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Fine root dynamics for forests on contrasting soils in the colombian Amazon

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Abstract

It has been hypothesized that in a gradient of increase of soil resources carbon allocated to belowground production (fine roots) decreases. To evaluate this hypothesis, we measured the mass and production of fine roots (<2 mm) by two methods: 1) ingrowth cores and, 2) sequential soil coring, during 2.2 years in two lowland forests with different soils in the colombian Amazon. Differences of soil resources were determined by the type and physical and chemical properties of soil: a forest on loamy soil (Ultisol) at the Amacayacu National Natural Park and, the other on white sands (Spodosol) at the Zafire Biological Station, located in the Forest Reservation of the Calderón River. We found that mass and production of fine roots was significantly different between soil depths (0–10 and 10–20 cm) and also between forests. White-sand forest allocated more carbon to fine roots than the clayey forest; the production in white-sand forest was twice (2.98 and 3.33 Mg C ha^{-1} year^{-1}, method 1 and 2, respectively) as much as in clayey forest (1.51 and 1.36–1.03 Mg C ha^{-1} year^{-1}, method 1 and 2, respectively); similarly, the average of fine root mass was higher in the white-sand forest (10.94 Mg C ha^{-1}) than in the forest on clay soils (3.04–3.64 Mg C ha^{-1}). The mass of fine roots also showed a temporal variation related to rainfall, such that production of fine roots decreased substantially in the dry period of the year 2005. Our results suggest that soil resources play an important role in patterns of carbon allocation in these forests; carbon allocated to above-and belowground organs is different between forest types, in such a way that a trade-off above/belowground seems to exist; as a result, it is probable that there are not differences in total net primary productivity between these two forests: does belowground offset lower aboveground production in poorer soils?

1 Introduction

Tropical forests play a central role in the global carbon cycle (Dixon et al., 1994; Vogt et al., 1996) due to their potential to reduce atmospheric levels of CO_2 through its capture

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by photosynthesis (Dixon et al., 1994; Vogt et al., 1996; Brown, 2002). A lot of effort has been dedicated in last years to study net primary productivity (NPP) because its tremendous importance as a product of forest metabolism and its role in the global carbon cycle (Clark et al., 2001a).

However, understanding NPP in many ecosystems, tropical included, is still poor due to the scarcity of information on several of its components, mainly in the belowground portion. Fine root dynamics is not usually measured despite its importance for carbon economy and functioning of the ecosystem; in the few studies that this variable has been evaluated technical limitations of the methods used have complicated the comparisons (Clark et al., 2001a, b; Hendricks et al., 2006; Vogt et al., 1996).

It has become common that global-scale models of NPP consider only the aboveground components, mainly because they can be observed from satellites (Goward et al., 1993). However, not including the belowground portion of NPP could produce significant biases in the quantification of carbon fluxes in ecosystems (Woodward and Osborne, 2000). Despite this lack of information, it has been estimated that about 33% of annual global NPP is used to produce fine roots (Jackson et al., 1997).

Fine root dynamics can contribute significantly to the ecosystem-scale biogeochemical cycling, which is particularly important in tropical forests, where biomass and rates of production and decomposition of fine roots are high (Silver et al., 2005). The apparent paradox of the exuberance and large size of tropical humid forests growing on intensively leached soils, suggests that fine roots play an important role in optimizing nutrient acquisition and maintaining a close nutrient cycling in tropical rain forests (Gower, 1987). Additionally, the role of tropical forests as places to capture carbon and the relationship of this process to global climate change and plant growth has evidenced the necessity for more precise estimations of stocks and production rates of fine roots (Vogt et al., 1998), as well as their relationship with climatic variables.

The information on biomass and productivity of fine roots in tropical forests, and specifically in Amazonia, is scarce (Vogt et al., 1998; Clark et al., 2001b; Silver et al., 2005). This study contributes on carbon allocation to belowground productivity

(fine roots ≤2 mm) in two forests of *Terra firme* developing on contrasting soils in the colombian Amazon. In particular, we aimed to answer the following questions: "How different are the mass and production of fine roots between these forest types? How is the variation of these variables with soil depth (0–10 and 10–20 cm) in each forest

5   and between them? Is there any temporal variation in fine roots mass? And if so, is it related to rainfall? Due to during the period of data collection in 2005 occurred a strong dry period, we added one more question: did the drought of 2005 affect the production of fine roots?". To answer these questions, we estimated the mass, production, and relative growth rates of fine roots.

10   Hendricks et al. (1993) summarize two contrasting hypotheses proposed to explain the control of soil resources on carbon allocation and NPP. The first one, is called the "differential allocation hypothesis", and states that total NPP increases with the increase in the availability of resources, and that allocation between above- and below-ground components is differential, with a higher allocation to foliage and wood than to

15   fine roots in richer sites (Gower et al., 1992; Albaugh et al., 1998). The other hypothesis is the "constant allocation hypothesis", also proposes an increase in total NPP with the increase in the availability of soil resources, but the allocation of NPP to above-and belowground organs remains relatively constant (Aber et al., 1985; Nadelhoffer et al., 1985; Raich and Nadelhoffer, 1989).

20   Other hypotheses have been proposed to explain the effect of soil nutrient availability on biomass and production of fine roots (Grier et al., 1981; Keyes and Grier, 1981; Vogt et al., 1983, 1985). For example, Gower (1987) proposed that fine root biomass is controlled by the most limiting mineral nutrient in the forest ecosystem. Alternative hypotheses have considered not only soil nutrients, but also the role of soil texture,

25   which is a good indicator of several soil conditions that can influence root growth, such as nutrient and water availability, and soil aeration (Cuevas and Medina, 1986; Silver et al., 2000).

This study is orientated by the differential allocation hypothesis, which has been one of the most accepted for tropical forests (Albaugh et al., 1998; Gower et al., 1992;

Keyes and Grier, 1981). In consequence, we predict a decrease of mass and production of fine roots with the increase of soil resources (review in Hendricks et al., 1993). Soils were an Ultisol with clayey texture and greater nutrient content than a sandy Spodosol with lower nutrient content (Table 1). We also predict that the pattern of fine root production is opposite to the results of wood production of Malhi et al. (2004), who found a positive relationship between wood productivity and soil fertility in the Amazonian basin.

2   Material and methods

2.1   Study sites

This Study was carried out in two types of *Terra firme* forest in the colombian Amazon, located in the department of Amazonas (*Trapecio Amazónico*, Leticia) (Fig. 1). One sampling was done in two 1-ha permanent plots named AME and AMU located in a forest on well-drained Ultisols with clayey texture (Table 1) from the Amacayacu Natural National Park (Rudas and Prieto, 2005), at 3°43′10.5″ S and 70°18′25.8″ W, and, 3°43′20.2″ S and 70°18′25.8″ W, respectively and elevations between 90 and 115 m a.s.l. The other sampling was done in 1-ha permanent plot named ZAB located in a forest on a white-sand soil from the Zafire Biological Station, located in the Forest Preserve of the Calderón river, at 4°0′20.9″ S and 69°53′55.2″ W, and an elevation of 80 m a.s.l.

AME and AMU belong to the geologic unit named *Pebas* or *Solimoes* Formation; the terrain is slightly undulated and uniform, with soils moderately deep, well drained, and strongly acidic with texture moderately fine (Herrera, 1997). Soils from ZAB belong to the *Terciario Superior Amazónico* unit (Herrera, 1997; PRORADAM, 1979), probably originated from the Guiana Shield (Hoorn, 1994, 2006), and composed mainly by quartz. The terrain is flat and uniform, with a hard-pan at 90–100 cm depth (Quesada et al., 2008).

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This region shows a mean monthly rainfall of 277.9 mm with a drier period from June to September (mean monthly rainfall of 189.8 mm), and a rainy season from October to May (mean monthly rainfall of 323.9 mm) (data from the Vásquez Cobo airport of Leticia for the period 1973–2006). Mean temperature is about 26°C and does not fluctuate significantly along year (Fig. 2). Relative humidity is high, with a yearly average of 86%.

In 2005, in the middle of the sampling, a strong drought period occurred from June to September. The annual rainfall in 2005 was 2873.2 mm, substantially lower than previous and posterior years (3249.7 in 2004 and 3710.1 in 2006), and than the multi-annual average (3334.8 mm).

2.2 Fine root mass and production

To study the seasonal variation of fine root mass (FRM) (diameter≤2 mm) and to estimate the production (FRP) in the 0–20 cm soil depth, we used two of the three most used direct methods (Vogt et al., 1989, 1998): 1) Ingrowth cores, and 2) Sequential soil coring.

2.2.1 Ingrowth cores method

We selected 13 areas for sampling of fine roots approximately 40 m apart of each other along each plot of the clayey forest (AME and AMU) and 14 areas in the white-sand forest (ZAB). Ingrowth cores were established in three dates: 1) February 2004, 2) September 2004, and 3) February 2006; we did not establish cores in ZAB in the first date. Ingrowth cores were located at a distance of about 1–2 m from large trees (Diameter>10 cm) to avoid biases produced by high root concentration next to trees; cores were also 0.20–1 m apart of each other.

In plots of clayey forests, soil cores were extracted with a root auger 8 cm-diameter and 20 cm-length; in the white-sand plot we used a soil core sampler 5 cm-diameter and 15 cm-length. Samples were divided into two depths, 0–10 cm and 10–20 cm.

To prepare soil samples for the study of ingrowth cores, each core was sieved twice (through 6 and 1 mm mesh size, respectively), and then roots and fragments were extracted by hand with forceps. Finally, this root-free soil was sown in the same hole and depth level of the original sample.

In total we collected 105 and 80 cores from AME and AMU, respectively, during the sampling period for the establishment date 1; for the establishment date 2 we collected 63 and 59 cores, respectively, and for the establishment 3 we harvested 39 cores only in AME. In the white-sand forest we collected 136 and 39 cores for the establishments 2 and 3, respectively.

In all cases, the first collection of ingrowth cores was done 5–7 months after establishment; subsequent collections were done at 2–4 month intervals. Selection of the time interval for the first collection was based on reports of mean life of fine roots for several tropical forests, which ranges from 6 to 12 months (Priess et al., 1999); previous samplings showed that starting collection after a shorter period is too early to allow root growth into the root-free soil cores.

Soil cores were packed in previously labelled polyethylene bags and received a preliminary washing and sorting in the streams of each place. Then, samples were air-dried until transportation to the lab, where they were washed with deionised water and received a final sieving (mesh size 0.1 mm), and manual extraction of remaining material with forceps. Roots were packed in paper bags and oven-dried for 24 h at 80°C, and then weighed (0.001 g precision).

2.2.2 Sequential soil coring method

In the same areas described previously for sampling of ingrowth cores in each plot, we did a first collection of undisturbed cores six months after the initiation of the ingrowth study; subsequent collections were carried out every 2–4 months. Monitoring interval was from September 2004 to December 2006 in AME and ZAB and, from September 2004 to July 2006 in AMU. We collected 110 and 82 soil cores during the monitoring period in AME and AMU, respectively and, 233 cores in ZAB. Handling and

processing of samples was the same as described above for ingrowth cores.

2.3 Statistical methods

We tested for differences between forest types, time and soil depths. Differences among groups were evaluated with one way ANOVA. Data were previously checked for normality of distributions with the Kolmogorov-Smirnov and Shapiro-Wilk tests and, for homogeneity of variances with the test of Levene (Dytham, 2003). When ANOVA was significant ($p<0.05$), we used the *post hoc* test of Tukey to compare means. When the requirements of ANOVA were not met, we used non-parametrical tests, such as the test of Kruskal-Wallis followed by the test U of Mann-Whitney between pairs of data until the differences of the entire group were evaluated. Statistical analyses were done with the software SPSS 11.5.0 (6 September 2002, LEAD Tecnologies, Inc.).

FRP ($Mg\,ha^{-1}\,yr^{-1}$) was calculated between the time of ingrowth core installation (time zero) and the subsequent 6–10 months, scaled to a yearly basis (Vogt et al., 1998). In this way, for the first establishment in clayey forest, calculation of yearly production was based on growth between February and December 2004; for the establishment 2, on growth between September 2004 and April 2005; and for the white-sand forest, on growth between September 2004 and July 2005; for the establishment 3 in both forest types, production was based on growth between February and December 2006.

To compare FRP in standard units between forests and time intervals, we calculated the relative growth rate (RGR), defined by Fogg (1967) and Kozlowski et al. (1991) as:

$$\text{RGR} = \frac{\ln W_1 - \ln W_0}{t} \tag{1}$$

Where, ln=natural logarithm; W_1 and W_0=final and initial dry weight of fine roots, respectively; t=time between two collections, in days.

Due to the occurrence of a strong drought period in the middle of our sampling in 2005 (Fig. 2), we tested its effect on root production through the comparison of

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RGR before (September–December 2004), during (April–July 2005), and after drought (September–December 2006). For the white-sand forest, we also analyzed the RGR in the time interval between the installation and the harvest 370 days later, and between measurements separated 89 days, with the purpose of having an estimate of RGR during drought, between July and September 2005.

Annual production of fine roots ($Mg\,ha^{-1}\,year^{-1}$) was also estimated from the data of sequential cores as the difference between maximum and minimum biomass measured in one year (Vogt et al., 1998). Due to length of monitoring was different between plots and with the purpose of analyzing the same time intervals for all plots, we selected two years (April 2005–2006 and December 2005–2006) for this analysis. The initial period, from September 2004 to April 2005 was not used for calculations because the sharp seasonality of FRM observed in clayey forests during this period could introduce biases in the estimations.

Turnover rate was calculated as the FRP divided into the average FRM for that year; carbon content in fine roots was assumed to be equal to 50% of dry mass (Silver et al., 2005).

To evaluate the association between FRM ($Mg\,ha^{-1}$) – from data of sequential cores – and mean daily rainfall ($mm\,day^{-1}$), we used the Spearman's correlation coefficient (r_s) (Dytham, 2003).

Several works have correlated the production and mass of fine roots with rainfall (Gower et al., 1992; Kavanagh and Kellman, 1992; Vogt et al., 1998; Yavitt and Wright, 2001). However, the speed of the response and its temporal scale is unknown. It is presumed that this response can be variable depending on soil conditions and rainfall regimes (Yavitt and Wright, 2001). For this reason, we explored a wide range of time intervals with respect to rainfall; therefore, we selected the average daily rainfall of last 7, 15, 30, 60, 90, 100, and 120 days until the sampling day. We also explored the existence of a lagged response of FRM to rainfall; for this purpose we considered the average daily rainfall for fixed time periods of 15, 30, 60, and 90 days with time lags of 7, 15, 30, 120, and 150 days from the sampling date.

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3 Results

3.1 Mass and production of fine roots from ingrowth cores

FRM in each collection date and soil depth (0–10, 10–20, and 0–20 cm) did not show significant differences ($p > 0.05$) between plots of clayey forest (AME and AMU). For this reason, these plots were considered as a unique site in subsequent analyses and were significantly different ($p < 0.05$) from the white-sand forest plot (ZAB).

Mass and production of fine roots were higher in the 0–10 cm than in the 0–20 cm soil depth for all the establishment dates and forests (Fig. 3 and Table 2). FRM in the clayey forest showed significant differences ($p < 0.05$) between soil depths (0–10 cm and 10–20 cm) in most collection times of each establishment date, with the exception of the collection of April 2005 for the second establishment. Similarly, in the forest on white sands, FRM showed significant differences between soil depths in many collection dates; differences between depths were not significant in the first collection dates after sowing; however, differences were consistent in both forest types.

Figures of FRP were higher in the forest on white sands than in the forest on clays in all depths and establishment dates (Table 2). Differences of FRP in the 0–20 cm layer were significant ($p < 0.05$) in the establishments 2 and 3; however, in the establishment 2, differences between forest types were not significant ($p > 0.05$) when were evaluated independently at each soil depth (0–10 cm and 10–20 cm); in the establishment 3, we found significant differences ($p < 0.05$) of FRP between forest types at all soil depths. Results for FRM had similar trends: in establishments 2 and 3 showed significant differences ($p < 0.05$) between the two forest types at each soil depth in most dates of collection, except for the establishment 2 in April 2005, in which differences were not significant between sites at any soil depth, and in April 2006 at the 10–20 cm depth; however, for this collection date, the other depths (0–10 cm and 0–20 cm) showed significant differences ($p < 0.05$) between forests.

The rates of FRP in the first 20 cm of soil ranged from 1.60 in clayed forest to 6.00 Mg ha^{-1} year^{-1} in sandy soil, both rates obtained in the establishment 3 (Table 2). Likewise, mean FRP was lower in the clayey forest (3.02 Mg ha^{-1} year^{-1}) than in the white-sand forest with 5.97 Mg ha^{-1} year^{-1} (Table 2). Relative growth rates (RGR) for the three periods evaluated were higher in the white-sand forest than in the clayey forest (Fig. 4). RGR in the clayey forest before and after drought were higher than during drought in 2005; before drought RGR were 4.47 and 3.94 year^{-1} for AME and AMU, respectively, and after drought RGR was 1.21 year^{-1} for AME; figures of RGR during drought were lower: −1.00 and −0.72 year^{-1} for AME and AMU, respectively. RGR before and after drought in the forest on white-sands were similar: 2.94 and 2.08 year^{-1}, respectively, while the RGR estimated during the final part of the drought period also presented a low value (−0.77 year^{-1}), similar to those obtained for the forest on clays.

3.2 Mass, production, and turnover of fine roots from sequential soil coring

Similar to results obtained for the ingrowth cores, FRM was significantly higher ($p<0.05$) at the 0–10 cm depth than at the 10–20 cm (Fig. 5 and Table 3). Temporal variation of FRM along the monitoring period also showed significant differences among collection dates for all plots: AME ($F_{8,101}=4.754$, $p<0.01$), AMU ($X^2=23.130$, D.F.=6, $p=0.001$), and ZAB ($X^2=49.258$, D.F.=8, $p=0.000$) (Fig. 5). December 2005 had the highest value of FRM (5.04 Mg ha^{-1}) in AME. In AMU September 2004, April and December 2005 showed higher values (3.90, 4.27 and 5.04 Mg ha^{-1}, respectively) while July 2006 showed the lowest value (2.44 Mg ha^{-1}). In ZAB September 2004, July 2005, and December 2006, showed significant differences (Fig. 5). In the clayey forests (AME and AMU) the FRM increased between September and December, while in the white-sand forest the increase occurred between March and July.

FRM also showed significant differences ($p<0.05$) in each collection date at all soil depths (0–10, 10–20 and 0–20 cm) between plots (Fig. 6); however, differences between plots of clayey forests (AME and AMU) were not significant ($p>0.05$) in most

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sampling dates, with the exception of April 2005. The plot on white sands (ZAB) showed values significantly higher ($p<0.05$) than plots on clayey soils in almost all collection dates.

On the other hand, FRM measured along the whole monitoring time (2.2 years) showed significant differences ($p<0.05$) between plots in all soil depths considered (Table 3). The average FRM for all time monitored was almost three times higher in the plot of white-sand forest than in plots of clayey forests (10.94 Mg ha^{-1} in ZAB and 3.04 and 3.64 Mg ha^{-1} in AME and AMU, respectively).

For the two years evaluated independently, FRP was higher in the white-sand forest (8.92 and 4.41 Mg ha^{-1} year^{-1} for years 1 and 2, respectively) than in the clayey forest (2.77 and 2.67 Mg ha^{-1} year^{-1} for AME, respectively, and 2.05 Mg ha^{-1} year^{-1} for AMU in year 1) (Table 3).

Turnover rates (year^{-1}) estimated from sequential cores for each year (Table 3), varied between 0.53–0.84 in the clayey forests, and between 0.51–0.81 in the white sand forest. Averages per plot were 0.84 and 0.53 for AME and AMU, and 0.66 for ZAB.

3.3 Relationship between fine root mass and rainfall

We found a significant correlation between FRM and rainfall (mm day^{-1}) in both forest types (Appendix A). For plots in the clayey forest (AME and AMU), the correlation was positive and significant between FRM and mean daily rainfall with and without time lag. Rainfall variables that showed a positive correlation (R between 0.1884 and 0.2397) in AME were average daily rainfall of last 90 days, average rainfall of last 60 and 90 days with time lags of 7 and 15 days, and average rainfall of last 60 days with time lag of 30 days. In AMU we obtained a higher number of rainfall variables with positive and higher correlations (0.2397–0.4702); variables with significant correlations were average daily rainfall of last 60, 90, 100 and 120 days, as well as rainfall with time lags of 7 days in all the fixed periods considered (15, 30, 60 and 90 days), rainfall with time lag of 15 days for fixed periods of 30 and 60 days, and rainfall with time lag of 30 days

with a fixed period of 15 days. Rainfall with the longest time lags (120 and 150 days) and almost all fixed periods considered, showed negative correlation with FRM in plots of clayey forests (-0.2593 to -0.3719).

In the white-sand plot FRM showed negative correlations with daily averages of rainfall of last 7, 15, 30, 60, 90, 100 and 120 days without time lag, and with rainfall for fixed periods of 15, 30 and 60 days and time lags of 7 and 30 days, and finally, with rainfall of last 30 days with time lag of 120 days. Contrary to the results in clayey plots, correlations for long time lags were positive: correlations varied from 0.1657 to 0.1943 for a time lag of 150 days and fixed periods of 30 and 60 days.

4 Discussion

4.1 Carbon allocation to fine roots

Spodosols had a much higher average of FRM (10.94 Mg ha^{-1}) than the forest on clays (3.04 and 3.64 Mg ha^{-1}) which agrees with several reviews, wich show that higher values of FRM in tropical forests occur in soils with low nutrient content, such as Spodosol and Caatinga (Cavelier, 1992; Vogt et al., 1996). These results are inside the range reported in the Amazon basin and other similar forests in Venezuela (Table 4), which varied between 2.18 and 39.50 Mg ha^{-1} for a forest on clays (Ulti/Oxisol) in Brazil and a transition between well drained and Caatinga forest in Venezuela, respectively.

Values of FRM reported in Table 4 for forests on Spodosols (ranging from 4.98 to 20.00 Mg ha^{-1}) are higher than those for forests on Ultisols (from 2.18 to 3.64 Mg ha^{-1}), which were close to the values obtained for forests on the same soil type of this study; however, the value for forests classified by Duivenvoorden and Lips (1995) as belonging to well-drained soils on Ulti/Oxisols in the middle Caquetá (colombian Amazon) is out of this range (12.00 Mg ha^{-1}).

Our estimations of FRP for the white-sand forest are high as compared with the range shown in Table 4 (5.97 Mg ha^{-1} year^{-1} with the ingrowth core method and

6.67 Mg ha^{-1} year^{-1} with sequential cores), while estimations for the clayey forest are intermediate (3.02 Mg ha^{-1} year^{-1} with ingrowth cores and 2.05 Mg ha^{-1} year^{-1}, 2.72 Mg ha^{-1} year^{-1} with sequential cores).

The decrease of FRM and FRP with soil depth found here is a general trend reported in tropical forests (Cavelier, 1992; Duivenvoorden and Lips, 1995; Klinge, 1973; Pavlis and Jeník, 2000; Silver et al., 2000) due to the proliferation of fine roots near surface. These roots are considered important for resource acquisition because allow the direct cycling of nutrients from organic matter, which probably is an adaptation to the low nutrient supply in unfertile soils (Sayer et al., 2006).

Both FRM and FRP were significantly higher in the white-sand than in the clayey forest. These results show that in white-sand forests, with lower nutrient content, the ratio total amount/belowground mass allocation is higher than in clayey forests. This result has been found in other forests on soils with low nutrient availability and content (Cavelier, 1992; Priess et al., 1999), and specifically in sites such as the mountains in Guiana (Priess et al., 1999) and other Amazonian Caatingas (Klinge and Herrera, 1978).

Differences found here between forest types support our hypothesis about the decrease of stocks and production of fine roots with the increase of soil resources and agree with other hypotheses proposing the increase of FRM and carbon allocation with the decrease of site quality, nutrient availability or under more xerophytic conditions (Shaver and Aber, 1996; Landsberg and Gower, 1997). The investment in leaf compounds, such as tannins, for retarding litter decomposition and, in this way, to slow down the nutrient cycling, could result in an increase of belowground productivity to improve the supply the nutrient requirements. These authors found that FRP was highly correlated with leaf tannin content and the genetic composition of individual trees, which suggests a potential genetic control of the compensatory growth of fine roots in response to the accumulation of secondary compounds of foliage in the soil. This is a factor that could be evaluated as a potential mechanism of allocation to belowground productivity, particularly in white-sand forests which could contain high amounts of tannins in the foliage.

Several studies show that soil plays an important role in the carbon allocation to be-lowground production (Block et al., 2006; Cavelier, 1992; Haynes and Gower, 1995; Yavitt and Wright, 2001), and Malhi et al. (2004) found that soil is an important factor for aerial NPP. However, they found that does not exist an obvious relationship be-tween wood productivity and climatic variables such as rainfall, length of dry season or solar shine, but they did evidence a trend between wood productivity and general classes of soil fertility in the Amazonian basin. Haynes and Gower (1995) analyzed how soil fertility affected carbon allocation to belowground productivity in a plantation of *Pinus resinosa* Ait. on fertilized and unfertilized soils, and found that fertilization de-creased the relative carbon allocation to belowground production. Gower et al. (1992), analyzed how the availability of water and nutrients affected the NPP in a coniferous forest (*Pseudosuga menziesii* var. *galuca*), and found a negative relationship between water and nutrient availability and carbon allocation to belowground organs. In the case of the forests studied, the fact that they are subject to the same climatic regime, we conclude that soil is the factor playing the principal role on the amount of carbon allocated to roots. In this way, both FRM and FRP decreased with the increase of soil fertility, which is opposite to the results of Malhi et al. (2004) for aerial NPP.

On the other hand, integrating above-and belowground productivity of the forests studied (Table 5) makes clear that allocation of NPP between above (wood and foliage)- and belowground (fine roots) is differential, just as the differential allocation hypothesis proposes. Even though carbon allocation to the aboveground portion was higher than that to fine roots, this difference is more accentuated in the clayey forest than in the for-est on white sands. Differences of total productivity (above plus belowground) between the two forests were not high (between 8.66 and 8.76 Mg C ha^{-1} year^{-1} for the clayey forest and, 7.12 Mg C ha^{-1} year^{-1} for the white-sand forest). These results on above – and belowground productivity show the large variation of Amazonian forests at smaller scales than that presented by Malhi et al. (2004), which reflects the importance of soil and widen the knowledge about the allocation to above- and belowground productivity in different forest types and soils of the Amazon region (see Aragão et al., 2008).

4.2 Turnover rates of fine roots

Turnover rates of this study (0.51–0.84 year^{-1}) are similar to values reported for other Amazonian forests (0.14 and 0.70 year^{-1}) (Table 4). However, the average turnover rate for the plot AME in the clayey forest was comparatively high (0.84 year^{-1}). Fine roots are tissues energetically expensive to build (Yavitt and Wright, 2001) and their longevity is critical for the functionality of the root system. Short longevity supposes higher energetic demands for the formation of new roots to replace dead roots and to maintain the concomitant absorption surface. Aber et al. (1985) propose that turnover rates of fine roots are higher on rich soils than on poor ones. However, turnover rates in both forest types showed similar values (0.53–0.84 years^{-1} for the clayey forest, and 0.51–0.81 years^{-1} for the forest on white sands). The large variability of turnover rates in each forest type could mask differences between them.

4.3 Temporal variation of fine root mass

Several authors have correlated environmental variables with biomass or production of fine roots (Gower et al., 1992; Kavanagh and Kellman, 1992; Vogt et al., 1998; Yavitt and Wright, 2001). Among these variables, rainfall has been one of the most influential of FRM and its longevity in tropical forests (Green et al., 2005). Fine root mass showed a clear temporal variation during the monitoring period, a result in line with numerous studies showing that in certain periods of the year occurs a higher growth of fine roots in response to specific climatic events (Vogt et al., 1986). Though results suggest that differences in carbon allocation to fine roots between forest types are governed by the availability of soil resources, patterns of temporal variation of FRM are explained by their correlation with rainfall, which has been reported for other tropical forests (Green et al., 2005; Kavanagh and Kellman, 1992; Yavitt and Wright, 2001).

Though FRM responded to the average daily rainfall in both forest types, such response showed an inverse behaviour between them. In plots of the clayey forest FRM increased with rainfalls of the last three months and decreased with rainfalls occur-

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ring with long time lags (120–150 days). In the forest on white sands FRM decreased with rainfall of last 4 months, and increased with the rainfall with long time lags (until 5 months). Differences of the response of both forest types to rainfall are explained by differences of their soils: soils of the white-sand forest contained a hard pan at 90–100 cm depth, which produces water logging during rainy season and impedes growth of fine roots; this is shown by the negative correlation of FRM with rainfall of last 4 months. This phenomenon does not occur in the clayey forest which responds positively to the increase of rainfall.

On the other hand, the effect of rainfall on FRP was evident in the drought season of 2005. RGR during the drought showed that both forests responded in similar way, because both decreased the FRP. However, in the white- sand forest this decrease was more obvious in last months of drought (Fig. 4). The hard pan present in the white-sand soil probably plays an important role in the soil water content of this forest by storing extra water during the rainy season which is slowly released during the dry season, and therefore delaying the forest response to the drought. The general behaviour during drought suggests that both forest types are susceptible to strong changes of rainfall. However, the main difference between them is the speed of the response of each forest: the clayey forest showed a faster decrease of FRP as a response to drought than the white-sand forest.

Likewise, in both forest types RGR before drought were higher than after drought. This probably is related with the higher rainfall of last months before the first collections (year 2004), than that after the drought, in 2006 (Fig. 4). In the clayey forest of AME, the periods between collections that showed an increase of FRM were October–December 2005, and September–December 2006, which coincided with the rainy season. Also in AMU October–December 2005 was the period of increase of FRM. In both plots the FRM was higher in December 2005 than in the same month of 2006, which could be explained by the higher rainfall of the two previous months in 2005 than in 2006 (Fig. 2).

In the white-sand forest the periods of increase of the FRM occurred between April–July 2005, and March–July 2006, when rainfall decreased and therefore the water logging of soil caused by hard pan also decreased. On the other hand, FRM was higher in July 2005 than in July 2006, which could be explained by the decrease in the soil water logging in July 2005 when the first months of drought occurred, which allowed an increase of FRM. The two preceding months to July 2006 showed a mean rainfall higher than in 2005, which suggests that water logging conditions of soil were greater at this time than in 2005, which was expressed in a lesser FRM.

Results show that rainfall plays a crucial role in the seasonal variation of fine root growth in both forests; in the clayey forest the pattern accords with reports for other well drained forests (Green et al., 2005; Metcalfe et al., 2008; Priess et al., 1999; Silver et al., 2005), where FRM increased in the rainy season and decreases during the dry season. The white-sand forest showed a different pattern, similar to that of flooding forests. This behaviour is apparently conditioned by the hard pan that causes water logging during the rainy season which limits growth of fine roots and lags the time of fine root growth in response to rainfall.

4.4 The methods of estimation used

The selection of methods for the estimation of FRP and its controlling factors is tremendously important and has raised great interest nowadays (Hendricks et al., 2006; Lauenroth et al., 1986; Majdi et al., 2005; Makkonen and Helmisaari, 1999; Metcalfe et al., 2007; Vogt et al., 1986, 1998). Hendricks et al. (2006), used a wide range of common methods to estimate FRP in three types of ecosystems in a gradient of soil humidity, with different soil characteristics and resource availability and found that FRP was not negatively correlated with the availability of soil resources. Their results support in some cases the hypothesis of differential resource allocation and in some others the constant allocation hypothesis. With respect to the methods used in the present study-sequential cores and the ingrowth cores-these authors mention, as well as others (Madji et al., 2005; Vogt et al., 1986, 1998), that they probably underestimate

FRP; however, they seem to be the most appropriate to compare sites and to evaluate the temporal variation of FRP and FRM (Makkonen and Helmisaari, 1999; Vogt et al., 1998).

Results of FRP did not show large differences between the two methods used here in each forest type. The Clayey forest showed similar results of FRM between the two methods, but differences in the white-sand forest were marked: FRM estimated by the ingrowth cores was about $5.00\,\mathrm{Mg\,ha^{-1}\,year^{-1}}$, while by the sequential cores was about twice ($10.94\,\mathrm{Mg\,ha^{-1}\,year^{-1}}$). This result suggests a stronger effect of the changed physical properties of soil on root growth in white sands and that those soils require a longer time to reach the original root density after the disturbance implied by the ingrowth method.

Despite the different results of FRP obtained with the different estimation methods widely documented by several authors (Hendricks et al., 2006; Vogt et al., 1998), all of them continue being used because the lack of consensus about the most appropriate one to study the dynamics of fine roots. For these reasons, the combination of different methods seems to be a good strategy for the estimation of FRP.

5 Conclusions

Carbon allocation to fine roots was different between forest types. As expected in a gradient of availability of soil resources, the clayey forest, with less limitation in soil resources, showed a lower carbon allocation to fine roots than the white-sand forest, which has more limitations in the availability of soil resources. FRM and FRP also showed differences with soil depth, with higher values in the first 10 cm than in the 10–20 cm layer of soil.

Temporal variation of FRM was correlated with mean daily rainfall; however, this relationship was inverse between forest types: in the clayey forest FRM increased with the increase of rainfall of last three months; in the white-sand forest FRM decreased with the increase of rainfall of last four months. Likewise, RGR of fine roots were

different before, during, and after the drought period. Both forest types showed lower RGR during drought, which suggests that severe changes of rainfall could strongly affect both forest types.

Results of productivity of the forests studied suggest that they allocate resources of NPP differentially to above-and belowground components. However, considering the total NPP differences between forest types seem not to exist, which raises the hypothesis that total NPP probably does not vary with respect to soil as it does occur for wood productivity (Malhi et al., 2004) and for belowground organs (this study).

This study shows that variation in the functioning of amazonic ecosystems at small spatial and time scales is large; it also shows that both rainfall patterns and soils act in different ways on the carbon allocation to fine roots in these forests and finally, that understanding how amazonian ecosystems can respond to these factors is fundamental in face to the events expected by the climate change.

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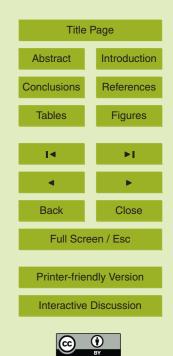
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Table 1. Main characteristics of soils and vegetation of the study sites in the colombian Amazon: The Amacayacu National Natural Park (two 1-ha plots: AME and AMU), and The Biological Station Zafire (one 1-ha plot: ZAB).

Characteristics	Amacayacu NNP		Biol. Stat. Zafire
	AME	AMU	ZAB
Soil type[a]	Ultisol clay, clay loam		Spodosol loamy sand
Chemical properties (depth 0–30 cm)[b]			
pH	4.50	4.29	4.27
P ($mg\,kg^{-1}$)	1.07	1.34	11.52
Mean N (%)	0.15	0.16	0.11
Mean C (%)	1.23	1.37	2.43
C/N	7.97	8.21	27.13
Ca ($c_{mol}c\,kg^{-1}$)	0.60	0.55	0.25
Mg ($c_{mol}c\,kg^{-1}$)	0.29	0.34	0.20
K ($c_{mol}c\,kg^{-1}$)	0.11	0.12	0.14
Na ($c_{mol}c\,kg^{-1}$)	0.00	0.02	0.05
Al ($c_{mol}c\,kg^{-1}$)	5.20	5.24	0.07
SB ($c_{mol}c\,kg^{-1}$)	1.00	1.02	0.64
CIC ($c_{mol}c\,kg^{-1}$)	6.21	6.26	0.71
Al Saturation ($c_{mol}c\,kg^{-1}$)	83.81	83.64	9.82
Bases saturation (%)	16.19	16.36	90.18
Physical properties[b]			
Sand (%)	20.63	19.19	74.75
Clay (%)	42.12	43.1	0.64
Silt (%)	37.25	37.71	24.61
Main root depth (cm)	20.00	20.00	10.00
Total root depth (cm)	50.00	50.00	100.00
Available water capacity, cm water per cm depth			
0–30 cm	3.75	3.51	2.82
Vegetation[c]			
Richness (No. sp ha^{-1})	225	244	25
Mean height of crown (m)	30	30	20
Mean stem diameter (cm)	17.29	21.02	14.94
Stem density (n ha^{-1})	647	606	866
Aboveground biomass (Mg ha^{-1})	281.305	276.464	160.870

[a] SSS (1999), USDA Texture Classification. [b] Quesada, CA, et al., 2008. [c] Amazon Forest Inventory Network RAINFOR: http://www.geog.leeds.ac.uk/projects/rainfor.

Table 2. Fine root production ($Mg\,ha^{-1}\,year^{-1}$) in the first 20 cm of soil depth in two forests with different soil types in the Colombian Amazon, estimated from ingrowth cores established in three times: 1) February 2004, 2) September 2004 and, 3) February 2006.

Soil depth	Forest on clay soil N	Mean	Forest on white sands N	Mean
Establishment 1 (0.83 years)				
0–10 cm	24	3.082 (0.196)	—	—
10–20 cm	25	1.153 (0.144)	—	—
0–20 cm	24	4.215 (0.307)	—	—
Total C		2.108		
Establishment 2 (0.52 and 0.77 years, respectively)				
0–10 cm	22	2.104 (0.357) a	26	3.530 (0.520) a
10–20 cm	22	1.243 (0.212) a	26	2.404 (0.414) a
0–20 cm	22	3.346 (0.472) a	26	5.934 (0.773) b
Total C		1.680		2.967
Establishment 3 (0.82 and 0.81 years, respectively)				
0–10 cm	13	1.210 (0.178) a	13	3.910 (0.990) b
10–20 cm	13	0.390 (0.078) a	13	2.091 (0.589) b
0–20 cm	13	1.600 (0.203) a	13	6.001 (1.388) b
Total C		0.800		3.001
Mean[*]				
0–20 cm		3.022		5.968
Total C		1.511		2.984

In parenthesis is the time elapsed between the installation and the harvest of cores. Standard errors in parenthesis. Different letters shows significant differences ($p < 0.05$) in the production between the forests. [*] Weighted arithmetic mean with respect to time in every establishment.

Table 3. Fine root mass (Mg ha^{-1}), production (Mg ha^{-1} year^{-1}) and turnover rates (year^{-1}), in two forests with different soil types in the colombian Amazon: one forest on clay soils (two 1-ha plots: AME and AMU), and other on white sands (one 1-ha plot: ZAB), estimated by the sequential core method.

	Forest on clay soil		Forest on white sands
	AME	AMU	ZAB
Mean mass by soil depth[a]			
00–10 cm	2.331 (0.114) a	2.758 (0.148) b	7.861 (0.240) c
10–20 cm	0.711 (0.053) a	0.879 (0.056) b	3.077 (0.174) c
00–20 cm	3.043 (0.151) a	3.637 (0.181) b	10.938 (0.327) c
Mean mass by year (0–20 cm)			
Apr 2005–2006	3.30 (0.24)	3.85 (0.24)	10.94 (0.65)
Dec 2005–2006	3.17 (0.23)	—	8.69 (0.46)
Maximum and minimum values of annual stocks			
Apr 2005–2006	5.042 (0.547)	5.196 (0.648)	16.710 (1.288)
	2.273 (0.327)	3.145 (0.258)	7.794 (1.156)
Dec 2005–2006	5.042 (0.547)	—	10.943 (1.046)
	2.374 (0.403)	—	6.530 (0.824)
Production[b]			
Apr 2005–2006	2.769	2.051	8.916
Dec 2005–2006	2.668	—	4.413
Mean	2.719	2.051	6.665
Total C	1.359	1.026	3.332
Turnover rates			
Apr 2005–2006	0.84	0.53	0.81
Dec 2005–2006	0.84	—	0.51
Mean	0.84	0.53	0.66

Standard errors in paranthesis.

[a] Mean Fine root mass for the whole monitoring time (2.2 years).

[b] Difference between the maximum and minimum fine root mass measured during a year.

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Table 4. Total Biomass (FRB), production (PRF) and turnover rates (TR) of fine roots (<2 mm) in forests of the Amazon basin.

Forest type	Soil Depth (cm)	FRB (Mg ha^{-1})	FRP (Mg ha^{-1} year^{-1})	TR (years^{-1})	Reference
Brazil					
Campina on humus (Podzol)	29	4.98	—	—	Klinge (1973)
TF Forest (Oxisol)	27	5.33	—	—	Klinge (1973)
TF Forest (Oxisol)[1a]	30	—	3.70	—	Metcalfe et al. (2007)
TF Forest (Oxisol)[1b]	30	—	11.40	—	Metcalfe et al. (2007)
TF Forest (Oxisol)[1b]	30	—	5.00	—	Metcalfe et al. (2007)
TF Forest (Oxisol)[1b]	30	—	5.60	—	Metcalfe et al. (2007)
TF Forest (Oxisol)[1b]	30	—	2.10	—	Metcalfe et al. (2007)
TF Forest (Oxisol) (sand plot)	30	14.00	4.00	0.29	Metcalfe et al. (2008)[**]
TF Forest (Oxisol) (dry plot)	30	10.00	3.00	0.30	Metcalfe et al. (2008)[**]
TF Forest (Oxisol) (clay plot)	30	15.00	4.00	0.27	Metcalfe et al. (2008)[**]
TF Forest (Oxisol) (fertile plot)	30	11.00	7.00	0.64	Metcalfe et al. (2008)[**]
Forest on clay soils (Ulti/Oxisol) – year 1	10	2.18	2.04	0.70	Silver et al. (2005)
Forest on clay soils (Ulti/Oxisol) – year 2	10	2.18	1.57	0.69	Silver et al. (2005)
Forest on sandy loam soils (Ultisol) – year 1	10	2.92	2.54	0.57	Silver et al. (2005)
Forest on sandy loam soils (Ultisol) – year 2	10	2.92	1.49	0.39	Silver et al. (2005)
Mature forest (Ulti/Oxisol)[2a]	10	2.60	0.35	0.14	Trumbore et al. (2006)[**]
Mature forest (Ulti/Oxisol)[2b]	10	2.60	0.92	0.35	Trumbore et al. (2006)[**]
Mature forest (Ulti/Oxisol)[2c]	10	2.60	1.18	0.45	Trumbore et al. (2006)[**]
Mature forest (Ulti/Oxisol)[2d]	10	2.60	0.52	0.20	Trumbore et al. (2006)[**]
Secondary forest of 17 years old (Oxisol or Ultisol)[2d]	10	3.42	0.85	0.25	Trumbore et al. (2006)[**]
Colombia					
Flooded forest on well drained soils (Enti/Inceptisol)[3*]	20	10.00	—	—	Duivenvoorden and Lips (1995)
TF Forest on well drained soils (Ulti/Oxisol)[3*]	20	12.00	—	—	Duivenvoorden and Lips (1995)
TF Forest on white sands (Podzol)[3*]	20	20.00	—	—	Duivenvoorden and Lips (1995)
Secondary forest of 18 years old in low terraces in the Caquetá river	20	12.82	—	—	Pavlis and Jeník (2000)
Secondary forest of 25 years old in low terraces in the Caquetá river	20	11.24	—	—	Pavlis and Jeník (2000)
Secondary forest of 37 years old in low terraces in the Caquetá river	20	16.87	—	—	Pavlis and Jeník (2000)
Mature forest in low terraces in the Caquetá river	20	30.61	—	—	Pavlis and Jeník (2000)

TF: *Terra firme*

[*] Fine root diameter<5 mm

[**] The TR was calculated from production and FRB reported for each forest.

[1] The FRP was estimated in the same site by two methods: [a] ingrowth cores method (all roots) and [b] rhizotrons.

[2] They make reference to method used to estimate the production: [a] maximum-minimum, [b] decision matrix, [c] flow compartment, and [d] decomposition model.

[3] The values of FRB are the averages for different forests for landscape unit.

[4] They make reference to method used to estimate the production: [a] ingrowth cores and [b] maximum-minimum.

[8] This sites were included due the similar conditions with the study sites.

Table 4. Continued.

Forest type	Soil Depth (cm)	FRB (Mg ha^{-3})	FRP (Mg ha^{-1} year^{-1})	TR (years^{-1})	Reference
Colombia					
TF Forest on clay soils (Ultisol)[4a]	20	—	3.02	—	Present study
TF Forest on white sands/Caatinga (Podzol)[4a]	20	—	5.97	—	Present study
TF Forest on clay soils (Ultisol)[4b]	20	3.04	2.72	0.84	Present study
TF Forest on clay soils (Ultisol)[4b]	20	3.64	2.05	0.53	Present study
TF Forest on white sands/Caatinga (Podzol)[4b]	20	10.94	6.67	0.66	Present study
Venezuela[8]					
High Caatinga	—	—	1.20	—	Cuevas and Medina (1988)
TF Forest (Oxisol)[*]	—	—	2.01	—	Jordan and Escalante (1980)
TF Forest (Oxisol)[*]	—	—	11.17	—	Jordan and Escalante (1980)
High forest (Oxisol)	20	11.40	3.12	0.27	Priess et al. (1999)[**]
Medium forest (Oxisol)	20	12.20	3.06	0.25	Priess et al. (1999)[**]
Low forest (Oxisol)	20	9.63	4.20	0.44	Priess et al. (1999)[**]
TF Forest	30	13.80	—	—	Rev. in Cavelier (1992)
Bana	30	15.70	—	—	Rev. in Cavelier (1992)
Transitional forest Caatinga/Bana	30	15.70	—	—	Rev. in Cavelier (1992)
Caatinga	30	17.90	—	—	Rev. in Cavelier (1992)
Transitional forest TF/Caatinga	30	39.50	—	—	Rev. in Cavelier (1992)
TF Forest	10	—	15.4	—	Rev. in Nadelhoffer and Raich (1992)
TF Forest	10	—	1.90	—	Sanford (1990)
TF Forest	10	—	1.00	—	Sanford (1990)
TF Forest	10	—	1.00	—	Sanford (1990)

TF: *Terra firme*

[*] Fine root diameter<5 mm

[**] The TR was calculated from production and FRB reported for each forest.

[1] The FRP was estimated in the same site by two methods: [a] ingrowth cores method (all roots) and [b]. rhizotrons.

[2] They make reference to method used to estimate the production: [a] maximum-minimum, [b] decision matrix, [c] flow compartment, and [d] decomposition model.

[3] The values of FRB are the averages for different forests for landscape unit.

[4] They make reference to method used to estimate the production: [a] ingrowth cores and [b] maximum-minimum.

[8] This sites were included due the similar conditions with the study sites.

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Table 5. Above- and belowground productivity ($Mg\,C\,ha^{-1}\,year^{-1}$) in two forests with different soil types in the colombian Amazon: one forest on clay soil in the Amacayacu National Natural Park (two 1-ha plots: AME and AMU), and other on white sands in the Biological Station Zafire (one 1-ha plot: ZAB).

Productivity ($Mg\,C\,ha^{-1}\,year^{-1}$)	Forest on clay soil		Forest on white sands
	AME	AMU	ZAB
Above ground productivity			
Wood productivity[a]	3.354	3.843	1.316
Litterfall production[b]	3.87a	3.65a	2.67b
Total	7.22	7.49	3.99
Below ground productivity (fine roots)[c]			
Ingrowth cores		1.51	2.94
Sequential soil coring	1.36	1.03	3.33
Mean	1.44	1.27	3.14
Total productivity	8.66	8.76	7.12

[a] Jiménez and Peñuela (data not publ.). [b] Navarrete (2006). [c] Mean production, results from the present study. Different letters show significant differences ($p<0.05$).

Table A1. Spearman coefficients (r_s) for the fine root mass in two forests with different soil types in the colombian Amazon, correlated with the precipitation as averages daily (PD) of the last ones 7, 15, 30, 60, 90, 100 and 120 days until the day of collection date and, with the precipitation as averages daily with a time lag in the time (TL) of 7, 15, 30, 120 and 150 counted days starting from the day of collection date with fixed intervals of time of 15, 30, 60 and 90 days.

Mean precipitation (mm Day⁻¹)	Forest on clay soil AME	AMU	Forest on white sands ZAB
PD-7	−0.0844	−0.0244	−0.2581**
PD-15	−0.0560	0.0691	−0.2872**
PD-30	−0.0118	0.1700	−0.1414*
PD-60	0.1479	0.3052**	−0.2857**
PD-90	0.2169*	0.3422**	−0.1612*
PD-100	0.1721	0.2397*	−0.1544*
PD-120	0.1492	0.2397**	−0.1294**
TL7-15	0.1835	0.4666**	−0.3223
−30	0.0455	0.3548**	−0.1502*
−60	0.2190**	0.4702**	−0.2769**
−90	0.2397*	0.2845**	−0.1222
TL15-15	0.0068	0.1314	0.0555
−30	0.0142	0.2494*	−0.0240
−60	0.2015*	0.3422**	−0.1168
−90	0.1884*	0.1820	−0.1100
TL30-15	0.1417	0.2512*	−0.1563
−30	0.1195	0.1941	−0.2261**
−60	0.2060*	0.1820	−0.1652**
−90	0.1831	0.1820	−0.0601
TL120-15	−0.2813**	−0.2653*	−0.0779
−30	−0.3719**	−0.2805	−0.1562*
−60	−0.3260**	−0.2603*	−0.1283
−90	−0.2775**	−0.3871**	0.0923
TL150-15	−0.3369**	−0.0254	0.1179
−30	−0.2834**	−0.2777*	0.1943**
−60	−0.2627**	−0.3449**	0.1657*
−90	−0.2593**	−0.4480**	0.1120

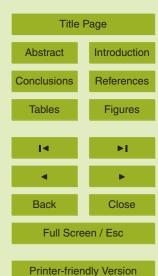* Significance level $p < 0.05$. ** Significance level $p < 0.01$

Fig. 1. Localization of the study sites in the colombian Amazon (*Trapecio Amazónico*, Leticia): the Amacayacu National Natural Park and also territory of the Indigenous preserve of the Ticuna-Cocama Yagua, and The Biological Station Zafire in the Forest Reservation of the Calderón river.
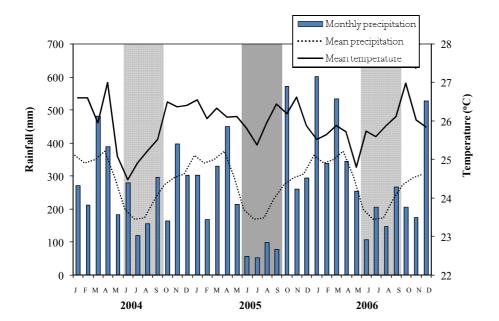
Fig. 2. Patterns of monthly and mean monthly precipitation (1973–2006) and mean temperature from the meteorological station of the Vásquez Cobo airport, Leticia (Amazonas, Colombia) during the time of the research. Shady areas show the dry period of each year, the dark one represents the drought periods. Mean monthly precipitation is plotted repeatedly for every year.

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Fig. 3. Fine root production (Mg ha^{-1}) in the first 20 cm of soil depth estimated by the ingrowth core method in two forests with different soil types in the colombian Amazon. Cores were established in three times: 1) February of 2004, 2) September of 2004 and, 3) February of 2006. Values are the means and the standard errors. The shady area is the drought period of the year 2005. * Significant differences ($p<0.05$) of fine root mass in relation to: 1) differences between soil depths (0–10 cm and 10–20 cm) per collection date in each plot, 2) differences between all soil depths per collection date and forest type.
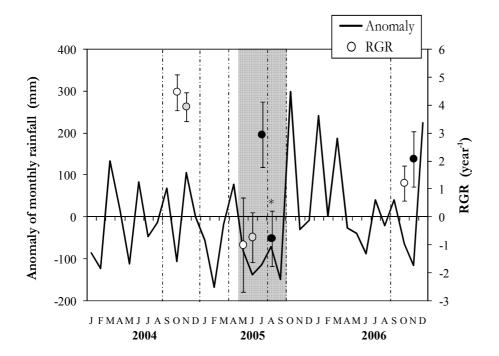
Fig. 4. Anomaly of rainfall along the period of study, calculated as the precipitation of each month minus the mean monthly precipitation (1973–2006) and relative growth rates (RGR) of fine root mass (year^{-1}) for the forests studied. Dotted vertical lines show the time intervals considered for the estimation of RGR from ingrowth cores; the portion dashed shows the drought of 2005. Circles with vertical bars represent the mean and standard errors of RGR; white and gray circles for plots of forests on clay soils (AME and AMU, respectively) and black circles for the plot on white sands (ZAB). *RGR for ZAB, calculated between the former harvest (July 2005) and the following harvest (September 2005).
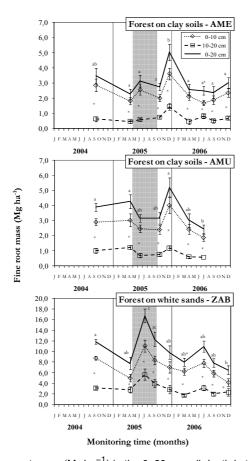
Fig. 5. Temporal variation of fine root mass (Mg ha^{-1}) in the 0–20 cm soil depth in two forests on different soil types in colombian Amazon: one forest on clay soils (plots AME and AMU) and another on white sands (plot ZAB), estimated with the method of sequential cores. Values are averages and standard deviations. The area dashed shows the drought period in 2005. Different letters in each plot show significant differences ($p < 0.05$) of fine root mass (0–20 cm) between collection dates. *Significant differences ($p < 0.05$) of fine root mass in each collection date between depths 0–10 and 10–20 cm.
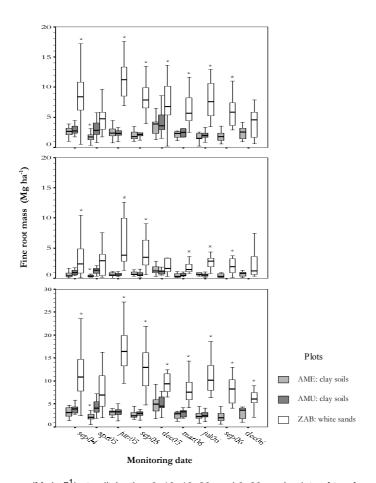
Fig. 6. Fine root mass (Mg ha^{-1}) at soil depths: 0–10, 10–20, and 0–20 cm, in plots of two forests on different soils in colombian Amazon: one forest on clay soils (plots AME and AMU) and other forest on white sands (plot ZAB), estimated by the sequential core method. *Significant differences ($p<0.05$) of fine root mass in each collection date among plots.