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Increased litterfall changes fine root distribution in a moist tropical forest

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Abstract

Root proliferation into the Oa and Oe soil horizons in tropical forests is often substantial and allows direct cycling of nutrients from the organic matter; this was thought to be an adaptation to the low nutrient supply in infertile soils. In this study, we show that experimentally increased litter inputs promote root proliferation into the Oi and Oe horizons in a relatively fertile soil, suggesting that it is a response to a more readily available nutrient source rather than an adaptation to nutrient shortage, and the absence of root mats on fertile tropical soils is simply a consequence of the lack of persistent organic horizons due to high decomposition rates.

Introduction

Tree roots often proliferate in the organic layers of the forest floor to obtain nutrients directly as they are mineralized (Jordan, 1985; Richards, 1996), this "direct cycling" of nutrients from organic matter via superficial roots and mycorrhizal hyphae can be seen as a nutrient conserving mechanism in infertile and highly leached soils (Herrera et al., 1978; Stark and Jordan, 1978; Stark and Spratt, 1977; St. John, 1982). Tropical forest soils are generally nutrient-poor (Jordan, 1985; Richards, 1996), nutrient cycling is tight (Vitousek, 1984) and the direct cycling of nutrients from organic matter therefore plays a major role in their nutrient budget (Herrera et al., 1978; Stark and Jordan, 1978). In some, but not all, tropical forests growing on infertile soils extensive root mats form in the humus (Oa) and fermentation (Oe) horizons (Chuyong et al., 2002; Coomes and Grubb, 1996; LaClau et al., 2004; Stark and Jordan, 1978; Stark and Spratt, 1977) and even where root mats are not formed, root proliferation into the organic layer is often substantial (Hertel et al., 2003). There exists evidence that roots colonise not only older decomposing organic matter but also freshly fallen leaves (Jordan and Escalante, 1980; Herrera et al., 1978), and in a site in Southern Venezuela it has been shown that root contact with fresh litter accelerates the decomposition process and the release of Ca and Mg from the litter (Cuevas and Medina, 1988). However, root proliferation into organic matter has only been studied in sites where decomposition is limited and a gradual build-up of organic matter on the soil surface over time has lead to the formation of distinct Oe and Oa horizons (Vogt et al., 1986) and root growth into the litter standing crop (Oi horizon; defined as partially decomposed litter that is still in fragments larger than *c.* 10 mm and still often identifiable to species) has been largely ignored, with the notable exception of Cuevas and Medina (1988). Comparative studies of root proliferation into organic matter layers have only been conducted in different forest types, forests on different soils, or in different successional stages. Within a particular forest, it is not known whether root foraging into the litter layer will change

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if litter inputs are changed. Litterfall in forests has been shown to increase as a consequence of elevated CO_2 (Allen et al., 2000; DeLucia et al., 1999; Finzi et al., 2001; Schlesinger and Lichter, 2001; Zak et al., 2003); increased litter production and the predicted decrease in litter quality (Berntson and Bazzaz, 1998; Hattenschwiler et al., 1999; King et al., 2001; Norby et al., 2001) may lead to a build-up of fresh organic matter on the soil surface, with consequences for fine root distribution, production and turnover.

Our study investigates the relationship between root biomass and aboveground litter inputs. We combined experimental litter manipulation treatments (addition and removal) with measurements of root biomass in the soil and in the litter layer to address the following questions: 1. Do increased leaf litter inputs promote fine root proliferation into the litter layer even on relatively fertile tropical soils? 2. Does a thicker litter layer increase overall fine root biomass? 3. Does increased root proliferation into the litter layer affect the vertical distribution of fine roots?

Methods

This study was carried out within an ongoing large-scale, long-term litter manipulation experiment located on the Gigante Peninsula of the Barro Colorado Nature Monument in Panama, Central America. Nearby Barro Colorado Island (*c*. 5 km from the study site) has a mean annual rainfall of 2600 mm with a strong dry season from around January to April and an average temperature of 27 °C (Leigh, 1999). The forest under study is old-growth seasonal moist tropical forest. The soil is an oxisol with pH *c*. 5.0, low 'available' P concentration, but high base saturation and cation exchange capacity (Cavalier, 1992).

Fifteen 45 m × 45 m plots were set up in 2000. The plots were trenched to a depth of 0.5 m to minimize nutrient- and water import via the root/mycorrhizal network, the trenches were double-lined with plastic and backfilled; a 7.5 m buffer was left around the inside of the trenches to eliminate trenching effects, resulting in a measurement plot size of 30 m × 30 m. Starting in January 2003, the litter in five plots was raked up once a month, resulting in low, but not entirely absent, litter standing crop (L− plots). The removed litter was immediately added to five further plots, where it was spread out as evenly as possible, effectively doubling the litterfall (L+ plots); five plots were left undisturbed as controls (CT plots).

In order to quantify root proliferation into the litter layer, the leaf litter was cleared from five randomly chosen areas of *c*. 0.5 m^2 in each of the 15 plots in September 2003. A 250 mm × 250 mm square of 1.2-mm fibreglass mesh was then placed on the soil surface in the centre of each of the cleared areas and the mesh anchored firmly to the soil surface using five corrosion-resistant hooks, one in each corner, and one in the centre. The locations of the screens were marked with PVC flags to ensure that they would not be disturbed, and the leaf litter was replaced in each area in the CT and L+ plots. The sites were left undisturbed for one year to allow growth of roots through the screens.

The screens were collected in September 2004. The first four screens per plot were collected by clearing enough loose litter to expose one corner of the mesh, and removing the anchoring hook. Roots growing through the screen were severed at the soil surface with a long, sharp knife as the mesh was carefully lifted to avoid roots being pulled out of the mesh during collection. Loose leaf litter was removed from the top of the screens, and the screen, along with debris attached to the mesh by roots, was sealed in a polythene bag. In order to obtain measurements of root biomass in the litter above the screens, the fifth screen in each plot was collected by placing a wire frame of the same dimensions over the edges of the mesh and cutting around the edges of the frame before carefully severing the roots at the soil surface and sealing the screen with all the covering litter in a polythene bag.

The number of fine roots growing through each of the five screens per plot was counted. Roots growing horizontally through the screen and passing through it several times were counted only once and removed to avoid confusion. Once all the counts had been completed, the litter collected above the fifth screen was cut away and the fine roots picked out of the debris using forceps. Almost all roots growing through the screens were fine roots (< 2 mm diameter) and were therefore not divided into size classes. The

roots were washed and dried to constant weight in the oven at 70 °C to obtain dry fine root biomass in the litter layer above each screen.

Litter standing crop depth was measured from the mineral soil surface to the surface of the litter layer to the nearest 5 mm at 10 randomly chosen locations in each of the CT and L+ plots.

In order to determine the root biomass in the soil, ten 51-mm diameter soil cores were taken in each plot from 0 to 100 mm depth in June and July 2004 using a soil split-corer with slide-hammer attachment (AMS Inc., American Falls, USA). Each soil core was cut into two equal segments, giving nominal sampling depths of 0–50 mm and 50–100 mm. In the lab, live roots (and those recently dead but indistinguishable from live roots) were separated from the soil by first soaking the soil cores in water and then sieving away the soil under a continuous stream of water using a fine-mesh (0.5 mm) sieve. The washed roots were sorted into fine roots (<2 mm), small roots (2–5 mm), and coarse roots (>5 mm). The coarse roots were discarded as large roots had been avoided during coring and the samples would not have been representative. All other roots were dried to constant weight at 70 °C to obtain dry fine root biomass for both sampling depths. Total root biomass henceforth refers to the biomass of all roots with a diameter of ≤ 5 mm and all root biomass values are given as grams dry weight per m^2.

The gravimetric water content of the litter layer was determined from 10 samples of the litter standing crop in each of the CT and L+ plots. Gravimetric soil water content was measured one month before, during, and after root sampling by taking four soil cores per plot using a 20-mm diameter punch-corer.

Soil bulk density from 0 to 150 mm depth was measured in February 2005 by taking two cores per plot using lubricated stainless steel sleeves (98-mm inner diameter) in a drop-hammer soil corer to minimize soil compaction. Soil bulk density was determined separately for five 30-mm sections of each core and given as dry weight per volume.

Analyses

In order to test whether the number of roots growing through the mesh (ingrowth counts) could be used to estimate root biomass in the litter layer, the relationship between ingrowth counts and biomass of roots in the litter above the screens was examined by linear regression, as was the relationship between the depth and water content of the litter standing crop and root biomass in the litter layer. The L− plots were excluded from these analyses because there was no measurable litter standing crop.

As all data were approximately normally distributed, differences between litter treatments in ingrowth counts, root biomass in the soil, root biomass in the litter layer, soil water content, litter water content, and soil bulk density were analysed by one-way ANOVAs; comparisons between the controls and each of the treatments (CT vs. L+, CT vs. L−) were analysed by independent sample *t*-tests. Percentage data of vertical root distribution were arc-sine transformed prior to analysis.

The relationship between root biomass in the litter and root biomass in the soil was analysed using the Pearson correlation. SPSS 11.0.2 for Mac (SPSS Inc. Chicago, USA) was used for all analyses.

Results

The counts of roots penetrating the mesh screens gave a good estimate of root biomass in the litter layer; root biomass was strongly related to the number of roots growing through the screens ($R = 0.78$, $P = 0.001$, Pearson correlation). In the litter layer, root biomass in the L+ plots was 20.2 g/m^2, which was significantly higher than the 5.7 g/m^2 in the CT plots ($P = 0.016$, *t*-test; Figure 1.). The mean number of roots passing through the mesh was higher in the L+ plots (123) than in the CT plots (95); but this difference was only marginally significant ($P = 0.07$, *t*-test). Roots penetrating the mesh in the L− plots (mean count = 15) were growing into soil that had been deposited on the mesh by surface runoff and root biomass above the screens was negligible (<0.005 g per sample).

In the mineral soil, fine root biomass from 0 to 100 mm depth in the L+ treatment averaged 135 g/m^2 and was lower than in the control with 214 g/m^2 ($P < 0.01$, *t*-test); fine root biomass in the L− plots (173 g/m^2) did not differ significantly

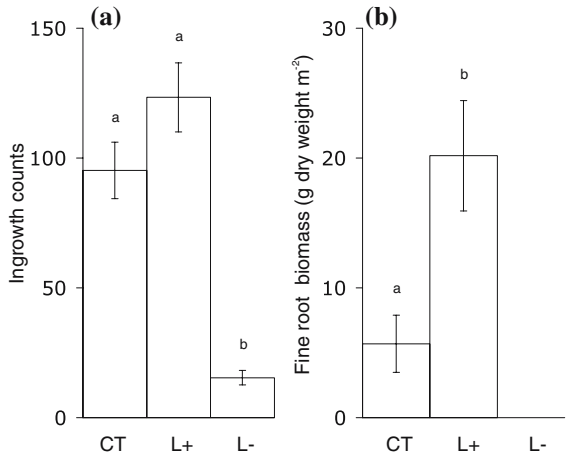

Figure 1. (a) The number of roots growing through mesh screens (ingrowth counts) and (b) the fine root biomass in the litter layer above the screens in litter manipulation plots in moist tropical forest in Panama, Central America: CT = control, L+ = litter addition, L− = litter removal; error bars are standard errors of means; treatments with different letters are significantly different at $P < 0.05$.

from the controls. The lower fine root biomass in the L+ plots was apparent at both sampling depths (Figure 2.) but the difference relative to controls was greatest at 50–100 mm depth (0–50 mm: $P = 0.022$; 50–100 mm: $P = 0.014$, *t*-tests). Small root (2–5 mm) biomass did not differ between treatments at either depth.

The vertical distribution of fine roots differed between treatments (Figure 3.). Compared to the controls, the L+ plots had a higher percentage of fine roots in the litter layer ($P < 0.01$, *t*-test) and a significantly lower percentage of fine roots at 50–100 mm depth in the mineral soil ($P = 0.049$, *t*-test).

Mean LSC depth in the L+ plots (34 mm) was greater than in the CT plots (14 mm; $P = 0.044$, *t*-test). Root biomass in the litter layer in the CT and L+ plots was strongly related to LSC depth ($R^2 = 0.69$, $P = 0.003$, linear regression; Figure 4.). Root biomass in the litter layer did not differ between treatments when calculated per volume of litter rather than per area.

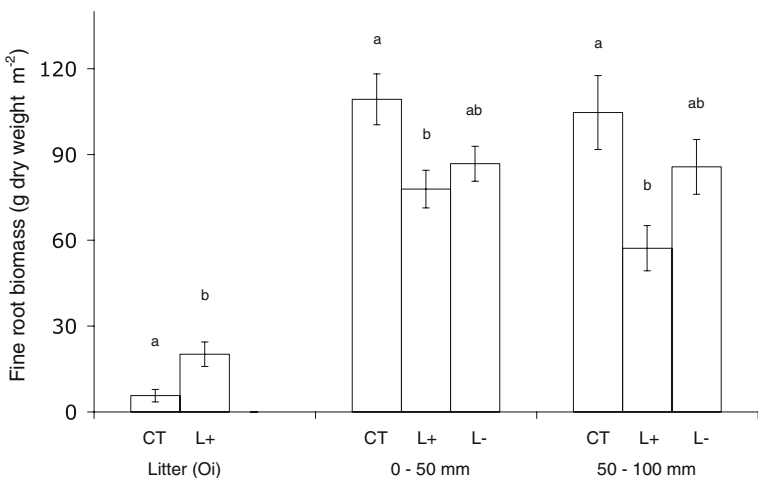

Figure 2. The root biomass in the litter layer and in the mineral soil at 0–50 mm and 50–100 mm depth in litter manipulation plots in moist tropical forest in Panama, Central America: CT = control, L+ = litter addition, L− = litter removal; error bars are standard errors of means; within horizons, treatments with different letters are significantly different at $P < 0.05$.

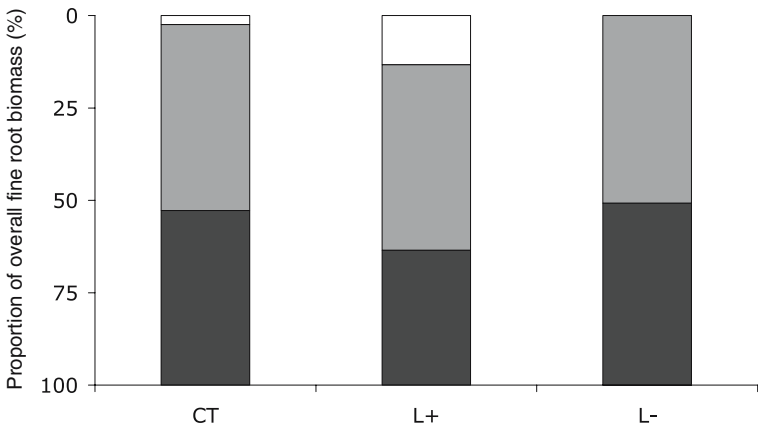

Figure 3. The vertical distribution of roots as a percentage of the overall root biomass in litter manipulation plots in moist tropical forest in Panama, Central America; CT = control, L+ = litter addition, L− = litter removal; white = litter layer, light grey = mineral soil from 0–50 mm depth, dark grey = mineral soil from 50–100 mm depth.

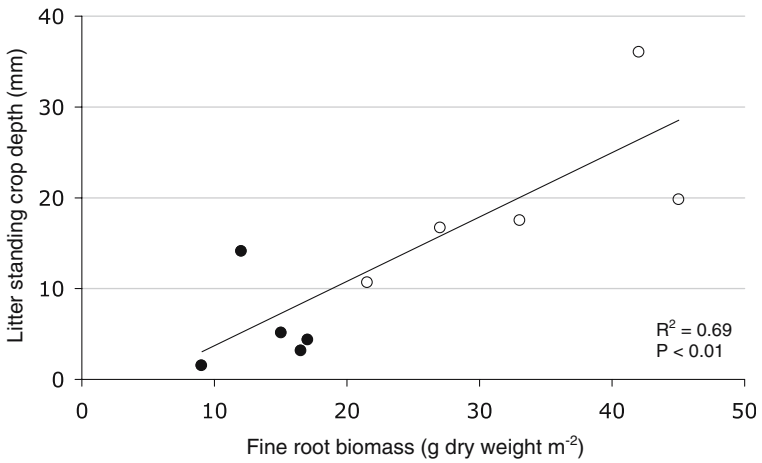

Figure 4. Relationship between the mean depth of the litter standing crop (LSC) and Oi fine root biomass in litter manipulation plots in moist tropical forest in Panama, Central America; closed circles = control plots, open circles = litter addition plots.

Higher root biomass in the litter was related to lower fine root biomass in the soil at 50–100 mm depth ($R = -0.47$, $P = 0.038$, Pearson correlation), but not at 0–50 mm depth.

The total biomass of small and fine (< 5 mm) roots in the soil and litter layer together (overall root biomass) was significantly lower in L+ plots than in the controls ($P = 0.013$, *t*-test; Table 1), as was the biomass of fine (< 2 mm) roots ($P = 0.019$, *t*-test). Overall root biomass in the L− plots did not differ from the controls.

There were no differences between treatments in soil or litter water content. During the study period, soil water content from 0–100 mm depth ranged from 30–35%, and litter water content from 29–40%. Root biomass in the litter layer was not related to litter water content.

Soil bulk density from 0–150 mm was *c*. 1.0 g/cm^3 and did not differ between treatments. However, bulk density from 0–30 mm was higher in the L− plots (1.1 g/cm^3) than in the CT or L+ plots (0.7 g/cm^3; $P = 0.016$, ANOVA).

Discussion

The differences in root biomass between litter manipulation treatments demonstrate that the

Table 1. Overall small- and fine root biomass in the litter and soil surface layers (0–100 mm) in litter manipulation plots in moist tropical forest in Panama, Central America, given as g dry weight m^{-2}: CT = control, L+ = litter addition, L− = litter removal. Standard errors for $n = 5$ plots per treatment are given in parentheses

	Root diameter class		
	< 2 mm	2–5 mm	all < 5 mm
CT	219 (±18)	97 (±10)	316 (±22)
L+	155 (±13)*	73 (±10)	228 (±17)*
L−	173 (±14)**	94 (±16)	267 (±27)

*Differs significantly from the controls at $P < 0.05$.
**Differs from the controls at $P < 0.1$.

quantity of leaf litter on the soil surface affects the foraging behaviour of fine roots. Root mats are generally formed on tropical forest soils with a clearly defined Oa horizon (Vogt et al., 1983); the thick organic layers (Oe and Oa horizons) that have accumulated in some late successional forests are also known to contain higher fine root biomass per area than the mineral soil both in the tropics (Hertel et al., 2003) and in the temperate zone (Berendse et al., 1989; Coomes and Grubb, 2000; Fahey and Hughes, 1994). In addition to the concentration of fine root growth into old established Oe and Oa layers, we have shown that roots also respond rapidly to relatively recent increases in fresh leaf litter.

Litterfall and fine root growth in the forest under study are highly seasonal (Cavalier, 1992; Yavitt and Wright, 2001). Leaf fall peaks during the dry season, and the lack of moisture impedes the breakdown of the litter during this period. The accumulated litter starts to decompose with the first heavy rains, and by the end of the rainy season most of the litter has disappeared (Wieder and Wright, 1995). Fine root production in the soil is also seasonal; root production is greatest at the beginning of the rainy season and remains high during the first half of the rainy season, but declines towards the beginning of the dry season (Yavitt and Wright, 2001). Although fine root growth during the dry season is mainly water-limited, it is worthy of note that fine root production during the rainy season closely follows the pattern of litter decomposition, suggesting a strong relationship between nutrient release during litter decay and fine root growth. Our study took place in the mid rainy season during the period of rapid root growth.

The total fine root biomass in the forest under study is similar to that found on the very fertile soils at La Selva in Costa Rica and lower than that on the infertile soils at La Selva (Gower, 1987) – suggesting that the soil on the Gigante peninsula at BCNM is fertile. Compared to soils collected in lowland tropical forests in Bolivia, Ecuador, and Peru (43 soils from 13 sites all analysed in the same lab), the surface soils in the study site are around the mean for total nitrogen, have low concentrations of available (Bray's) phosphorus, and high concentrations of exchangeable calcium, magnesium, and potassium (O. Phillips, J. Lloyd, S. Lewis, pers. comm.). The nitrogen, phosphorus and calcium contents of the leaf litter in our site (143 kg ha^{-1} yr^{-1}, 6 kg ha^{-1} yr^{-1} and 139 kg ha^{-1} yr^{-1}, respectively) are among the highest for lowland tropical forests with similar annual precipitation (Vitousek, 1984), which suggests that plants in this forest are not limited by nitrogen, phosphorus, potassium, calcium, or magnesium.

Despite the relatively fertile soil, greater amounts of leaf litter on the soil surface increased root proliferation into the Oi and Oe horizons in the L+ plots. The soil and litter water contents were favourable to root growth in all treatments and did not explain the differences in fine root biomass. The lower overall root biomass in the L+ plots suggests that nutrient uptake has been improved by increased root biomass in the litter layer and the necessary nutrients for growth can be obtained with a lower net investment in root production, as lower root biomass is often associated with greater nutrient availability (Coomes and Grubb, 2000; Jordan, 1985; Vitousek and Sanford, 1986). These findings suggest that root proliferation into organic horizons occurs in response to the more easily obtainable nutrients in organic matter, rather than as an adaptation to low soil fertility and

thus that root proliferation into organic matter will occur on any site regardless of soil fertility provided there is a persistent organic layer and sufficient moisture. We suggest that the lack of extensive root mats in fertile sites is due to the absence of thick organic horizons as a consequence of high decomposition rates (Vogt et al., 1983), and not necessarily a result of higher soil nutrient availability, as has been previously hypothesized (Berish, 1982; Herrera et al., 1978; Jordan, 1985; Klinge and Herrera, 1978). Our suggestion is supported by calculations of root biomass per volume of organic matter rather than per area; in our study root density per volume of litter did not differ between treatments. Similarly, Hertel et al. (2003) found that fine root biomass was 4–6.5 times higher in the organic horizons in old-growth montane forest compared to early successional forest, but the volume of the organic layer in the old-growth forest was also 5 times greater on average.

Our findings that only fine root biomass differed significantly between treatments are in agreement with Fitter's (1994) observations that increased production of roots of small diameter in response to patches of increased soil fertility minimizes the potential cost of foraging in a possibly unprofitable or short-lived nutrient source. The difference between the CT and L+ plots in fine root biomass in the litter layer was much greater than the difference in the number of ingrowth counts (Figure 1.), thus it appears that fine roots foraged vertically into the litter layer to a similar extent in both treatments, but the greater nutrient availability in the litter layer of the L+ plots greatly enhanced fine root ramification and proliferation (Persson, 1980); this response of root growth to high-nutrient patches is well-known for mineral soil (e.g. Fitter, 1994; Robinson, 1994).

Increased root biomass in response to a source of nutrients is usually compensated by lower fine root biomass elsewhere in the soil (Fitter, 1994); in our study, increased root proliferation into the litter layer was associated with a decrease in fine root biomass at 50–100 mm depth in the soil. A more superficial distribution of fine roots in response to increased litter inputs will maximise nutrient uptake; root proliferation into the litter layer allows the direct uptake of the bulk of nutrients from the decaying organic matter (Richards, 1996; Stark and Jordan, 1978), fine roots in the soil surface layers intercept any potential losses due to leaching from the litter, and fine roots deeper in the soil are therefore more expendable. However, fine roots are also very sensitive to changes in moisture levels (Persson, 1980) and a strongly superficial root distribution may cause increased fine root mortality during dry periods (Joslin and Henderson, 1987) and strongly affect the forest carbon cycle (Fahey and Hughes, 1994). It is very likely that the majority of fine roots in the litter die during the dry season and as the production of new fine roots is costly in terms of carbon, the acquisition of nutrients from the litter layer needs to be sufficiently high to justify the carbon lost by high root mortality during dry periods, otherwise increased root proliferation in the litter layer in the L+ plots may become a disadvantage over the long term.

As low soil fertility generally leads to increased belowground allocation of plant resources (Gower, 1987; Haynes and Gower, 1995; Jordan, 1985), fine root biomass was expected to increase with nutrient depletion following litter removal; it therefore appears that 18 months of litter removal has not depleted soil nutrients to the extent that would elicit a below-ground growth response from the vegetation. The slightly lower root biomass in the upper 50 mm of the soil in the L− plots (Figure 2.) may be attributed to compaction in the superficial soil layers as a result of trampling and raindrop impact in the absence of a protective cover of leaves, as evidenced by the higher bulk density in the upper 30 mm of the mineral soil.

The surface-root ingrowth technique (SRIT) employed in this study proved a reliable method for estimating the fine root biomass in the litter layer in the tropical forest under study. Horizontally installed screens have previously been used to determine root biomass in the litter layer by severing all roots growing through the screens at the soil surface and weighing them (Jordan and Escalante, 1980); in our study, the positive correlation between the counts of roots growing through the mesh and the root biomass in the litter above the mesh shows that reasonably reliable comparative values can be obtained by simply counting the number of roots passing through the mesh, which is less time-consuming; this allows greater sample sizes and therefore

a more representative plot mean. A similar technique was used to estimate fine root production and turnover in the forest floor by mapping roots growing through screens *in situ* over a period of several months (Fahey and Hughes, 1994), and the results compared favourably with data from minirhizotron measurements (Tierney and Fahey, 2001). Although the depth of the litter layer and the formation of root mats limit the use of *in situ* mapping in tropical forests, direct estimates of root production and turnover in the litter layer can be made using the SRIT technique if screens are sequentially collected at different time intervals.

Thus, from this study, we can conclude that root proliferation into leaf litter is related to the depth of the litter standing crop and is probably driven by greater nutrient availability in the litter rather than low soil nutrient concentration. Increased leaf litter inputs promoted the proliferation of fine roots into the litter layer, resulting in a more superficial fine root distribution and lower overall fine root biomass. Thus root proliferation in litter layers is a response to nutrient availability in the litter rather than due to the lack of nutrients in the soil.

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