhas predominaram na liteira sobre o solo (353 $g.m^{-2}$).

PALAVRAS-CHAVE: Acesso ao dossel; Liteira de dossel; Queda de liteira; Técnica de escalada por cordas; Camada de liteira do solo.

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As the awareness on environmental issues accelerates, including the biosphere-atmosphere interactions, studies of forest canopies become essential to our understanding of biodiversity, global atmospheric changes, and forest conservation. The development of canopy access methods has enabled scientists to conduct quantitative research in tree crowns, shifting the biological canopy science from a descriptive autoecology of specific individuals to a complex ecosystem approach (Lowman & Wittman 1996).

Fine litter dynamics within the canopy may differ from litter dynamics on the forest floor for many reasons such as differences in microclimate, substrate, disturbance level, *stratum* influence, decomposition rates, among others (Nadkarni & Matelson 1991). Despite several studies evaluating litterfall and litter accumulation on the forest floor, there are just a few works published on the amounts, characteristics or dynamics of suspended leaf litter in subcanopy (Alvarez-Sanchez & Guevara 1999; Dearden & Wardle 2008) and within tree canopy crowns (Nadkarni & Matelson 1991; Nadkarni *et al.* 2004). To the best of our knowledge this study is the first attempt to quantify fine litter accumulated in the canopy of a Central Amazonian Rainforest, with the following questions addressed: (1) How accumulated canopy litter in this type of forest can be compared to fine litter-layer on forest floor and to other tropical forests? (2) Which components of the fine litter are mostly accumulated within tree canopy in Amazonian Forests?

This study was carried out in the Cuieiras Reserve of the National Institute for Amazonian Research (INPA), located 60 km north from Manaus (2°35'S, 60°06'W), during the end of the dry season, from October to November 2008. The climate type is "Am" in the Köppen classification with total annual rainfall about 2,700 mm and the rainiest months from December to May and driest from August to November. Daily mean relative humidity varies from 75% to 92% throughout the year (Araújo *et al.* 2002). Mean annual temperature is 26.7 °C with average monthly air temperature varying between 24 °C and 27 °C (Leopoldo *et al.* 1987).

To estimate the canopy fine litter accumulation we collected the fine litter (*sensu* Proctor 1983, comprising leafy and reproductive materials, plus wooden material with diameters ≤ 2 cm) resting on accessible branches segments within 3 m from the central trunk on five trees with diameter at breast height (DBH) larger than 35 cm and possible to be climbed by rope techniques. Despite recent advances in techniques, access to the upper canopy remains problematic (Baker & Sutton 1997), what generally induces a low number of samples. Thus, to make our sample more meaningful, by the criteria of commonness, we selected trees of the most common species present in a 500-m^2 plots, in a plateau area. These species belong mainly to families with greatest species richness and importance value, Lecythidaceae and Sapotaceae (Oliveira *et al.* 2008) and also to Caryocaraceae.

Insufficient replication due canopy access difficulties generally induces inappropriate collection of pseudoreplicated data, a problem that has not yet received sufficient attention amongst canopy researchers (Barker 1997). To avoid pseudoreplication and to represent better the variability within trees, at each tree we collected composite samples, that consist of the sum of five branch sub-samples. The branch surface area was determined by its length x width in meters defining canopy fine litter unit as grams of litter mass per branch surface area (g.m^{-2}). To quantify fine litter accumulated on soil surface, we also collected five sub-samples (summing a composite sample) under the crown area of each tree sampled for canopy litter, using a 20 x 20 cm aluminum frame. Each composite sample was sorted into six components – leaves, wood < 2 cm, reproductive parts (i.e., fruits and flowers), bryophytes, roots and miscellaneous – and than oven-dried at 60 °C for 50 hours (or until constant weight) and weighed. The wind speed (m.s^{-1}) was recorded at each 30 minutes during the 2008 year by sonic anemometers (for details, see Araújo *et al.* 2002) located in a flux tower at two heights: above the canopy (60 m) and in the sub-canopy (28 m).

The nonparametric Two Sample Wilcoxon Rank Sum test (W) was performed to compare the amount of accumulated litter in tree canopy with that on soil surface and also the annual mean wind speed amongst sub-canopy and above canopy. Differences on amount of litter components within samples were assessed by Kruskal-Wallis Rank Sum tests (KW). All analyses were carried out using the free software R 2.6.2 (R Development Core Team 2008).

The mean canopy fine litter mass accumulated in the tree canopies was 294 g.m^{-2} of the branch surface area, with a large amplitude of variation (range = 79–677 g.m^{-2}). This large variation can be explained somehow by branch structural characteristics which had a general influence on canopy litter accumulation. The branch segments sampled covered a wide variation of branch width that exists within tree crowns ('pers. obs.'). In a Costa Rican Cloud Forest, Nadkarni & Matelson (1991) found a mean canopy fine litter mass around 170 g.m^{-2} of the branch surface area (range = 4.5–1,268 g.m^{-2}), which corresponded to *ca.* 1% of fine litter-layer mass on that area. Therefore, comparing these two forest formations, our study site in a Central Amazonian Tropical Rainforest area presents higher values of canopy fine litter mass than a Costa Rican Cloud Forest. These results were somehow expected considering that (1) wind is one of the main within–canopy disturbances on canopy fine litter interception, besides rains and the impact of arboreal animal activities, and (2) winds are strongest and consequently a more important factor in the Costa Rican Cloud Forests than on Amazonian Lowland

Rainforests. In a Costa Rican Cloud Forest the wind speed above the canopy range between 18 and 180 $m.s^{-1}$ (Nadkarni & Matelson 1991), while we detected a mean daily wind speed above canopy of 1.92 (± 0.90 SD) $m.s^{-1}$ quite constant throughout the 2008 year (Figure 1b), for the plateau areas of our study site on Central Amazon, with its maximum values reaching 8.3 $m.s^{-1}$.

e mean ne litter mass accumulated on soil surface in Central Amazonian Forest was 833 $g.m^{-2}$ (8.33 $t.ha^{-1}$; range = 567–1,385 $g.m^{-2}$). is value fell in the range of another study in the same area (Monteiro 2005) that found the highest amount of ne litter mass on soil surface in the plateau areas (mean = 580 $g.m^{-2}$ or 5.8 $t.ha^{-1}$ range = 3.6 to 9.2 $t.ha^{-1}$) at the end of the dry season, when higher amounts of litter are accumulated. Since we also sampled at the time of greatest litter accumulation (Luizão & Schubart 1987), we found high values of litter mass.

Evaluating vertical variation of litter accumulation, litter mass on forest oor di ers signi cantly from canopy (W = 1; $p < 0.05$ – Figure 1a). It should be closely related to wind speed vertical strati cation. Wind reaches higher speeds in the canopy than in lower forest *strata*; therefore wind is supposed to remove more litter from higher canopy branches. e annual mean wind speed in sub-canopy was about 0.3 $m.s^{-1}$, which was 6.4 times slower than the above canopy wind speed (W = 278155723; $p < 0.001$ – Figure 1b). Even more, lower forest *strata* (i.e., sub–canopy and understory) may have a substantial cumulative contribution to the of ne litter accumulation at forest oor.

A detailed comparison of the ne litter composition showed differences in the amounts of such component accumulated in the canopy (KW = 20.115; df = 5; $p < 0.01$) and in soil surface (KW = 25.739; df = 5; $p < 0.001$ – Figure 2). e wooden component with less than 2 cm diameter dominates the canopy litter (174 $g.m^{-2}$) while leafy component predominate in soil surface litter (353 $g.m^{-2}$), followed by wood component (273 $g.m^{-2}$). Branches and twigs are less susceptible than leaves to the in uence of winds, facilitating the prevalence of wood components in the canopy. Leaves use to be the main ne litter component on soil surface, and subject to high decomposition rate, contributing signi cantly to faster nutrient cycling process (Luizão 1989). Canopy leaf litter turnover time recorded for Costa Rican Tropical Forests was 2.8 years, twice that of leaf litter turnover time on soil

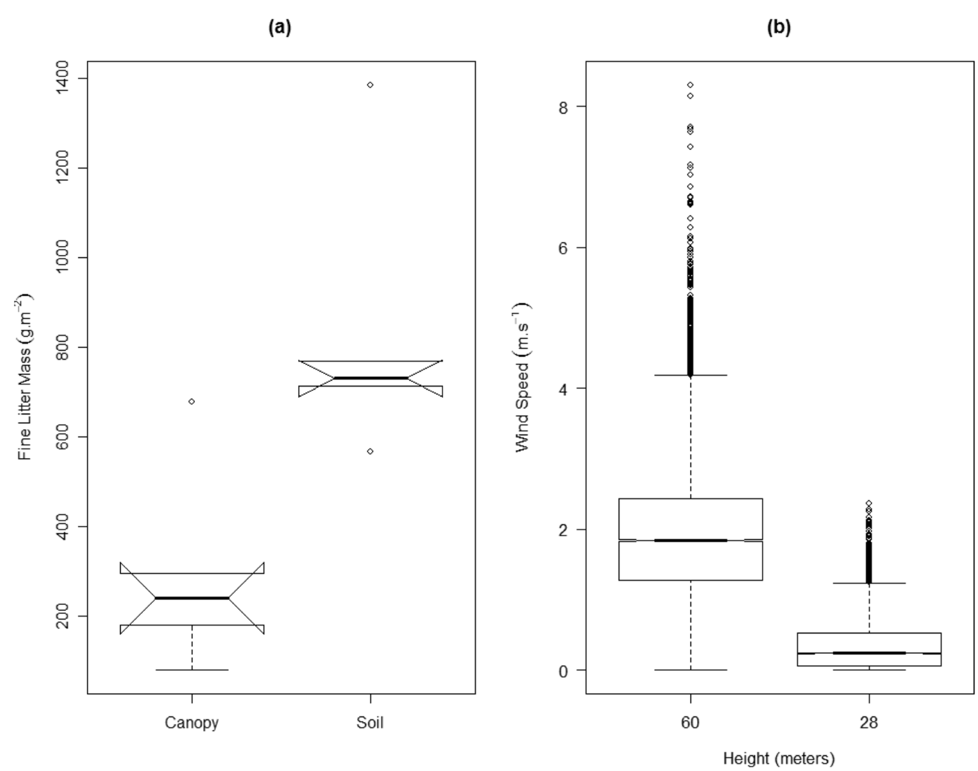

Figure 1 - Boxplots comparing (a) fine litter accumulated in canopy and on soil surface; (b) Wind speed ($m.s^{-1}$) above the canopy (60 m) and in the sub-canopy (28 m) in Central Amazon Forest for the 2008 year. The box stretches from the lower to the upper hinges (defined as the 1st–3th quartiles) and the bold line shows the median of the data sample. The whiskers extend to the most extreme data point, which is no more than 1.5 times the interquartile range from the box. Open dots correspond to outlier data points that fall beyond 1.5 times the interquartile range. Notches in the boxes represent roughly a 95% confidence interval for the difference in two medians. Non-overlapping notches are strong evidence that the two medians differ significantly.

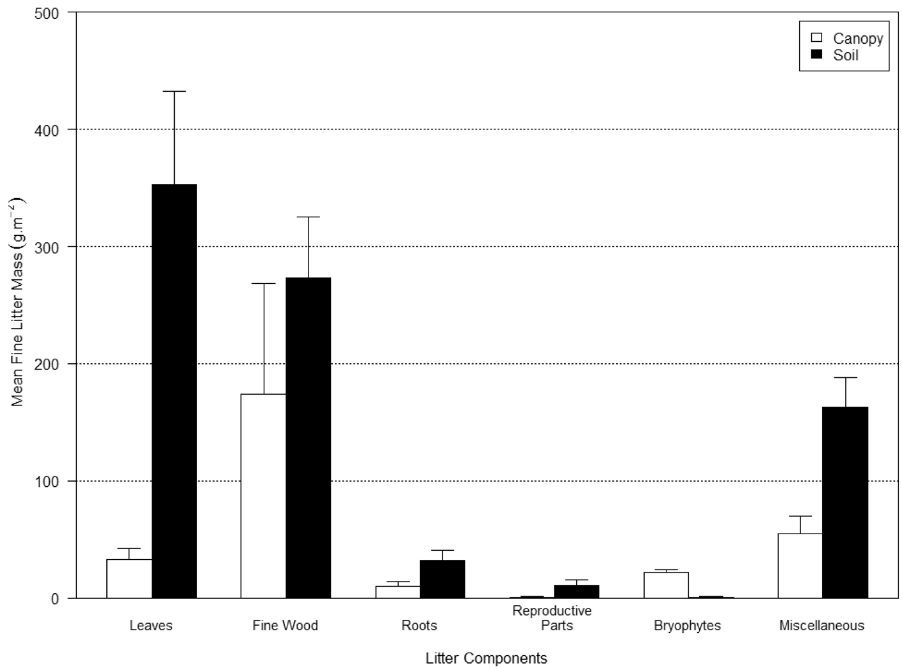

Figure 2 - Dry mass (g.m^{-2}) of litter components accumulated in canopy and on soil surface. Values in bars are means (n=5) and error bars represent standard errors.

surface that was 1.4 years (Nadkarni & Matelson 1991).   us, the few leaves that do remain in the canopy decompose slower than on the soil. According to Nadkarni & Longino (1990), this low decomposition rate in the upper *stratum* should be attributed to drier environmental conditions and lower densities of key decomposers in the tree crowns. On the other hand, the bryophyte component of litter was found just in the canopy samples suggesting that its soft material is quickly decomposed in the canopies and do not reach the forest   oor, at least in a recognizable way.

More detailed studies concerning long term   ne litter turnover and decomposition rate in Amazonian tropical rainforests canopy are still needed and essential to increase our knowledge on nutrient cycling at di erent forest layers and for further discussions on biosphere-atmosphere interactions. In the same way, long term studies addressing di erent vegetation types (primary and secondary forests) and topographic positions (i.e., plateau, slope and valley) are necessary to clarify the seasonal dynamic of canopy   ne litter accumulation and to make comparisons between di erent forest types possible.

Concluding, the studied Central Amazonian Rainforest intercepts greater   ne litter mass in the canopy compared to other forest formations with higher winds speed, as in a Costa Rican Cloud Forest.   e mean canopy   ne litter mass accumulated at the end of the dry season was less than a half of that on soil surface.   e   ne wood component dominates the canopy samplings suggesting a slower litter decomposition rate at this *stratum*.

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