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Variation of carbon and nitrogen cycling processes along a topographic gradient in a central Amazonian forest

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Abstract

It is well recognized in the literature that topography can influence soil nutrient stocks and dynamics in temperate regions, but for tropical forests, this source of variation has sometimes been ignored. The nature of such variations may depend upon the soil type, which in turn, is closely linked to local or regional topography. This study characterizes the soil and describes the status of carbon and nitrogen in vegetation, litterfall, litter-layer and soil upper layers along the main positions of a topographic gradient (plateau, slope and valley), 60 km north of Manaus, on Cuieiras Reserve watershed. Nitrogen concentrations in living leaves, fresh litterfall, litter-layer and soil upper layers were lower in the valley than in both slope and plateau plots. Carbon concentrations in plant material were not significantly different among the three topographic positions, resulting in higher C : N ratios in valley plots. Local topography (plateau, slope and valley) clearly was an influential factor in the nutrient distribution along the study locations. Lower rates of N cycling processes in the valley are probably related to its sandy soil texture and seasonal flooding.

Keywords: litter decomposition, nitrogen dynamics, soil texture, C : N ratio, topographic gradient

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Introduction

Tropical rain forests generally have high biomass and very high diversity (Pires & Prance, 1985), even though they usually grow on deeply weathered, nutrient-poor soils. It has often been assumed that this richness results, apart from abundant sunlight and rainfall, from efficient mechanisms for nutrient conservation and recycling (Herrera *et al*., 1978). In Amazon rain forests there is substantial variability in forest types and forest biomass, even at small spatial scales where there is also variability in soil nutrition, soil texture and drainage. Such spatial correlations could point to limitations by water, but also by nutrient availability. It is hard to prove the existence of nutrient limitation in the field, but investigating simultaneously varying properties of soils and vegetation can at least suggest where to look for limiting processes. Also, C : N ratios in plant material should be fairly large where N limitations occur (Lloyd, 1999).

Many questions still remain about the role of texture on soil C storage and ecosystems processes, such as primary productivity and decomposition. In most terrestrial ecosystems, the majority of the net primary production (NPP) enters the decomposition systems as plant litter, where it has important 'afterlife effects' (Findlay *et al*., 1996). Topography and associated texture variation can affect decomposition rates as well as soil nutrient transformations. For temperate forests, it is well known that nitrogen mineralization may be highly variable within a forest ecosystem (Hill & Shackleton, 1989), and that N transformation rates vary between different soil types within the same watershed (Van Miegroet *et al*., 1990). At the Walker Branch forest watershed (Tennessee, USA), it was shown that valley floors had greater total N concentrations, lower soil C : N ratios, greater potential net nitrification, and greater microbial activity (Garten *et al*., 1994). Several other important variables related to soil N dynamics

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were significantly correlated with topography. In the tropics, forest on highly weathered white sand soils are considered to be N-poor systems indicating that soil texture, sometimes associated with topography, influences biogeochemical and ecological processes (Cuevas & Medina, 1986; Livingston *et al*., 1988; Vitousek & Matson, 1988; Silver *et al*., 2000). At San Carlos, Venezuela, litter decomposition and turnover rates on sandy soils were slower due to nutrient and water limitations on decomposition (Cuevas & Medina, 1986). In Amazonian forests, Livingston *et al.* (1988) found nitrogen in low supply in lower topographic positions with increased sandy soil. Silver *et al.* (2000) also found lower nitrogen transformation in sandy soils along a sand to clay gradient.

Near Manaus, eddy correlation measurements of net ecosystem carbon exchange (NEE) in the Cuieiras forest reserve, 60 km north of Manaus, suggest that carbon uptake varies depending on the part of the landscape where the fluxes are originating from and the percentages of high tall statured and short statured forests within those 'footprints' (Araújo *et al*., 2002; Kruijt *et al*., in press). This forest area is representative of the dominant landscape type of vast areas in the central Amazonia: the so-called 'Terra Firme' landscape, effectively a dissected sedimentary plateau (Chauvel *et al*., 1987). It is likely that variability in carbon uptake, biomass and diversity are related to soil properties associated with topography. This study, therefore, aims to characterize soils and describes the status of carbon and nitrogen in both vegetation, litterfall, litter-layer and soil upper layers along a topographic gradient in this area of Terra Firme landscape, and seeks to establish whether these sources of variation are related and possibly associated with nutrient limitations.

Material and methods

Site description

The Manaus LBA site was installed 60 km north of Manaus, in the Cuieiras Reserve of the Instituto Nacional de Pesquisas da Amazônia (INPA). The Cuieiras Reserve has an area of 22 735 ha and is part of a vast area of pristine tropical rainforest (Andreae *et al*., 2002). It is accessed via ZF-2, an unpaved road running west from the main BR-174 Manaus-to-Caracas highway. The study concentrated on a watershed around the medium-sized plateau area near one of the micro-meteorological towers of the LBA Programme known as K34 (2°35″21.08″ S, 60°06″53.63″ W) (Araújo *et al*., 2002). There is very little seasonal variation of air temperatures at the site, with mean monthly values only varying between about 24 °C and 27 °C; mean annual temperature is 26.7 °C (Leopoldo *et al*., 1987). The total annual rainfall is 2200 mm, with a distinct dry season during July–September with usually less than 100 mm of rain per month. Daily mean relative humidity varies from minimum values of 75% during the relatively dry month (August) to 92% during the height of the rainy season in April (Araújo *et al*., 2002).

The topography is undulating with very little large-scale relief in this region, but at a smaller scale the dense drainage network has formed a pattern of plateaus and valleys with a maximum height difference of about 60 m (from 60 to 120 m). The Tertiary sediments of the Alter-do-Chão formation are covered mostly by Oxisols on plateaus, Ultisols on slopes and Spodosols associated with small streams in small valley bottoms (Bravard & Righi, 1989). When moving from plateau to valley, clay content of the top 5 cm of soil decreases strongly while sand content increases. The vegetation covering the watershed corresponds to a highly diverse Lowland Evergreen Rainforest (Floresta Densa de Terra Firme) (Guillaumet, 1987). The variation in soil type and topography creates distinct habitats for the forest vegetation. On plateaus, well drained clay soils favour high biomass forest with 35–40 m in height with several trees emerging (> 45 m) such as *Dinizia excelsa*. Usually there are several stemless palms such as *Attalea attaleoides* and *Astrocaryum sciophilum*. On slopes, where the layer of sandy soil is deepening in the lower portions, forest biomass is lower and height is around 25–35 m. Few emerging trees are found in this location, and there are some tree species that only occur in this habitat. In valleys, sandy soils are usually waterlogged during the rainy season, supporting low biomass and low tree height (20–35 m), with very few emerging trees. Several trees have aerial and adventitious roots, and there are also various species of arboreal palm trees, such as *Oenocarpus bataua* and *Mauritia flexuosa*. The understorey is dense with other species of stemless palm (e.g. *Attalea microcarpa*) and several species of herbs common to waterlogged habitats, belonging to the families Rapateaceae, Marantaceae and Cyclanthaceae (Guillaumet, 1987).

Field sampling

From the plateau where the K34 micro-meteorological tower is located, a 600 m transect crossed the topographic gradient down to the small stream in the bottom of the valley. Three replicate plots of 20 m × 50 m were selected in each of three topographic positions located on plateau, slope and valley, respectively, with clear differences in clay content.

To study the relationship between C and N concentrations, composite samples of mature leaves were collected from 20 canopies of trees belonging to various species, randomly selected along a 1 km × 10-m transect, in each of the topographic positions. After climbing the trees, samples were taken from three canopy positions (top, middle and lower parts). Sun and shade leaves (which did not turn out to differ in C and N concentrations) were mixed and analysed together.

To assess soil properties and nitrogen dynamics in each plot, three composite samples made up of five topsoil (0–10 cm) cores were taken randomly around the sampled trees. Additionally, five soil pits randomly selected were excavated to a depth of 2 m in each topographic position, crossing all three assigned plots within each topographic position. For the purpose of the present study, only the two upper soil layers, 0–5 and 5–10 cm, were analysed.

Fine litterfall, including woody material with a diameter of up to 2 cm (Proctor, 1983), was sampled semi-monthly in ten 50 cm × 50 cm traps, randomly located within three 20 m × 80 m plots assigned for each topographic position. Litter samples were sorted into four main components: leaves, woody material (diameter ≤2 cm), reproductive structures and fine fractions. Of each component, dry weight and chemical content were measured.

The litter-layer on the forest floor was sampled in the same plots as those used for litter traps, five times during 1 year covering all different seasons, including the transitional periods. In each plot, five composite samples (made of five subsamples each) were taken randomly, using a 20 cm × 20 cm wooden frame.

In order to assess the litter dynamics in forests at the three topographic positions, the turnover rate (k_L) was calculated using the equation: $k_L = L/S$, where L is annual litterfall (total litter produced annually), and S is the mean amount of litter stored on the soil surface along the year.

Laboratory analyses

Soil measurements included texture, pH, water-holding capacity (WHC) and gravimetric moisture, C and N concentrations, initial mineral N, net N mineralization and nitrification. Texture, WHC and gravimetric moisture followed the methodology described by EMBRAPA (1997). Soil C and total N concentrations were measured after air-drying and sieving samples through a 2 mm mesh, using a CHN Fisons NA-1500 Auto-Analyzer. Net N mineralization and nitrification were measured by incubating samples for 10 days in aerobic conditions as described by Hart et al. (1994): two 20 g subsamples of field moist soil were weighed into glass flasks, of which one was immediately extracted with 100 mL 2 M KCl to measure the concentrations of N-NH_4^+ and N-NO_3^-, to be considered as the initial mineral N content. The other set was incubated at ambient temperature (approximately 25 °C) for 10 days before extraction. All values were expressed on a soil dry weight basis.

Estimates of net nitrification, measured as nitrate production in incubated soils, provide an index of N availability in a soil at the time of sampling.

Plant material (leaves from living trees and litter), was oven-dried at 65 °C and finely ground. C and N concentrations were measured on a CHN Fisons NA-1500 Auto-Analyzer.

Results

Variation of soil properties along the topographic gradient

Soil texture varied significantly with altitude along the topographic gradient, where clay content decreased from 65% in the plateau to 43% in the slope and 5% in the valley (Table 1). Along with texture, some other properties also showed significant trends along the gradient, such as organic matter content (soil organic matter) and soil moisture ($P < 0.001$ for both) (Table 1). For soil pH, lower values were found in the valley than in the other two topographic positions. The opposite difference ($P < 0.01$) was found (Table 1). Soil C and N concentrations were similar in the two higher topographic positions: plateau and slope, but concentrations in the

Table 1 Physical and chemical properties of the topsoil (0–10 cm) in the three main positions of the toposequence in the Cuieiras area

Topographic position	Altitude (m)	Clay (%)	SOM (%)	C:N (0–5 m)	C:N (5–10 cm)	pH (H_2O)	Moisture (g H_2O g^{-1} dry soil)	WHC
Plateau	120 ± 6	65a ± 2.0	6.6a ± 2.0	12.2a ± 3.1	12.5a ± 1.9	3.9a ± 0.6	0.354a ± 0.04	0.441a ± 0.001
Slope	95 ± 8	43b ± 0.8	3.5b ± 1.1	13.2a ± 1.1	12.7a ± 0.9	3.8a ± 0.6	0.257b ± 0.02	0.474a ± 0.02
Valley	70 ± 6	5c ± 1.7	2.1c ± 1.4	15.5b ± 2.3	14.2a ± 2.0	4.4b ± 0.2	0.176c ± 0.05	0.357b ± 0.02

Values are means and standard deviations of five samples in each plot. Means within a column followed by the same letter are not significantly different from each other (Tukey's test, $P = 0.05$).
SOM, soil organic matter; WHC, water-holding capacity.

valley were significantly lower ($P < 0.01$) (Fig. 1, Table 2). Irrespective of locations, decreasing C and N concentrations were found with depth (Fig. 1), but no significant differences occurred between the 0–5 and 5–10 cm layers (Fig. 2).

C and N in living vegetation

Carbon concentrations of mature tree leaves did not vary significantly among the three topographic levels. However, as for soil upper layers, nitrogen concentrations were significantly lower ($P < 0.001$) in tree leaves from the valley ($1.3 \pm 0.2\%$) than in the plateau ($1.9 \pm 0.\%5$) and slope ($2 \pm 0.5\%$) (Fig. 2, Table 2). Thus, C : N ratios of leaves were significantly higher ($P < 0.001$) in valley trees (C : N = 36.6) than in trees of either plateau (C : N = 26.1) or slope (C : N = 25.9).

Litterfall

During the dry season, the highest mean monthly litter production was found on the plateau (1.17 t DW ha^{-1}), while the smallest amount was measured in the valley plots (0.67 t ha^{-1}). This spatial pattern was found throughout the year (July 2001–June 2002). The annual

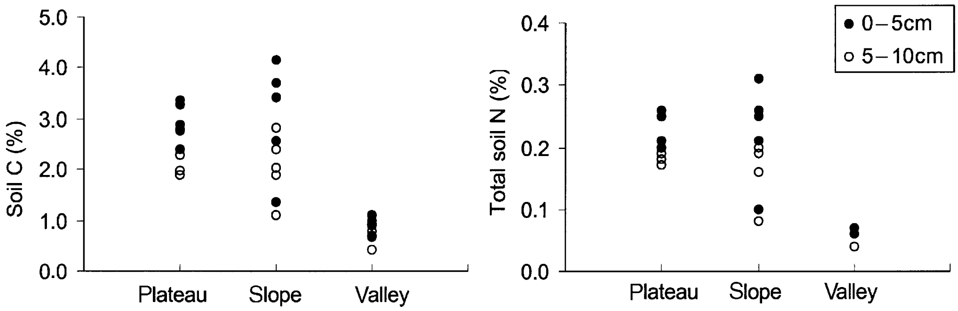

Fig. 1 Concentrations of C and total N in the 0–5 and 5–10 cm layers of the soil in the three main positions of the topographic gradient on Cuieiras watershed.

Table 2 Values of significance for one-way ANOVA between the three main topographic positions (plateau, slope and valley) for soil and plant characteristics

Characteristics	*F*	*P*	Differences found (Tukey at 5%)
Upper soil layers			
Clay content	36.3	0.000	Plateau > slope > valley
Soil moisture	47.6	0.000	Plateau > slope > valley
WHC	9.31	0.002	Plateau = slope > valley
Soil pH (H_2O)	40.0	0.000	Plateau = slope < valley
SOM	111.8	0.000	Plateau > slope > valley
Soil total C (0–5 cm)	8.84	0.006	Plateau = slope > valley
Soil total C (5–10 cm)	10.7	0.003	Plateau = slope > valley
Soil total N (0–5 cm)	11.9	0.002	Plateau = slope > valley
Soil total N (5–10 cm)	15.2	0.000	Plateau = slope > valley
Soil NO_3 N (0–5 cm)	3.73	0.039	Plateau = slope > valley
Soil NH_4^+ N (0–5 cm)	4.24	0.023	Plateau = slope > valley
Net N mineralization (0–5 cm)	12.5	0.000	Plateau = slope > valley
Net N nitrification (0–5 cm)	23.8	0.000	Plateau = slope > valley
Leaves of living trees			
Leaf N concentration	13.9	0.0000	Plateau = slope > valley
Leaf C : N ratio	19.5	0.0000	Plateau = slope < valley
Litterfall			
Fine litter production	5.36	0.008	Valley < plateau = slope
Woody fraction (%)	3.48	0.031	Plateau = slope < valley
Leaf-litter C concentration	11.9	0.000	Plateau < slope = valley
Leaf-litter N concentration	29.6	0.000	Plateau = slope > valley
Leaf-litter C : N ratio	46.3	0.000	Plateau = slope < valley

SOM, soil organic matter; WHC, water-holding capacity.

litter production on the plateau ($8.9\,t\,ha^{-1}$) was significantly higher ($P<0.01$) than in the valley ($6.6\,t\,ha^{-1}$). A greater proportion of leaf litter (81%) was measured in the plots located on the slopes, compared to 78% in the plateau and 74% in the valley plots. On the other hand, more woody material (17%) was found in the valley plots than in both plateau (15%) and slope (13%); the differences between valley and slope plots were significant ($P<0.05$) (Table 2).

The concentrations of C in the leaf litterfall were significantly lower ($P<0.001$) on the plateau (45%) (Table 2) than in the valley and slope plots (ca. 47%) and N concentrations varied substantially, ranging from 1.09% in the valley to 1.44% at the plateau (Fig. 3, Table 2).

Thus, the valley plots showed significantly higher C:N ratio (43.3) in litterfall ($P<0.001$) than in the plateau (C:N = 31.8) and slope plots (33.6). Nitrogen retranslocation rates, calculated as the ratio of N concentrations in leaves collected from living trees by the concentrations in fresh leaf litter showed trends for higher values on the plateau (1.33) and on the slope (1.44) compared with the valley plots (1.22), but they were not statistically significant.

Litter-layer and turnover quotient (k_L)

The greatest density of litter in the litter-layer was found on the slope ($6.3\,t\,DW\,ha^{-1}$), and the smallest occurred in the valley floor ($5.4\,t\,DW\,ha^{-1}$), but values for plots within each topographic position were highly variable, and no significant differences were found among topographic positions (Tables 2 and 3).

The greatest turnover quotient (k_L) was found for the plateau forest (1.5), while the forest in slope and valley plots showed similar values (1.2), but the differences were not significant (Table 3).

Soil mineral nitrogen, net N mineralization and nitrification

Soil mineral nitrogen concentrations showed significant ($P<0.001$) differences along the topographic gradient for both $N\text{-}NH_4^+$ and $N\text{-}NO_3^-$ (Fig. 4). There were lower inorganic-N concentrations, especially $N\text{-}NO_3^-$, in the valley location when compared with the other locations, either on the plateau or on the slope (Table 2).

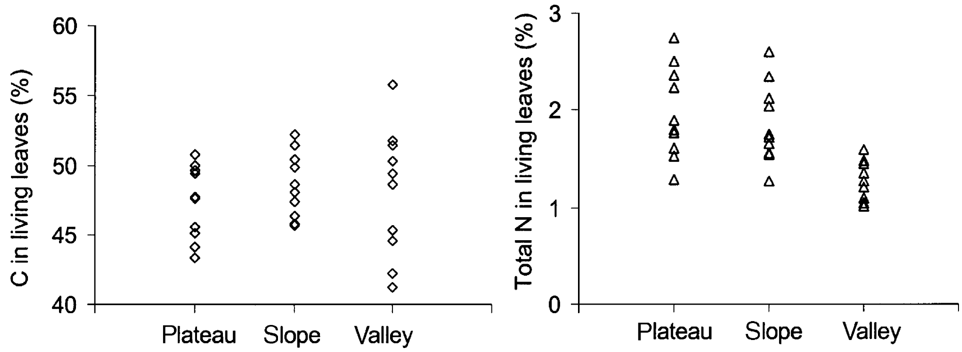

Fig. 2 Concentrations of C and total N in the living leaves in the three main positions of the topographic gradient on Cuieiras watershed.

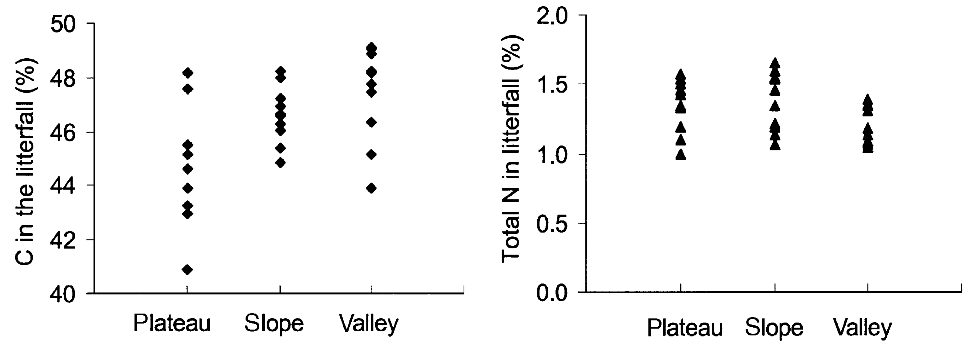

Fig. 3 Concentrations of C and total N in the leaf litterfall in the three main positions of the topographic gradient on Cuieiras watershed.

Net N mineralization in the dry season (October 2001) showed the same pattern observed for inorganic-N concentrations along the topographic gradient, with the same positive rate of net N mineralization on the plateau and slope locations, and negative values (net N immobilization) observed in the valley ($P<0.001$) (Fig. 5). In the rainy season, because of the high variability within each location, no significant differences were found among the topographic positions for net N mineralization.

Net nitrification in the dry season again showed the same trend with topography as shown for the inorganic-N concentrations, with higher rates of net nitrate production ($P<0.001$) on the plateau and slope locations than in the valley (Fig. 6), where available nitrogen was either in low supply or immobilized by the microbial population. During the rainy season, lack of available nitrate was even more drastic (Fig. 6), with negative values for net nitrification at all three locations of the topography.

Table 3 Annual litter production (t ha^{-1}), litter-layer mass on soil surface (t ha^{-1}) and turnover quotient (k_L) in the forest at the three topographic positions (plateau, slope and valley) in the Cuieiras areas

Topographic positions	Litter production (t ha^{-1} yr^{-1})	Litter-layer (t ha^{-1})	Turnover ratio (k_L)
Plateau	8.9a ± 1.9	6.0a ± 2.1	1.5a ± 0.14
Slope	7.6a ± 0.5	6.3a ± 2.0	1.2a ± 0.14
Valley	6.6b ± 0.8	5.4a ± 2.1	1.2a ± 0.08

Value are means and standard deviations. Means within a column followed by the same letter are not significantly different from each other (Tukey's test, $P=0.05$).

Discussion

Soil organic C and total N concentrations were higher in the first soil layers, decreasing with depth, a well-known characteristic of these soils (Chauvel *et al.*, 1987). Higher concentrations of total N in the upper soil layers are associated with greater biological activity and consequently a higher intensity of the mineralization processes. The mean values were similar for the plateau and slope plots, but both were significantly greater than

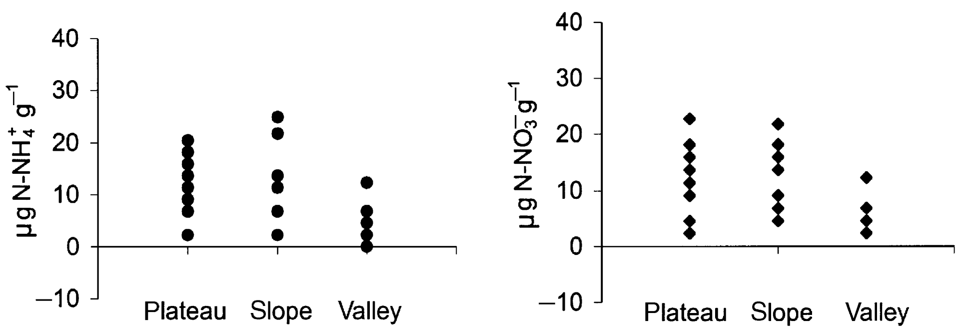

Fig. 4 Soil N mineral concentrations (N-NH$_4^+$ and N-NO$_3^-$) in the three main positions of the topographic gradient on Cuieiras watershed.

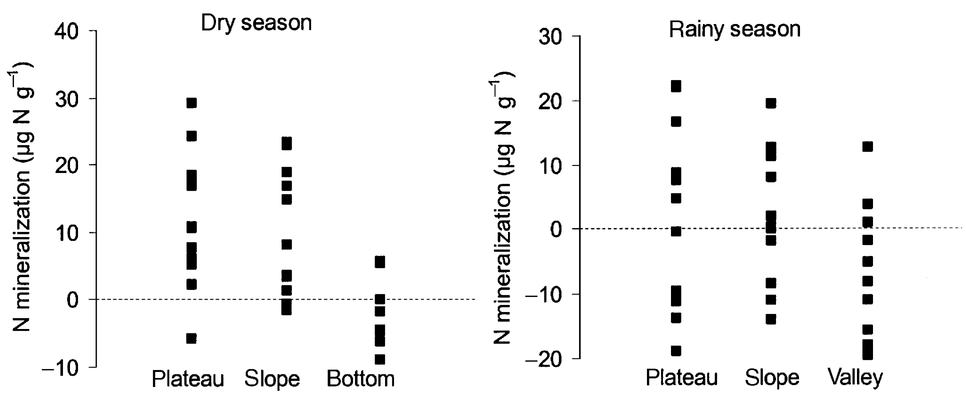

Fig. 5 Net nitrogen mineralization during the 10 days incubation of topsoil (0–10 cm) collected in the dry season (October 2001) and the rainy season (April 2002) in the three main positions of the topographic gradient on Cuieiras watershed.

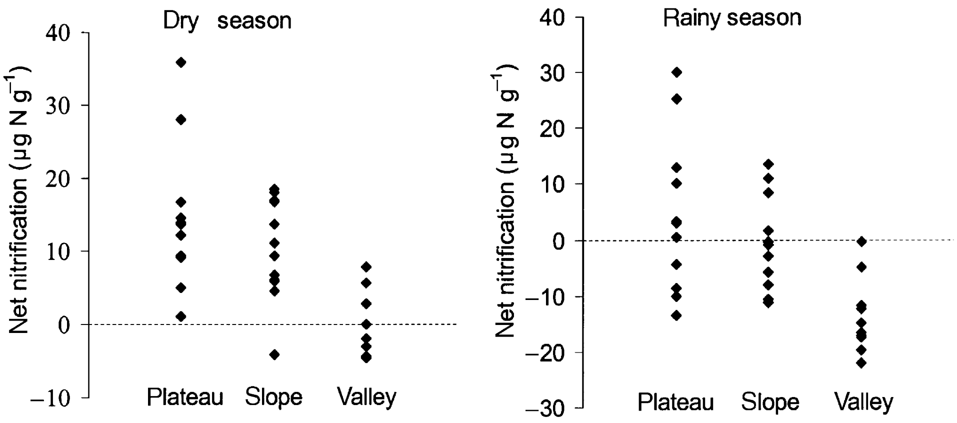

Fig. 6 Net nitrification during the 10 days incubation of topsoil (0–10 cm) collected in the dry season (October 2001) and the rainy season (April 2002) in the three positions of the topographic gradient on Cueiras watershed.

in the valley, where markedly higher C:N ratio occurred. The decrease in total N concentrations seemed to follow the clay content in the topographic gradient, with higher concentrations in the clayey Oxisol and much lower for the sandy Podzol.

The lower N concentrations in living mature leaves of trees in the valley-plots is striking, since the number of Leguminous trees (five trees out of 20) sampled in those plots was similar to the plateau plots. As the C concentrations did not vary significantly along the topographic gradient, the lower N concentration resulted in a significantly higher C:N ratio in the leaves of the valley plots. C:N ratio has been widely used as an index of the quality of organic material: plant tissue is considered of high quality, and thus favourable for decomposers, when C:N <25, and of low quality when C:N>25; in the latter, the decomposition process is slower (Myers *et al.*, 1995). In the present study, C:N ratios indicated that canopy leaves from the valley forest have low quality, suggesting that decomposition rates might be lower than in the plateau and slope. The consequence of this should be a denser litter-layer deposited on the forest floor at valley plots, if no other factor would favour litter decomposition or removal.

The highest litterfall was measured in the plateau plots (8.9 t DW ha^{-1} yr^{-1}), which produced significantly more litter than the valley plots, agreeing with former results found in similar lowland evergreen forest nearby (Luizão, 1989). The lowest litterfall recorded at the valley plots is likely a consequence of the lower forest biomass (due to a lower density of large trees) and lower canopy cover at this location (Guillaumet, 1987). These vegetation characteristics may also explain the greatest variability in litterfall found in the valley. However, the annual litter production in both plateau and valley were higher than all previous measurements made in central Amazonia, and higher than that measured by Luizão (1989) in the period 1979–1982.

Adding the litterfall production in the plateau forest to the annual stand mass increment (6.4 t DW ha^{-1}, including 0.9 t DW ha^{-1} of damaged trees) measured by Chambers *et al.* (2001) from a nearby plot, the above-ground NPP of the forest would reach 15.3 t DW ha^{-1} yr^{-1} which is equivalent to 7.7 t C ha^{-1} yr^{-1}.

The high proportion of leaves in the composition of the total litterfall, in all topographic positions, only confirmed the results of other studies in Amazonia, showing that leaves are by far the main components of fine litterfall for tropical forest in this region (Luizão, 1989). That was true in the three topographic positions where no significant differences was found among them. The leaf litter generally decomposes quickly, thus resulting in fast and effective nutrient cycling in this tropical rainforest.

The greatest C:N ratio of litterfall was found in the valley (43.7), while a smaller ratio was recorded on the plateau (31.8). The C:N ratio of the litter-layer was also significantly higher (C:N = 45) in the valley than in the plateau and slope, which showed similar values (C:N = 34) (Table 2). Although high C:N ratios in both litterfall and litter-layers suggest slow decomposition in the valley, decomposition rates were not significantly lower as shown by the k_L that were similar for both valley and slope positions. These results indicate that there may be other reasons for lack of litter accumulation on forest floor valleys. One reason might be related with two particular conditions found in that topographic position: a very sandy soil and a very open canopy above it.

Those conditions should allow the direct impact of the rain drops on forest floor, perhaps causing leaching and the burial of the litter into the soil. Considering that sandy soils are more subject to leaching, carbon deposited on forest floor may be washed from the system by the occasional heavy rains. Higher amounts of dissolved carbon measured on the stream in the bottom of the valley after rain events (Adriana Cuartas Piñeda, personal communication) confirmed the occurrence of such process.

Net nitrification was still substantial when net mineralization was positive, with the 51% of mineralized N found as nitrate. However, there were also many negative values of net N mineralization and net nitrification, especially in the valley at both seasons and for all locations during the rainy season. This rate of recovered net nitrification is in the lower range reported for other forested sites in Amazonia (Livingston *et al*., 1988; Piccolo *et al*., 1994; Verchot *et al*., 1999). Lower available N supply found in the sandy plots of the valley was also found by Livingston *et al*. (1988) in the quartz sands of Reserva Ducke, some kilometers away from ZF-2. They related the lower potential for NO_3 production in the valley compared with the other topographic positions with increasing sand content at lower positions.

Conclusions

In this study, the apparently low rates of net N mineralization and net nitrification in valley locations was associated with decline of clay content (below 10%), one of the main changes in the topographic gradient. Similarly, the nitrogen concentrations in tree leaves of the valley were also low, further indicating low availability of N in this ecosystems.

The local topography (plateau, slope and valley) clearly was an influential factor in the nutrient distribution along the study locations. Both soil texture and seasonal flooding in the valley can influence the N availability for plants, which was found in lower concentrations in plant material and in soil.

In spite of lower N concentrations in upper soil layer, living canopy leaves, litterfall, litter-layer and lower nutritional quality of litter in the valley plots, no significant differences were found in either litter layer mass or litter turnover quotient (k_L). This might be an indication that other factors are acting in the valley plots to remove litter form soil surface. Among those, leaching of the litter layer (removing soluble compounds) and transport of litter material to the stream (by intense rainfall events and/or waterlogging) may play a major role.

Results in this study showed the textural gradient along the topography can be an important source of variation for nitrogen dynamics. Several indicators of N availability, including litterfall, which is a major component of NPP varied significantly across the topographic gradient, with lower rates of N cycling and litterfall in seasonally inundated sandy soils in the valley bottoms.

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