

# Relationships among precipitation regime, nutrient availability, and carbon turnover in tropical rain forests

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**Abstract** The effect of high precipitation regime in tropical forests is poorly known despite indications of its potentially negative effects on nutrient availability and carbon (C) cycling. Our goal was to determine if there was an effect of high rainfall on nitrogen (N) and phosphorous (P) availability and indexes of C cycling in lowland tropical rain forests exposed to a broad range of mean annual precipitation (MAP). We predicted that C turnover time would increase with MAP while the availability of N and P would decrease. We studied seven Neotropical lowland forests covering a MAP range between 2,700 and 9,500 mm. We used radiocarbon ( $\Delta^{14}\text{C}$ ) from the atmosphere and respired from soil organic matter to estimate residence time of C in plants and soils. We also used C, N, and P concentrations and the stable isotope ratio of N ( $\delta^{15}\text{N}$ ) in live and dead plant tissues and in soils as proxies for nutrient availability. Negative  $\delta^{15}\text{N}$  values indicated that the wettest forests had N cycles that did not exhibit isotope-fractionating losses and were potentially N-limited. Element ratios (N:P and C:P) in senescent leaves, litter, and

live roots showed that P resorption increased considerably with MAP, which points towards increasing P-limitation under high MAP regimes. Soil C content increased with MAP but C turnover time only showed a weak relationship with MAP, probably due to variations in soil parent material and age along the MAP gradient. In contrast, comparing C turnover directly to nutrient availability showed strong relationships between C turnover time, N availability ( $\delta^{15}\text{N}$ ), and P availability (N:P) in senescent leaves and litter. Thus, an effect of MAP on carbon cycling appeared to be indirectly mediated by nutrient availability. Our results suggest that soil nutrient availability plays a central role in the dynamic of C cycling in tropical rain forests.

**Keywords** Carbon cycle · Nitrogen · Phosphorous · Radiocarbon · Stable isotopes

## Introduction

Evergreen tropical forests play a central role in the global carbon (C) cycle, as they are responsible for 31–36% of terrestrial annual C fixation despite covering only 14% of the earth's surface (Melillo et al. 1993; Field et al. 1998; Nemani et al. 2003). Determining the biotic and abiotic controls over C cycling in these forests is essential if we want to understand their role as a net source or sink of C to the atmosphere under changing climate conditions (Grace et al. 1995; Clark et al. 2003; Nemani et al. 2003; Saleska et al. 2003; Malhi and Phillips 2004). Water availability in the form of precipitation is typically a key climatic state factor that directly or indirectly controls the structure and function of tropical forest ecosystems since seasonal variation in temperature tends to be small (Richards and

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Caldwell 1987; but see Clark et al. 2003; Feeley et al. 2007). In dry to mesic tropical forests, water availability acts mainly as a resource for forest growth, and the effect of the dry season as well as drought caused by El Niño/La Niña cycles, have received significant attention (e.g., Wright et al. 1999; Nepstad et al. 2002; Saleska et al. 2003; Bruno et al. 2006; Feeley et al. 2007). However, evidence has also accumulated showing that long-term precipitations in excess of plant demand (i.e., when precipitation is greater than evapotranspiration) in everwet tropical forests can have a negative effect on forest growth because high water input is negatively correlated to the availability of other essential plant resources such as nutrients or light (Scott 1993; Wright et al. 1999; Schuur 2001, 2003; Schuur and Matson 2001; Graham et al. 2003; Nemani et al. 2003; Myneni et al. 2007). Currently, these everwet forests remain relatively understudied and it is not clear how they will respond to changes in climate (Christensen et al. 2007).

Knowledge of direct and indirect effects of precipitation over the ecosystem dynamics of everwet forests has been derived from studies of a mean annual precipitation (MAP) gradients in Hawaiian montane forests (Miller et al. 2001; Schuur 2001; Schuur et al. 2001; Schuur and Matson 2001). Measurements on these gradients show that both C cycling and nutrient availability are altered by excess precipitation. C cycling slows down largely due to a decline in litter decomposition rates in forests exposed to high MAP. Excess water in soils can cause fluctuating anaerobic conditions by limiting oxygen diffusion even in upland soils (Gale and Gilmour 1988; Nisbet et al. 1989; Updegraff et al. 1990; Magnusson 1992; Silver et al. 1999; Hobbie et al. 2000; Schuur 2001; Schuur et al. 2001). This low soil oxygen availability can directly reduce root metabolism (Crawford 1982), change concentrations of toxic elements (Ponnamperuma 1972) and reduce the activity of soil decomposers. The latter has an important effects on litter decomposition and mineralization rates which lead to increased soil C and a slower circulation of C in the ecosystem (Schuur et al. 2001). In addition, litter quality to decomposers declines with increasing MAP further reducing decomposition rates. High MAP can also decrease nutrient availability to plants due to increased ecosystem nutrient outputs that can remove inorganic and organic nutrients from the soil (Radulovich and Sollins 1991; Houlton et al. 2006) and lower mineralization rates which reduce the availability of nutrients and in turn cause a reduction in forest productivity (Schuur and Matson 2001; Schuur 2003). In addition, other resources such as light could be reduced if high rainfall is correlated with increased cloudiness (Clark and Clark 1994; Bruijnzeel and Veneklaas 1998; Wright et al. 1999; Graham et al. 2003; Nemani et al. 2003; Myneni et al. 2007).

Despite clear relationships among high precipitation, nutrient availability and ecosystem C-cycling in montane forests, our understanding of the potential effect of excess precipitation on lowland tropical forests exposed to high MAP is still limited. The negative effect of high rainfall on soil fertility and productivity observed in montane forest appears to be applicable across a broad range of tropical forests where NPP peaks at a MAP of 2,450 mm and then declines at higher MAP (Schuur 2003), yet baseline data from high rainfall areas are generally still scarce (but see Townsend et al. 2007). The Hawaiian precipitation gradient sites were dominated by a single tree species *Metrosideros polymorpha* and on the same parent material of similar age. While this provided valuable insights into the effect of changes in MAP on forest ecosystem dynamics, it is not clear if high rainfall has the same effect in species-rich lowland tropical forests over a diverse range of soil parent materials (Townsend et al. 2007). Here, our objective was to determine if increased rainfall had a negative effect on indexes of soil C cycling and nutrient availability in tropical forests. Our hypothesis was that an increase in MAP would increase the residence time of C in the ecosystem and decrease the availability of N and P due to higher leaching and slower mineralization rates. We sampled seven neotropical lowland forests exposed to a MAP between 2,650 and 9,510 mm to examine the relationships between average C turnover time, nutrient availability and rainfall. We used radiocarbon ( $^{14}\text{C}$ ) measurements of soil organic matter (SOM) respiration as an integrated signal of the turnover time of C (Trumbore 2000; Cisneros-Dozal et al. 2006; Schuur and Trumbore 2006), along with measurements of C, N, and P concentration and stable isotopes values of N in plant and soils as proxies of site fertility.

## Materials and methods

### Study sites

We sampled seven Neotropical lowland rain forest sites exposed to a broad range of MAP that varied almost fourfold, ranging from 2,650 to 9,510 mm/year (Table 1; Fig. 1 in Electronic Supplementary Material). These sites were chosen to be above 2,450 mm, the optimal MAP for forest growth predicted by a global relationship between MAP and NPP (Schuur 2003). The lowest MAP site in our study was Barro Colorado Island (2,650 mm/year), a 96-year-old artificial island located in the Panama canal area and covered with mature and secondary tropical forest. Sampling took place near the 50-ha permanent plot of the Center for Tropical Forest Science (CTFS). Amacayacu (2,910 mm/year) is a national park in Colombia located in

a region representative of the humid northwest Amazon basin. Sampling was done on an upland terra firme soil uphill from the floodplain forests that surround the Amazon river. Fort Sherman/Fuerte San Lorenzo (3,200 mm/year) is located on the Caribbean coast of Panama. Sampling was done in the old forest in the CTFS vegetation plot, in the vicinity of the canopy crane located at that site. Santa Rita (3,670 mm/year) is an inland forest also located in Panama and sampling took place in a large mature forest patch 17 km along the Santa Rita road. We sampled at La Selva Biological Station (4,260 mm/year), Costa Rica, in a site near Carboneo Project plot L4, which is located on residual (non-alluvial) soil. Gorgona (6,910 mm/year) is an island park 27 km off the Pacific coast of Colombia, with flora representative of the south portion of the biogeographical region of Chocó. Sampling took place in a mature forest on the western side of the island. Last, we sampled in a forest 2 km north of the town Pacurita (9,510 mm/year), which is located in the central valley of the Atrato river between the towns of Quibdó and Tutunendo (Chocó) in what is considered the wettest region on Earth (<http://www.noaa.gov>; Poveda and Mesa 2000). At Santa Rita and Pacurita, the forest sites we sampled were unprotected where selective logging most likely occurred to some extent, although the sampled area were in locations that appeared currently undisturbed with large canopy trees; all other sites were located in areas protected from logging. All sites were covered with mature and highly diverse tropical rainforests. Soils were derived from a range of volcanic and sedimentary parent materials (Table 1).

All sites have some seasonal variation in precipitation, although the only site with a relatively prolonged dry season was BCI (January–April; Fig. 2 in Electronic

Supplementary Material). Amacayacu precipitation is lower in July due to its location in the southern hemisphere, but no month had an average precipitation below 100 mm. Sherman and Santa Rita precipitation is low at the beginning of the year although the dry season is shorter than on BCI. The remaining sites had no well-defined dry season although monthly precipitation was consistently lower early in the year due to their location in the northern hemisphere. Samples were taken during wet months in all sites (Table 1 in Electronic Supplementary Material).

#### Field sampling

Given the elevated costs of the  $\Delta^{14}\text{C}$  analysis, we could only take a limited number of samples per site. Thus, we specifically targeted our sampling to well-drained soils, stratified to elevated topographic positions relative to rivers and floodplains to avoid soils that had alluvial influence. All sampled sites were chosen to be on small hills with gentle to moderate slopes ('hills' on a spatial scale of ca. 0.5–1 km). We sampled soils at 4–6 locations within an area covering ca. 2,000 m<sup>2</sup> in each forest. The sampling locations were selected randomly but distributed across the plot so that there were no duplicate samples under one canopy tree. We avoided forest gaps and microtopographic locations (spatial scale of ca. 1–10 m) where water would drain during a rainy period. This procedure ensured that we sampled in similar topographic conditions in all forest sites.

#### Soil analysis

We collected a fixed volume of surface soil with depth of 11.0 cm using a 5.5-cm-diameter corer, wrapped the cores

**Table 1** Name, geographical coordinates, mean annual precipitation (MAP), mean annual daily temperature (MAT), elevation and percent of stems (DBH  $\geq$  10 cm) that belong to the Family Fabaceae of seven neotropical lowland rain forest locations sampled in this study

Name	Country	Coordinates	MAP (mm) <sup>a</sup>	MAT (°C) <sup>a</sup>	Elevation (m)	Parent material	Percentage of Fabaceae <sup>a</sup>
Barro Colorado Island (BCI)	Panama	9°10'N, 79°51'W	2,650 (126)	27.2	60	Volcanic	7.8
Amacayacu (AMA)	Colombia	3°49'S, 70°16'W	2,910 (101)	25.8 <sup>c</sup>	80	Sedimentary	8.3
Fort Sherman (SHER)	Panama	9°17'N, 79°58'W	3,200 (127)	26.0	80	Sedimentary	7.5
Santa Rita (RITA)	Panama	9°22'N, 79°42'W <sup>b</sup>	3,670 (121) <sup>b</sup>	24.8 <sup>b</sup>	460 <sup>b</sup>	Volcanic	9.5
La Selva (SELVA)	Costa Rica	10°26'N, 84°00'W	4,260 (100)	26.2	50	Volcanic	14.4
Gorgona Island (GORG)	Colombia	2°59'N, 78°11'W	6,910 (188)	26.1	30	Volcanic	7.5
Pacurita (PACU)	Colombia	5°41'N, 76°36'W	9,510 (525) <sup>d</sup>	26.6 <sup>e</sup>	110	Volcanic	7.8

The values in parentheses are standard errors of the mean

<sup>a</sup> See the Electronic Supplementary Material for more details

<sup>b</sup> Agua Clara meteorological station

<sup>c</sup> Leticia airport

<sup>d</sup> Estimated by linear interpolation between Quibdó airport (4.4 km; MAP = 8,023 mm) and Tutunendo (6.0 km; MAP = 11,134 mm)

<sup>e</sup> Quibdó airport

in aluminum foil to minimize changes in soil structure during transport, and weighed them in the laboratory. The cores were frozen 5–6 days after collection, at the end of the incubations (see below), and then thawed before separating the different soil components. We separated live and dead roots, senescent leaves, leaf litter and the soil horizons from each individual soil core. We classified roots as live or dead based on their external appearance, flexibility and mechanical resistance to pulling. Senescent leaves consisted of leaves that appeared to have fallen recently, with an intact surface and with mechanical properties similar to that of live leaves. Leaf litter was any leaf or leaf fragment that was in process of decomposition. We visually separated organic and mineral horizons from the soil cores, in cases where horizons were present. All these soil components were oven dried at 60°C before analysis. Bulk density ( $\text{g}/\text{cm}^3$ ) was quantified by dividing the dry weight of each soil horizon by its volume; none of the samples had rocks or large roots that required a volume correction. We used bulk density and mineral percent nutrient content to calculate nutrient concentrations per unit area ( $\text{g}/\text{m}^2$ ) for a standardized 10-cm-deep mineral soil.

We measured N%, C%,  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  of plant tissues and soils with a Costech elemental analyzer (Valencia, CA, USA) connected to a Finnigan Delta XL Plus continuous-flow isotope ratio mass spectrometer (San Jose, CA, USA). Phosphorous in senescent leaves, leaf litter and live roots was measured using an ash digestion (Jones and Case 1996), followed by colorimetric determination of orthophosphate on an Astoria Pacific colorimetric autoanalyzer (Clackamas, OR, USA). Phosphorous in mineral and organic horizons was analyzed by ALS Chemex by four acid near total digestion (ME-ICP61 analysis; ALS Chemex, Sparks, NV, USA).

#### Soil incubations

Soil cores were transported to local laboratories in the field stations immediately after being collected. Then, they were incubated in sealed Mason jars equipped with two airtight stopcocks, while air humidity was maintained at saturation by adding a few millilitres of water to the bottom of the jar, and glass beads to elevate the soils above the water. During incubation, the cores were loosely wrapped in aluminum foil to maintain structure, but the upper portion and a side of the wrapped core was kept uncovered to permit an adequate airflow. Soils were initially incubated 3 days at ambient temperature in dark or shaded conditions before sample collection. Field experimentation has shown that soil respiration fluxes dropped by  $\sim 50\%$  within 3–5 days after girdling of trees in a high latitude forest (Högberg et al. 2001). We used that as an estimate of the length of

time during which roots plus mycorrhizae in the soil cores would have depleted a large proportion of their labile C reserves and would then contribute relatively little to the soil incubation  $\text{CO}_2$  flux (Schuur and Trumbore 2006). This appeared reasonable as none of the soil cores had large diameter roots that could sustain high root respiration rates for extended periods of time. After the initial 3-day period, the jars were completely scrubbed with  $\text{CO}_2$ -free air, and respired  $\text{CO}_2$  was allowed to accumulate until at least 3 mg of C were available in the jar atmosphere. Carbon accumulation took between 6 and 72 h and C in the air was subsequently extracted using an airtight pumping system that circulated air through a molecular sieve trap (Bauer et al. 1992). Carbon dioxide evolved from this stage of the incubation is dominated by heterotrophic decomposition of more labile SOM, and is largely devoid of passive soil C that can influence a  $^{14}\text{C}$  measurement of solid soil organic matter. We also used molecular sieve traps to collect  $\text{CO}_2$  from the atmosphere at each forest site to determine the background atmospheric value. Atmospheric sampling was done during moderately windy periods in elevated positions on open fields or above the forest canopy to obtain a well-mixed sample of the free troposphere. Air C was also captured using a pumping system that circulated air through molecular sieve traps. After the incubation period, the same cores were frozen and used to quantify soil components and fertility (see above).

#### Carbon isotopes

Molecular sieve traps were returned to the University of Florida where  $\text{CO}_2$  was liberated by baking them at 650°C in a vacuum line. The released  $\text{CO}_2$  was purified first through a dry ice/ethanol water trap and then condensed with  $\text{LN}_2$ . The  $^{13}\text{C}/^{12}\text{C}$  isotope ratio was measured from a subsample of purified  $\text{CO}_2$  with a Gas Bench III attachment to a Finnigan Delta XL Plus continuous-flow mass spectrometer. The remaining  $\text{CO}_2$  was converted to graphite by heating to 550°C in an  $\text{H}_2$  atmosphere in presence of a Fe catalyst (Vogel 1992). Then, the  $^{14}\text{C}/^{12}\text{C}$  isotope ratio in the resulting graphite was measured at the W.M. Keck Carbon Cycle AMS at the University of California, Irvine. The  $^{14}\text{C}$  results were expressed in terms of  $\Delta^{14}\text{C}$ , which corrects for mass-dependent fractionation using the  $^{13}\text{C}/^{12}\text{C}$  isotope ratio (Stuiver and Polach 1977). Carbon turnover time was calculated from SOM  $\Delta^{14}\text{C}$  respiration, annual average atmospheric  $\Delta^{14}\text{C}$  measurements (Table 1 in Electronic Supplementary Material), and atmospheric  $\Delta^{14}\text{C}$  measured over the past 50 years for the tropics (Levin and Hesshaimer 2000; Trumbore 2000). This turnover time is an estimate of the average residence time of a C atom in the ecosystem and integrates the residence time within living plants, litter, and SOM. Turnover time was estimated here

using a single-pool model where heterotrophic respiration  $\Delta^{14}\text{C}$  was dominated by a decomposable carbon pool (Trumbore 2000; Cisneros-Dozal et al. 2006; Schuur and Trumbore 2006; Trumbore 2009). This model is accurate for our incubations because although solid SOM is typically modeled with multiple pools, we removed the influence of several pools by: (1) delaying sampling beyond an initial period that removes the highly labile pool, and (2) avoiding the influence of a very old passive pool of C stabilized by soil minerals, which makes little or no contribution to  $\text{CO}_2$  released during an incubation. This experiment then largely isolates soil organic C pools which are most directly connected to the biological C cycling processes that were the subject of this study.

### Data analysis

We used simple least square regression to determine if there was a relationship between MAP and response variables. Data were transformed to meet the assumptions of regression and all regressions were done using mean site values. When a linear model was not appropriate, we used a one-way analysis of variance model with site as a fixed effect, followed by pairwise least square Student's *t* test to detect differences among forest sites.

### Results

We observed a significant increase in C content in the surface soil (top 10 cm mineral plus organic horizon) with MAP (Table 2; Fig. 3a in Electronic Supplementary Material;  $r^2 = 0.64$ ,  $p = 0.040$ ). The higher soil C in the wettest forests corresponded to a larger organic horizon compared to the more mesic sites, which tended to have no clearly defined organic horizons. In Pacurita, the wettest site, C in the organic horizon represented nearly 50% of total surface soil C (data not shown). Mean C content in the top 10 cm of mineral soil alone (i.e., excluding the organic horizon) was not related to MAP ( $r^2 = 0.01$ ,  $p = 0.843$ ) and tended to be low at either end of the precipitation gradient.

In contrast to C, we found no significant relationship between MAP and total soil N (Table 2;  $r^2 = 0.04$ ;  $p = 0.672$ ). The organic horizon in the wetter sites, Gorgona and Pacurita, contained 14 and 42% of total soil N, respectively, indicating that there was an important amount of N stored in this upper soil layer. However, Pacurita mineral soil had the lowest N content of all sites ( $F = 12.61$ ,  $p < 0.001$ ), offsetting increases in the organic layer. As a result of increasing soil C, soil C:N (all element ratios in this study are expressed in  $\text{mol mol}^{-1}$ ) increased significantly with MAP across the gradient (Fig. 3b in

Electronic Supplementary Material;  $r^2 = 0.63$ ,  $p = 0.034$ ). This increase in C:N suggests less decomposition in wetter sites and/or a decrease in tissue quality entering the SOM pool. The proportion of Fabaceae (i.e., Leguminosae) stems with a diameter at breast height  $\geq 10$  cm did not vary consistently with MAP and tended to be in the lower range in the two wettest sites (Table 1).

Carbon concentration (C%) of leaf litter and live root increased significantly with MAP ( $r^2 = 0.60$ ,  $p = 0.041$ ;  $r^2 = 0.94$ ,  $p < 0.001$ , respectively), while senescent leaves also followed an increasing trend, but were more variable and not significantly related to MAP ( $r^2 = 0.24$ ,  $p = 0.265$ ) (Table 2). The  $\delta^{13}\text{C}$  of senescent leaves, litter, live roots and soil was low in all sites suggesting, not surprisingly, that moisture availability in these forests was high (Table 2 in Electronic Supplementary Material). Similarly to soils, tissue N concentration (N%) was not significantly related to MAP for senescent leaves, litter and live roots. In contrast to the pattern for soils, C:N of senescent leaves and leaf litter showed a weak non-significant increasing trend with MAP, while live root C:N did not increase with MAP. In terms of individual sites, Pacurita, the wettest site, had a significantly higher C:N than all other sites for both senescent leaves (C:N = 64;  $F = 10.63$ ,  $p < 0.001$ ) and leaf litter (C:N = 48;  $F = 14.54$ ,  $p < 0.001$ ), while BCI, the driest site, and La Selva, with intermediate precipitation, had the lowest leaf litter C:N among all sites (21.4 and 22.2, respectively).

In contrast to N, P content ( $\text{mg g}^{-1}$ ) tended to decline with MAP, although the strength of this relationship varied across tissue types (Table 2). Live root P declined significantly with MAP ( $r^2 = 0.76$ ,  $p = 0.011$ ; transformed to  $\text{MAP}^{-1}$ ), while senescent leaves and litter P values followed the same trend but were not significantly related to MAP. Total soil P ( $\text{g m}^{-2}$ ) also followed a declining trend but was not significantly related to MAP (Table 2). In contrast, there were very strong positive relationships between C:P and MAP for senescent leaves ( $r^2 = 0.78$ ,  $p = 0.009$ ), leaf litter ( $r^2 = 0.80$ ,  $p = 0.007$ ), live roots ( $r^2 = 0.87$ ,  $p = 0.002$ ) and soils ( $r^2 = 0.92$ ,  $p = 0.001$ ). Senescent leaves and leaf litter C:P increased about an order of magnitude over the gradient (1,573 to 17,198 and 1,288 to 12,136, respectively), live root C:P increased about sixfold (1,287 to 7,563) and soil C:P increased nearly 25 times (71 to 1,746). The individual trends in N and P concentration in plant tissues across the gradient were more apparent in the analysis of N:P as N:P increased significantly with MAP for senescent leaves ( $r^2 = 0.82$ ,  $p = 0.005$ ), leaf litter ( $r^2 = 0.74$ ,  $p = 0.013$ ), live roots ( $r^2 = 0.82$ ,  $p = 0.005$ ) and soils ( $r^2 = 0.92$ ,  $p < 0.001$ ). A plot of normalized N:P showed that all components (senescent leaves, litter, live roots and soils) increased with MAP (Fig. 1a); there was a significant linear increase in the

**Table 2** Carbon (C), nitrogen (N), phosphorous (P), stable N isotope ratio ( $\delta^{15}\text{N}$ ), biomass of live fine roots of surface soils and bulk density along a MAP gradient in tropical wet forest (mean  $\pm$  SE). Also shown are element and isotope contents of senescent leaves, leaf litter and live fine roots

Site MAP (mm)	BCI (2,650)	AMAC (2,910)	SHER (3,200)	RITA (3,670)	SELVA (4,260)	GORG (6,910)	PACU (9,510)
<b>Soils</b>							
C (g/m <sup>2</sup> )	2,823 (151)	1,778 (187)	3,272 (265)	2,568 (132)	2,990 (144)	4,158 (118)	3,827 (702)
N (g/m <sup>2</sup> )	282 (17.2)	199 (13.6)	245 (15.7)	242 (15.3)	291 (9.3)	346 (10.5)	232 (19.8)
P (g/m <sup>2</sup> )	102.7 (7.13)	40.7 (1.67)	24.2 (1.07)	20.6 (1.97)	103.4 (6.88)	13.1 (0.55)	6.4 (0.84)
$\delta^{15}\text{N}$	7.10 (0.20)	6.57 (0.20)	4.10 (0.11)	5.50 (0.12)	7.18 (0.18)	2.48 (0.25)	4.17 (0.92)
Live roots <sup>a</sup> (g/m <sup>2</sup> )	N/A <sup>b</sup>	228 (79.6)	N/A <sup>b</sup>	N/A <sup>b</sup>	63 (17.4)	451 (252.2)	404 (65.5)
Bulk density (g/cm <sup>3</sup> ) <sup>c</sup>	0.63 (0.02)	0.85 (0.04)	0.47 (0.03)	0.52 (0.04)	0.59 (0.04)	0.41 (0.01)	0.64 (0.15)
<b>Senescent leaves</b>							
C (%)	42.6 (0.88)	44.7 (0.78)	47.5 (0.87)	41.9 (2.30)	38.7 (2.31)	43.8 (1.26)	49.5 (0.72)
N (%)	1.96 (0.10)	1.72 (0.19)	1.26 (0.12)	1.14 (0.04)	2.14 (0.09)	1.54 (0.19)	0.95 (0.14)
P (mg/g)	0.73 (0.083)	0.41 (0.074)	0.16 (0.023)	0.16 (0.019)	0.45 (0.108)	0.17 (0.041)	0.08 (0.005)
$\delta^{15}\text{N}$ (‰)	2.44 (0.61)	3.23 (0.44)	0.49 (0.18)	0.91 (0.24)	6.37 (0.36)	-2.04 (0.53)	-0.58 (1.00)
<b>Leaf litter</b>							
C (%)	35.6 (1.08)	42.2 (2.12)	44.4 (1.19)	37.6 (1.87)	39.9 (2.74)	43.7 (0.26)	49.8 (0.48)
N (%)	1.99 (0.16)	1.61 (0.11)	1.45 (0.12)	1.50 (0.12)	2.10 (0.09)	1.66 (0.08)	1.23 (0.09)
P (mg/g)	0.91 (0.267)	0.39 (0.028)	0.28 (0.022)	0.19 (0.011)	0.62 (0.044)	0.19 (0.019)	0.11 (0.009)
$\delta^{15}\text{N}$	3.33 (0.62)	2.51 (0.30)	0.82 (0.18)	1.72 (0.44)	6.12 (0.37)	-2.21 (0.20)	-1.64 (0.45)
<b>Live roots</b>							
C (%)	37.1 (1.37)	38.5 (0.47)	40.1 (0.92)	40.8 (0.70)	40.7 (1.07)	43.5 (0.92)	47.1 (0.16)
N (%)	1.56 (0.10)	1.73 (0.13)	1.45 (0.14)	1.15 (0.16)	1.37 (0.26)	1.60 (0.13)	1.47 (0.05)
P (mg/g)	0.78 (0.056)	0.45 (0.031)	0.40 (0.024)	0.31 (0.076)	0.44 (0.011)	0.16 (0.008)	0.16 (0.008)
$\delta^{15}\text{N}$	0.85 (0.72)	0.95 (0.55)	1.06 (0.22)	0.46 (0.67)	-1.10 (0.89)	-1.49 (0.21)	-1.93 (0.77)

Element concentrations in the soil were standardized to a 10-cm-deep mineral soil. If an organic horizon was present, its elements were added to the total; leaf litter was not considered

BCI Barro Colorado Island, AMAC Amacayacu, SHER Fort Sherman, RITA Santa Rita, SELVA La Selva Biological Station, GORG Gorgona Island PACU Pacurita

<sup>a</sup> <2 mm in diameter

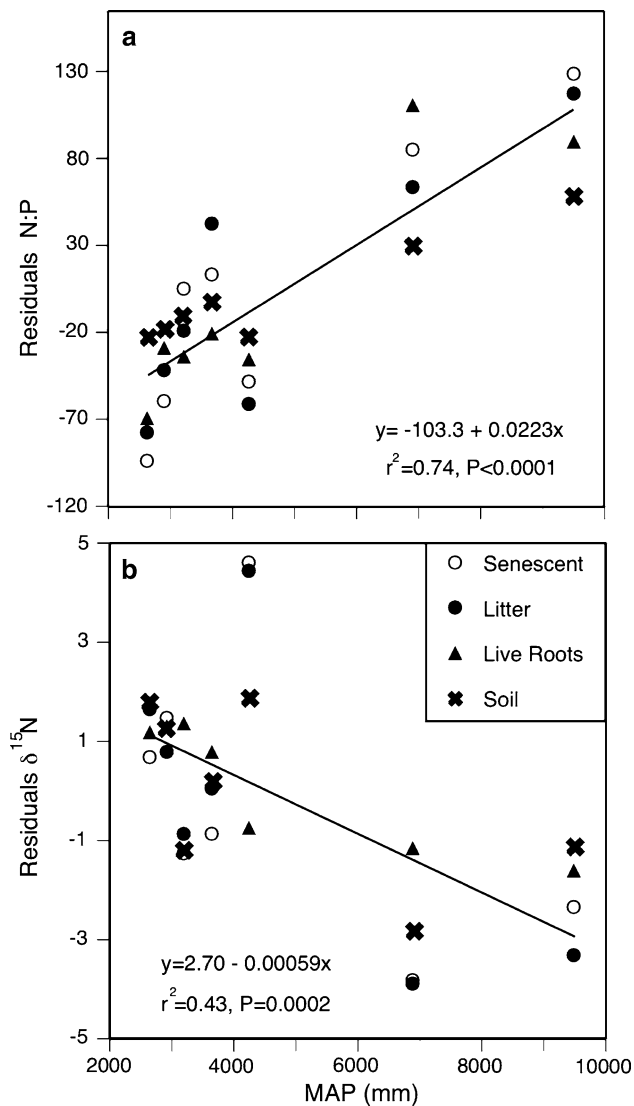
<sup>b</sup> Not available

<sup>c</sup> Including organic and mineral horizons; mineral horizon standardized to a depth of 10 cm

average residual value of N:P with MAP ( $r^2 = 0.74$ ,  $p < 0.001$ ). This increase in N:P was primarily caused by decreasing P%, while N% was less variable across the precipitation gradient.

We also quantified  $\delta^{15}\text{N}$  values in soils and plant tissues as an index of the dynamic of the ecosystem N cycle (Table 2). Positive  $\delta^{15}\text{N}$  values in leaves and litter have been associated with an 'open' nitrogen cycle, while negative  $\delta^{15}\text{N}$  values are expected to be indicative of a 'closed' nitrogen cycle when N availability is low relative to demand (Högberg 1990, 1997; Austin and Vitousek 1998; Martinelli et al. 1999; Amundson et al. 2003; Ometto et al. 2006; Pardo et al. 2006; Kahmen et al. 2008). There was a significant negative relationship between both leaf litter  $\delta^{15}\text{N}$  ( $r^2 = 0.63$ ,  $p = 0.032$ ) and live root  $\delta^{15}\text{N}$  ( $r^2 = 0.93$ ,  $p = 0.001$ ) with MAP (both variables log-transformed),

whereas senescent leaf and total soil  $\delta^{15}\text{N}$  followed a similar but non-significant trend. A comparison of the normalized  $\delta^{15}\text{N}$  values for each component showed a clear decline as MAP increased and that individual components generally mirrored each other (Fig. 1b); there was a significant regression between the average residual  $\delta^{15}\text{N}$  for each forest site and MAP ( $r^2 = 0.43$ ,  $p < 0.001$ ). The two wettest sites, Gorgona and Pacurita, had generally negative  $\delta^{15}\text{N}$  values, whereas more mesic sites had values that were mostly positive (Table 2) ( $F = 65.30$ ,  $p < 0.001$ ). These results suggest that nitrogen availability declined with MAP despite no clear changes in total N content in soils and plant tissues. We also found strong negative correlations between  $\delta^{15}\text{N}$  and N:P for senescent leaves ( $r = -0.76$ ,  $p = 0.048$ ), litter ( $r = -0.84$ ,  $p = 0.019$ ) and roots ( $r = -0.83$ ,  $p = 0.030$ ) and a marginally significant



**Fig. 1** Normalized **a** N:P and **b**  $\delta^{15}\text{N}$  for different ecosystem components as a function of MAP. The residuals are calculated as the deviation of a site from the mean across all seven forest sites for each individual component (i.e., the mean was calculated separately for senescent leaves, litter, live roots and soils). The continuous line is a linear regression calculated using average residual values for each forest site

relationship for soils ( $r = -0.74$ ,  $p = 0.059$ ) suggesting that a more closed N cycle was also accompanied by a decline in P availability.

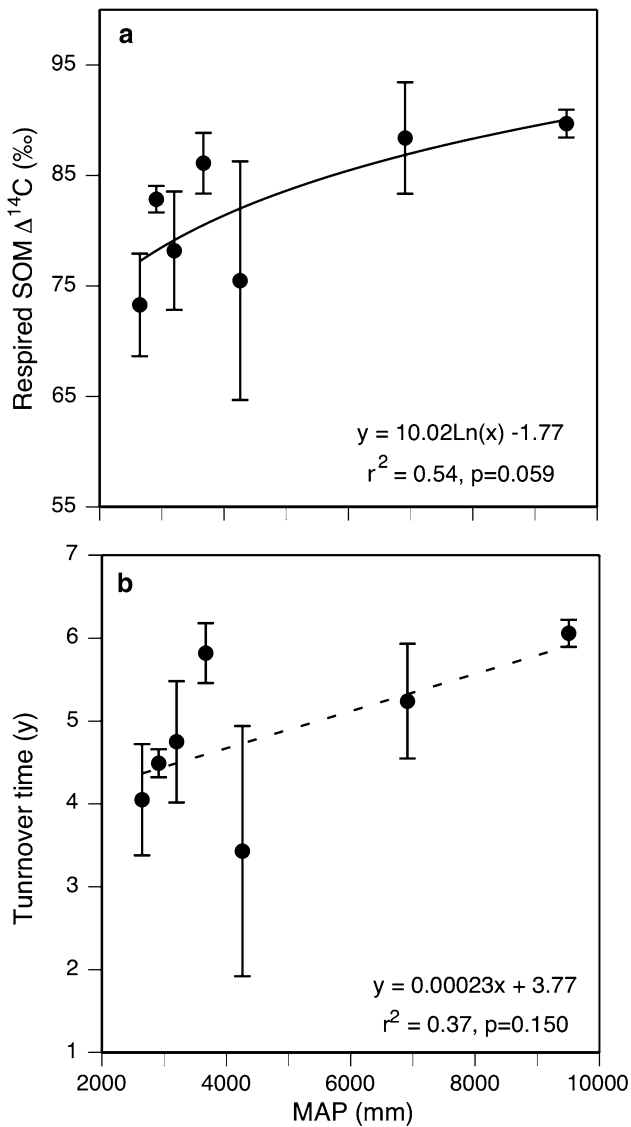
In addition to changes in C and nutrient pools across the MAP gradient, we quantified turnover time of C based on radiocarbon measurements. Radiocarbon measurements of  $\text{CO}_2$  respired from soil incubations provided a measurement of the age of C that is readily available to soil decomposers. Radiocarbon from SOM respiration varied between 73 and 90‰ across the MAP gradient, while atmospheric  $\Delta^{14}\text{CO}_2$  only varied between 53 and 60‰ during the 2004–2005 study period (Table 1 in Electronic

Supplementary Material). The elevated radiocarbon value of SOM respiration compared to atmosphere  $\Delta^{14}\text{CO}_2$  indicated that the soil microbes were respiring C that had resided in the ecosystem for several years as plant tissue and dead organic matter. Carbon that was photosynthetically fixed prior to the time of our study had elevated values due to atmospheric enrichment by bomb radiocarbon, which peaked in 1963 and is currently declining each year. Respired  $\Delta^{14}\text{CO}_2$  was marginally positively related to MAP (Fig. 2a;  $r^2 = 0.54$ ,  $p = 0.059$ ) and the wettest sites were respiring  $\text{CO}_2$  with higher radiocarbon values. However, we found a weaker non-significant relationship between turnover time and MAP (Fig. 2b). The overall mean turnover time was calculated to be 4.8 years, and the range across sites varied between 3.4 and 6.1 years. This turnover time relationship was weaker than that of respiration  $\Delta^{14}\text{CO}_2$  alone because sites sampled later in chronological time had the influence of a slightly lower contemporary atmosphere compared to sites sampled 1 year earlier (Table 1 in Electronic Supplementary Material). Neither respired  $\Delta^{14}\text{CO}_2$  ( $F = 1.72$ ,  $p = 0.177$ ) nor turnover time ( $F = 1.90$ ,  $p = 0.140$ ) were significantly different when comparing forest sites with an ANOVA model.

Since MAP is an ultimate state factor, rather than a proximal driver of ecosystem C cycling, we compared the calculated C turnover time directly to our nutrient availability indexes. Carbon turnover time decreased significantly with both  $\delta^{15}\text{N}$  of senescent leaves (Fig. 3a;  $r^2 = 0.64$ ,  $p = 0.031$ ) and N:P of senescent leaves (Fig. 3b;  $r^2 = 0.65$ ,  $p = 0.029$ ). Similar relationships for  $\delta^{15}\text{N}$  and N:P were observed for leaf litter and soil as well (not shown). These relationships indicated that turnover time of C was slower in forests with lower P availability (i.e., elevated N:P), and in forests with lower N availability (negative  $\delta^{15}\text{N}$ ).

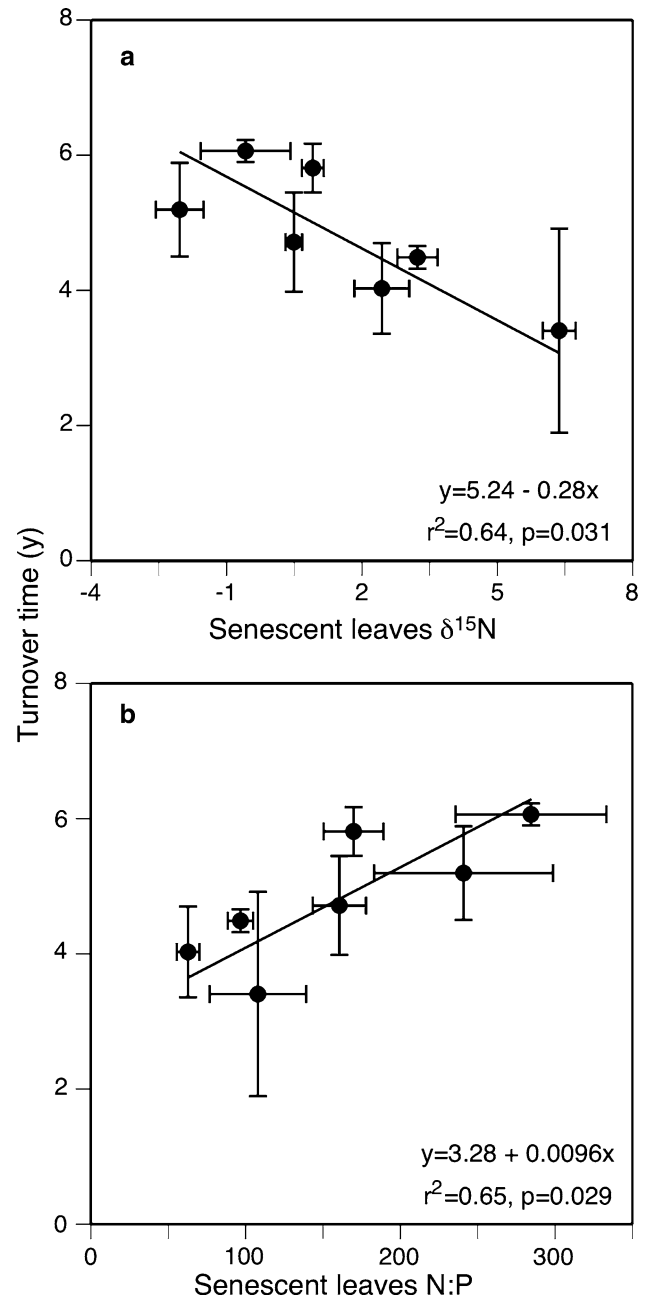
## Discussion

Our objective was to test the prediction that high precipitation regimes would be related to slower C turnover and a decrease in N and P availability in lowland everwet tropical forests. Consistent with this, we found an increase in surface soil C with increasing MAP, a pattern that has been observed in a larger global survey of non-wetland terrestrial soils (Post et al. 1982) and in mountain forests (Schuur et al. 2001). The observed relationship between soil C and MAP was contingent, however, on the wide range of MAP included in our study, and excluding the two wettest sites removed any significant relationship. This increase in soil C was caused by an accumulation of a gradually thicker organic horizon in the wetter sites, which could be caused



**Fig. 2** Relationship between mean annual precipitation and  $\Delta^{14}\text{C}$  respired by soil organic matter (mean  $\pm$  SE) (a). Relationship between MAP and turnover time of carbon (b) calculated with a one-pool carbon model and the  $\Delta^{14}\text{C}$  value

by slower decomposition rates of SOM, higher NPP rates or a combination of both. Yet, slower decomposition rate was a more likely cause because wet forests tend to have lower NPP than mesic forest (Schuur 2001) and litterfall input data for Gorgona are within the range of mesic lowland tropical forests (Posada et al., unpublished). Turnover time of labile surface soil organic C respired by microbes showed a weak, non-significant, increasing trend with MAP. Yet, this positive trend matched a stronger trend in decreased soil C turnover time with increased rainfall observed in montane forests (Schuur, unpublished data). The absence of strong relationship here was likely due to the relatively small range of soil C turnover times observed across the sites in this study (~3–6 years)



**Fig. 3** Relationship between senescent leaves  $\delta^{15}\text{N}$  and ecosystem C turnover time (a) and between senescent leaves N:P and turnover time (b) (mean  $\pm$  SE). The line is a linear regression calculated using mean values for each forest site

combined with considerable variability in soil parent material and substrate age across sites.

Despite this lack of relationship between turnover time and MAP, high rainfall had a significant effect on indices of N availability in these wet tropical forests. Nitrogen isotope ratios were consistently lower at high MAP, whether measured in senescent leaves, leaf litter, live roots or soils. These results agree with multiple studies that have shown that leaf  $\delta^{15}\text{N}$  declines with MAP (Austin and



Vitousek 1998; Handley et al. 1999; Schuur and Matson 2001; Santiago et al. 2004; Craine et al. 2009). Nitrogen isotope ratios have been suggested to reflect integrated changes in the ecosystem N cycle (Högberg 1990, 1997; Austin and Vitousek 1998; Martinelli et al. 1999; Amundson et al. 2003; Ometto et al. 2006; Pardo et al. 2006; Kahmen et al. 2008; Craine et al. 2009). In sites where N availability is relatively high, N losses are subject to isotopic fractionation and over time can lead to an overall enrichment in  $\delta^{15}\text{N}$  in plants and soil. Following this idea, increased rainfall in our sites appeared to decrease fractionating N losses, possibly reflecting lower N availability and a more conservative N cycle. Again, this pattern was detected only with the wide range of MAP in this study, with the mesic forests having consistently higher positive  $\delta^{15}\text{N}$  values, similar to other tropical lowland forests, and the wetter sites having negative  $\delta^{15}\text{N}$  representative of N-limited ecosystems (Martinelli et al. 1999; Ometto et al. 2006). The increase in soil C with MAP suggests that N limitation in Gorgona and Pacurita could, at least in part, be attributed to low decomposition and mineralization rates, but other factors, such as nutrient leaching or complete denitrification of nitrate pools that removes all  $^{15}\text{N}$  enriched substrates, may also play a role (Radulovich and Sollins 1991; Houlton et al. 2006; Craine et al. 2009). The percentage of Fabaceae (Leguminosae) stems (DBH  $\geq 10$  cm) was in the lower part of the range when compared to legume distributions throughout the Amazon basin; however, percent root nodulation (as a proxy of potential N fixation) also tends to be high (ca. 70%) when the proportion of Fabaceae stems is around 10% (ter Steege et al. 2006). The percentage of Fabaceae was similar across forest sites (7.5–14.4%), implying that  $\delta^{15}\text{N}$  differences across sites were not directly influenced by the proportion of N-fixing vascular plants, although more detailed research is needed to determine if plant acquisition of N through mycorrhiza increases with MAP (Craine et al. 2009).

In contrast to  $^{15}\text{N}$ , N content and C:N in senescent leaves and litter were not related to MAP. This could have been caused by variability in soil parent material along the MAP gradient (Table 1) but also by a weak link between N in soils, plant N resorption and N content in plant tissues (McGroddy et al. 2004). The lack of relationship between leaf tissue N content and MAP could also be a consequence of a gradual ‘closing’ of the N cycle that effectively maintained tissue concentration relatively constant (Austin and Vitousek 1998). N content in senescent leaves from our study sites was not markedly different from a global average N content of tropical live leaves (1.87%) (Townsend et al. 2007), suggesting that average N resorption before leaf shedding was only 18.4%, a value that is low when compared to a global

average N resorption of ca. 48% (McGroddy et al. 2004). Furthermore, if  $\text{N} < 0.7\%$  is an indication of complete N resorption in senescent leaves, and if  $\text{N} > 1.0\%$  is an indication of incomplete resorption, and if any value inbetween is intermediate (Killingbeck 1996), then resorption in our study sites was incomplete for all sites but Pacurita, which was intermediate. Similarly, average C:N for senescent leaves (38.4) was lower than the average global value for the tropics (60.3) (McGroddy et al. 2004), which also suggests that N resorption was moderate in the studied forests. We did find that N concentration and  $\delta^{15}\text{N}$  values in senescent leaves and litter were positively correlated with each other, implying that forests with a more closed N cycle also had a lower N content in dead leaf tissues than forest with higher N availability, yet that effect was relatively small. Thus, there was evidence of N-limitation in the wettest forests (i.e., negative  $\delta^{15}\text{N}$  values), but this limitation had only a relatively modest effect on dead leaf N% and N resorption.

In contrast to these moderate site effects on N, C:P, and N:P increased significantly with MAP due to an important reduction in P rather than any large change in C or N. P concentration in senescent leaves was consistently lower than a global average P content ( $0.87 \text{ mg g}^{-1}$ ) of live tropical canopy leaves (Townsend et al. 2007) and, when compared to this global P concentration value, average P resorption was 64.4%, a value close to the global value of 68% (McGroddy et al. 2004). P content was below the threshold of complete resorption ( $P < 0.4 \text{ mg g}^{-1}$ ) in four forest sites and was in a range of intermediate resorption ( $P < 0.5 \text{ mg g}^{-1}$ ) in two forests (Killingbeck 1996); only BCI in Panama maintained a high P concentration in senescent leaves. This supports the prediction that many lowland tropical forests are limited by P availability (Vitousek 1982; Vitousek and Sanford 1986; Vitousek and Farrington 1997; Hedin 2004; McGroddy et al. 2004; Davidson et al. 2007). The very large increase in N:P and C:P and the decrease in P content in plant tissues with MAP shows that high MAP may have exacerbated P limitation appreciably (McGroddy et al. 2004). The N:P values of senescent leaves for Gorgona (241) and Pacurita (284) represent new extremes that extend the previously reported maximum N:P value of ca. 170 (McGroddy et al. 2004). Similarly, the C:P values of senescent leaves for Gorgona (8,704) and Pacurita (17,198) were much higher than the tropical average C:P value of 4,116. In contrast to our results, a review of leaf stoichiometry in the tropics found no relationship between N:P ratios of canopy leaves and MAP (Townsend et al. 2007). This could be explained by the fact that their study covered a smaller range of MAP and was based on N:P of live leaves which may not have

such a strong P-limitation signal as dead leaves, where P resorption occurred. In contrast to wet montane forests, P availability did not increase in the wettest sites, suggesting either that low redox conditions were not important in these soils in making P available through iron solubilization or that sufficient time and leaching had depleted the P capital that was made soluble by redox reactions, as the negative trend between total soil P and MAP suggests (Miller et al. 2001). In addition to these indexes of nutrient availability, the increase in surface fine root allocation with N:P, where measurements were available, indirectly supported the conclusion of lower nutrient availability in wetter sites (Fig. 4 in Electronic Supplementary Material).

Because rainfall is an ultimate state factor (Jenny 1941) that controls the availability of other plant and ecosystem resources, we examined direct correlations between C turnover time and indexes of nutrient availability across sites, independent of MAP. These analyses account for other state factors that may have varied among forests, such as changes in parent material and soil age, and have masked the effect of rainfall. Ecosystem C turnover time, which itself was weakly related to MAP (Fig. 2b), was negatively related to  $\delta^{15}\text{N}$  and positively related to N:P in senescent leaves (Fig. 3), litter and soil. Thus, in sites where P availability and N availability were low, soil C turnover time was also slower. This suggests that there was a concurrent effect of high precipitation and soil parent material on nutrient availability and C cycling. High MAP reduced N and P availability, and lower fertility promoted slower soil C turnover and higher C accumulation. Slower C turnover in infertile soils is consistent with either a direct nutrient effect on microbial decomposition (Mack et al. 2004; Kaspari et al. 2008) or an indirect effect of low fertility on the production of low quality plant litter available for decomposition (Hobbie and Vitousek 2000; Vitousek 2004).

The increase in C% in leaves and roots with MAP, although modest (ca. 10%), could indicate more plant allocation to carbon-based compounds such as fibers or waxes. Thus, as observed in montane forests in Hawaii (Schuur and Matson 2001), the quality of tissue for decomposers may have declined with increasing precipitation and decreasing soil fertility, which would have contributed to slower C cycling in the wettest forests. While our estimated C turnover time also encompasses the residence time of C in living plant tissue, there are not enough measurements available to conclude that there is an increase in tissue longevity with MAP or soil fertility across these sites. Yet, the observed increase C content in leaves with MAP could be associated to higher leaf mass per area (LMA) which is in turn related to an increase in longevity (Wright et al. 2004). In Panama, there was

support for a higher leaf lifespan in wetter forests than in more mesic sites (S.J. Wright, personal communication).

Tropical forests are generally expected to be limited by the availability of P while N limitation is more common in temperate latitudes (Walker and Syers 1976; Vitousek 1982, 1984; Vitousek and Sanford 1986; Vitousek and Farrington 1997; Martinelli et al. 1999; Hedin 2004; McGroddy et al. 2004). Our results confirm that P availability is generally low in lowland tropical forests and decreases considerably under high MAP regimes. Low N availability in the wettest sites was somewhat unusual because N is not thought to be limiting productivity in lowland tropical forests (Vitousek 1984), except for forests growing on oligotrophic white sands (Vitousek 1984; Cuevas and Medina 1988; Martinelli et al. 1999) or secondary forests found on abandoned agricultural soils (Davidson et al. 2007); evidence of N-limitation is more common in montane tropical forests (Vitousek and Farrington 1997; Tanner et al. 1998; Martinelli et al. 1999; Schuur et al. 2001; Schuur and Matson 2001). Thus, it appears that the wettest forest sites could have been co-limited by low N and P availability. A review of fertilization experiments indicates that forests respond to N and P fertilization independently of latitude (Elser et al. 2007). Yet, our study shows that there is considerable variation in nutrient availability within the tropics and suggests that the wettest forests should respond more strongly to N and P fertilization than mesic forests. A detailed long-term fertilization study done near BCI, our more mesic site, found that N and P fertilization had no effect on leaf production, although fertilization increased leaf nutrient concentration of these elements (Kaspari et al. 2008). These results are consistent with our observations.

In conclusion, given the range of parent material and ecosystem age along the MAP gradient, the effects of precipitation on ecosystem dynamics were most clear when our range of precipitation was large. Our results agree with previous studies that have shown a negative effect of increasing precipitation on nutrient availability (Schuur and Matson 2001). In addition, the strong correlations between nutrient availability and C cycling suggest that high MAP may affect forest C turnover indirectly, primarily by altering N and P availability. Further studies would be necessary to confirm the mechanistic links suggested by our findings, particularly by doing more detailed measurements and experimental manipulations of nutrient availability and rainfall exclusion in the wettest forests. This study brings new and valuable information for our general understanding of the biophysical determinants of C circulation and nutrient availability across the tropics. These results can also help us better predict how changes in precipitation regimes driven by climate change could alter the role of tropical forests in the global C cycle.

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