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Regional and temporal patterns of litterfall in tropical South America

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Abstract

The production of aboveground soft tissue represents an important share of total net primary production in tropical rain forests. Here we draw from a large number of published and unpublished datasets (n=81 sites) to assess the determinants of litterfall variation across South American tropical forests. We show that across old-growth tropical rainforests, litterfall averages 8.61±1.91 Mg/ha/yr. Secondary forests have a lower annual litterfall than old-growth tropical forests with a mean of 8.01±3.41 Mg/ha/yr. Annual litterfall shows no significant variation with total annual rainfall, either globally or within forest types. It does not vary consistently with soil type, except in the poorest soils (white sand soils), where litterfall is significantly lower than in other soil types (5.42±1.91 Mg/ha/yr). Litterfall declines significantly with increasing N:P. We also study the determinants of litterfall seasonality, and find that it does not depend on annual rainfall or on soil type. However, litterfall seasonality is significantly positively correlated with rainfall seasonality. Finally, we assess how much carbon is stored in reproductive organs relative to photosynthetic organs. Mean leaf fall is 5.74±1.83 Mg/ha/yr (71% of total litterfall). Mean allocation into reproductive organs is 0.69±0.40 Mg/ha/yr (9% of total litterfall). The investment into reproductive organs divided by leaf litterfall is negatively related to the N:P ratio, suggesting that on poor soils, the allocation to photosynthetic organs is prioritized over that to reproduction. Finally, we discuss the ecological and biogeochemical implications of these results.

1 Introduction

Since the early 1950s, an enormous amount of research has been devoted to the measurement of net primary production (NPP) in ecosystems, the amount of carbon that is fixed from the atmosphere into new organic matter. Of the 720 references reported in the Osnabrück dataset (Esser et al., 1997), only 21 were collected in tropical forest environments, an astonishingly small figure given that tropical rainforests account for a third of global terrestrial NPP, and savannas another quarter (Grace, 2004). Since that time, much progress has been made to quantify the carbon cycle in tropical forest ecosystems (Malhi et al., 2002, 2009; Keller et al., 2004), and there is still much activity around the development of global databases of the carbon cycle in terrestrial environments (Luyssaert et al., 2007).

In one of the most thorough recent reappraisals of tropical forest NPP quantification, Clark et al. (2001) compiled data from 39 tropical forest sites and they estimated total tropical forest NPP. Their estimates ranged between 3.1 and 21.7 Mg C/ha/yr, of which, 0.9 to 6.0 Mg C/ha/yr were allocated into soft tissues (leaves, reproductive organs and twigs). Tropical forest NPP was found to be poorly correlated with mean annual temperature and with annual rainfall (see also Schuur, 2003; Del Grosso et al., 2008). In a previous contribution, Malhi et al. (2004) explored the regional variation of the fraction of carbon fixed aboveground into woody parts in tropical South America (trunks and branches, wNPP). They focused on 104 permanent sampling plots where trunk diameter had been measured several times, and estimated the annual amount of carbon fixed into wood. Their major finding was that wNPP varied dramatically at the regional scale, and that a large part of this regional variation was due to soil type. Using the data available at 10 tropical forest sites in Amazonia, Aragão et al. (2009) showed that total NPP ranged between 9.3 and 17.0 Mg C/ha/yr, with a mean of 12.8 Mg C/ha/yr, much greater than recent regional tropical forest estimates (e.g. Luyssaert et al., 2007; Del Grosso et al., 2008).

Clark et al. (2001) also suggested that NPP was not strongly correlated with total litterfall, as had been previously suggested by Bray and Gorham's (1964) global model. They however acknowledged that their estimates were based on an indirect estimation of several key components of NPP. For Amazonian forests, Aragão et al. (2009) provide a most useful perspective on this question. Their analysis strongly supports Bray and Gorham's (1964) model: total NPP is consistently close to 3.1 times total litterfall. If their finding is general, this is a strong motivation for summarizing our current knowledge on the regional and temporal variation of total litterfall in the Amazon.

In the present contribution, we focus on the amount of carbon fixed into organs with short residence time, such as leaves, reproductive organs (flowers, fruits), and small branches. Like in most previous analyses, we assume that the ecosystem is at equilibrium, that is, the flux of carbon into this pool of carbon equals the flux of carbon outside of this flux. Then, the amount of NPP allocated annually to leaves, reproductive organs, and small branches should be equal to the annual litterfall. Leaf production and other components of litterfall should depend upon a large suite of environmental and geographical factors. In tropical South America, the determinants of this spatial variation remain poorly studied, and it is impossible to get even a superficial sense of the changes in litterfall production across environments and across regions. The goal of the present manuscript is to review the recent literature and explore whether available data are sufficient to draw general rules for the spatial variation of litterfall across South America.

We here bring together a large number of published and unpublished litterfall datasets, including a wide range of environmental conditions, such as terra firme rainforests, flooded rainforests, dry rainforests, and montane forests. We also partition litterfall into its main three components (leaves, fruits and flowers, and twigs, see Proctor 1983). We use this dataset to assess what determines the spatial and temporal variability in litterfall. Specifically, we address the following questions: (1) Is annual litterfall determined by edaphic or climatic factors? (2) Is the seasonality of litterfall determined by edaphic or climatic factors?, and (3) Does plant investment into photosynthetic organs and reproductive organs depend on environmental factors? Finally, we discuss the implications of our findings.

2 Methods

2.1 Dataset

We combed the literature for publications reporting figures on litterfall in tropical South America. In our analysis, we included the studies in central Panama, but not those of the rest of Central America. We also included a number of unpublished data. For each study, we reported the different parts of litterfall, including leaves, branches (usually less than 2 cm in diameter), flowers, fruits, and others, if available (Proctor, 1983). Litterfall was collected in litter-traps set up ca. 1–2 m above the ground to avoid disturbance by large mammals. We recorded the duration of the experiment, number of traps, and size of the traps. All litterfall figures (annual and monthly) were converted into Mg/ha/yr of dry biomass. We did not correct these figures for a possible loss to herbivory between censuses (Leigh, 1999; Clark et al., 2001), because this would have entailed making additional uncontrolled assumptions. Our litterfall estimates did not incorporate coarse woody debris, which may account for a sizeable fraction of carbon loss from the live vegetation (Chambers et al., 2001; Nepstad et al., 2002). In most cases, these estimates did not incorporate palm leaves which tend to be too large to be trapped by litter-traps, and the fruits and leaves produced by understory plants. This may result in a significant under-estimation of litterfall. For instance, in a wet rain forest of Costa Rica, over 10% of the total leaf area was below 2 m above ground (Clark et al., 2008).

In total, we report on 29 published studies (64 sites) and 7 unpublished ones (17 sites). The 81 sites included in the present analysis are detailed in Table 1. All of these studies comply with the minimal conditions for litterfall sampling proposed by Proctor (1983). The sampling duration varied from 1 year to 7 years (mean across sites: 1.97 yr), and the total area sampled (number of litterfall traps multiplied by the size of these traps, in m^2) varied from 1.92 to 60 m^2 (mean across sites: 10.1 m^2), with each trap at least 0.25 m^2 in area.

To evaluate the seasonality of litterfall, we created a database including the monthly litterfall data as reported in the published reports or in unpublished datasets. In a number of cases, these figures were reported in the form of figures. We scanned the figures, and retrieved the original data by digitizing the figure manually using the software DigitizeIt, version 1.5.8 (http://www.digitizeit.de/).

2.2 Environmental variables

Environmental variables included in the present analysis are soil type (see also Malhi et al., 2004), and rainfall data. Soil type, when available, was deduced from the publications, and mostly based on the World Reference Base Soil Taxonomy (WRB, 2006). More details on the distribution, area, and chemical properties of these soils type in Amazonia are available in Quesada (2008; see also Quesada et al., 2009). We classified the sites into four main soil categories, roughly increasing in soil fertility (concentration of phosphorus and of exchangeable cations in the soil, Quesada et al., 2009): A) highly permeable infertile soils (arenosols and podzols); B) relatively infertile ancient soils (ferrasols); C) relatively fertile acidic soils (acrisols, plinthosols and alisols) and D) fertile young or wet soils (cambisols, leptosols, histosols, gleysols or fluvisols). The one site with human-derived soil (archeo-anthrosol, CAX2 site: terra preta) was excluded from this classification.

When possible, we also reported the concentration of nitrogen and phosphorus in litterfall (N, P). The carbon to nitrogen ratio (C:N ratio) and the nitrogen to phosphorus ratio (N:P ratio) measure the depletion of nitrogen in plants, and the depletion of phosphorus relative to nitrogen, respectively. These values are tightly correlated with the resource availability of the soil on which the plants grow (McGroddy et al., 2004; Ågren, 2008; Quesada, 2008). If only data on N and P concentrations were available in live leaves (see e.g. Fyllas et al., 2009), we made use of these figures instead to compute the N:P ratio. This overestimates the concentration of both N and P in the litter because some of the N and P in leaves is retranslocated before leaf abscission (Chuyong et al., 2000). However as the same proportion of N and P appears to be retranslocated before leaf abscission (Chuyong et al., 2000), the N:P ratio should be similar in leaves and in litter. This finding is supported by a recent analysis at the scale of the entire Amazon (Quesada, 2008, chapt. 5). There, it was found that the correlation between leaf N and soil N was 0.33, while the correlation between leaf P and soil P was 0.56 (Kendall τ rank coefficient in both cases; values >0.19 are considered as significant).

Rainfall was derived from a climatic dataset that covers the period 1960–1998 (New et al., 1999), which minimizes the effects of interannual variability. For a few sites with strong climatic gradients near the Andes or close to the oceans, local meteorological data were preferred.

We also classified the data by forest type. The majority (n=51) was old-growth tropical rain forest (OG), but we also included a number of secondary (i.e. recently disturbed) rain forests (SEC, n=7), periodically or permanently flooded rainforest (FLO, n=10), montane rainforests (MON, n=5), and low vegetation (LOW, n=7). This last category is a composite of different vegetation types, including low vegetation growing on Colombian tepuis (Chiribiquete National Park), woodland savannas in Brazil and Colombia (cerrado), coastal oceanic vegetation in Brazil (restinga), and woodland savannas in Venezuela (caatinga).

2.3 Statistical analyses

We computed an index of seasonality as follows. We converted the month into a number from 0 (1 January) to 330 (1 December). This represents the number of days elapsed since the beginning of the year but also an angle in degrees. We used this convention to represent the data using a polar plot (Fig. 1), where the litterfall of month i are plotted using a vector starting from (0,0), with a length equal to the litterfall at month i (in Mg/ha/yr) and the angle equal to $30\times i$ (in degrees). The mean vector is obtained from the average of the projections along the x and the y axes. A similar analysis was performed to study the patterns of phenology across two seasonal rainforests (Zimmerman et al., 2007). The mathematical definition of the mean vector, $\boldsymbol{m}=(m_x, m_y)$,

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from the 12 monthly litterfall vectors $\boldsymbol{L}^i$ is:

$$m_x = \frac{1}{12}\sum_{i=0}^{11} \boldsymbol{L}^i \cos(30\times i)\,, \quad m_y = \frac{1}{12}\sum_{i=0}^{11} \boldsymbol{L}^i \sin(30\times i) \tag{1}$$

Here, $L^i = \|\boldsymbol{L}^i\|$ is the absolute value of litterfall (in Mg/ha/yr) for month i. Using these definition, annual litterfall is $L=\sum_{i=0}^{11} \boldsymbol{L}^i/12$. We finally define the seasonality index as follows

$$SL = \frac{\|\boldsymbol{m}\|}{L} \tag{2}$$

This index measures whether litterfall is evenly distributed throughout the year, in which case $SL\approx 0$. Alternatively, if litter falls only during one month, then $SL\approx 1$. Figure 1 represents polar plots with monthly litterfall data and the location of the mean vector, $\boldsymbol{m}=(m_x, m_y)$ for six of our study sites.

We also computed the seasonality in rainfall, based on monthly rainfall data, and called this parameter SR. Specifically, we defined SR as

$$SR = \frac{\|\boldsymbol{mr}\|}{R} \tag{3}$$

Where $\boldsymbol{mr} = (mr_x, mr_y)$, denotes the monthly rainfall vector defined like in Eq. (1) by

$$mr_x = \sum_{i=0}^{11} R^i \cos(30\times i)\,, \quad mr_y = \sum_{i=0}^{11} R^i \sin(30\times i) \tag{4}$$

Here, R^i is the monthly rainfall for month i measured in mm/mo. Then, annual rainfall is $R=\sum_{i=0}^{11} R^i$, a variable that appears in Eq. (3).

To investigate the relative investment into reproduction versus photosynthesis, we computed the RL ratio, the investment into reproductive organs divided by leaf fall. Hence a RL of 1 corresponds to an equal allocation into leaves and into reproductive organs. This excludes all non-photosynthetic organs which make up non-reproductive litterfall (twigs and trash) and provides a firm baseline for comparison across sites.

3 Results

3.1 Determinants of annual litterfall

In old-growth tropical rainforests, which cover the vast majority of the area under study, litterfall averaged 8.61±1.91 Mg/ha/yr (n=52, range: 5.19–12.47 Mg/ha/yr). We assessed Proctor's (1983) claim that one year of litterfall collection was enough to capture this variable. Of the 24 sites for which we had 2 years of data or more, mean interannual variability was found to be equal to 9.3% of the mean (range: 2–20%). Hence, one year of litterfall collection captures the long trend of litterfall within 10%.

Annual litterfall was higher in flooded forests than in old-growth tropical forests (Fig. 2), with a mean of 8.89±1.42 Mg/ha/yr (n=10, range: 6.6–11.21 Mg/ha/yr). Secondary forests had lower annual litterfall than old-growth tropical forests with a mean of 8.01±3.41 Mg/ha/yr (n=10, range: 5.01–14.74 Mg/ha/yr). The outlying secondary forest (14.74 Mg/ha/yr) was at the edge of the Mata de Piedade site, Atlantic rain forest of Brazil. Montane forests and low forests had lower mean annual litterfall (7.06±3.72 Mg/ha/yr and 3.01±1.67 Mg/ha/yr, respectively). Figure 3 shows the regional variation of litterfall across all the dataset (panel a) and restricted to old-growth forests (panel b).

Across forest types, annual litterfall showed no significant variation with total annual rainfall (Fig. 4). We excluded montane forests from this analysis because of the difficulty of estimating rainfall for these environments. With our analysis restricted to old-growth and flooded forests, the relationship between annual litterfall an annual rainfall was not significant (p=0.88 and p=0.23, respectively). Secondary forests showed a negative relationship of annual litterfall with annual rainfall, but this trend was not significant (p=0.18).

We limited our analysis of annual litterfall versus soil type to old-growth moist lowland rainforests (Fig. 5). The poor soils are found in group A (including white sand soils), and litterfall was significantly lower than in other soil types (5.27±1.86 Mg/ha/yr, n=6). Ferralsols (group B) also supported a forest producing less litterfall annually

(7.13 ± 2.53 Mg/ha/yr, $n=26$).

A similar analysis was performed by using the Redfield ratios C:N and N:P rather than soil types as independent variables (Ågren, 2008). Nitrogen-deprived plants have a large C:N ratio, while phosphorus-deprived plants have a large N:P ratio. Litterfall was found not to vary significantly with C:N across the entire dataset (Fig. 6, $p=0.43$, $n=47$), but it declined significantly with increasing N:P (Fig. 6, $p=0.02$, $n=36$).

3.2 Determinants of litterfall seasonality

Across all plots, the litterfall seasonality index *SL*, computed from 47 datasets, was of 0.166.

Litterfall seasonality was highest in small-statured forest sites (LOW), and lowest in montane and flooded forest sites (respectively MON and FLO, see Fig. 7). Litterfall seasonality did not depend on annual rainfall either across all datasets, or across old-growth forest sites only (in both cases, $p>0.4$, results not shown). Litterfall seasonality did not depend on soil type either.

Next we explored whether litterfall seasonality *SL* was related with the rainfall seasonality index *SR* (see the Methods section). We found a significantly positive relationship between litterfall seasonality and rainfall seasonality across all plots ($p=0.02$, $n=47$, Fig. 8). This result also held when the analysis was restricted to old-growth forests ($p=0.05$, $n=27$).

3.3 Carbon allocation in fast turnover plant organs

Finally, we asked how much carbon is stored in leaves and in reproductive organs. Across the dataset, 70.8 ± 8.5% of the litterfall was allocated to leaves ($n=74$, range 43.1–88.4%). Mean leaf fall was 5.74 ± 1.83 Mg/ha/yr. Likewise, 8.9 ± 5.6% of the litterfall was allocated to reproductive organs (0.8–18%). Mean allocation into reproductive organs was 0.69 ± 0.40 Mg/ha/yr. Notice however that some of these reproductive organs are designed to be eaten before they fall, hence our figure may be an underestimate.

Next we computed the *RL* ratio for our sites (investment into reproductive organs divided by leaf litterfall). Across sites, this ratio ranged between 0.008 and 0.89 and was 0.135 ± 0.119 on average (note that a ratio of 1 corresponds to an equal allocation into leaves and into reproductive organs). We did not find significant differences in the *RL* among forest types, except secondary forests where *RL* was significantly smaller (0.07 ± 0.018).

The *RL* ratio varied across soil types. It was smallest on group-A soils ($RL=0.081 \pm 0.036$, $n=5$), in acidic group-C soils ($RL=0.11 \pm 0.06$, $n=22$), in group-B ferralsols ($RL=0.17 \pm 0.21$, $n=16$), and finally in richer group-D soils (0.18 ± 0.07, $n=11$). Given that frugivore activity also correlates positively with nutrients, the actual *RL* ratios probably increase more steeply than this with soil nutrients. This suggests that plants growing on rich soils invest proportionally more into reproduction than into photosynthesis. We confirmed this finding by regressing *RL* against the N:P ratio, and we found a significant negative relationship ($p=0.07$, Fig. 9).

4 Discussion

Assuming that litterfall biomass contains 47% of carbon (cross-site mean taken from Fyllas et al., 2009), the total annual litterfall corresponds to a mean of 4.0 Mg C/ha/yr in old-growth tropical forests. This is in line with previous estimates of Amazon-wide allocation of carbon into the fast turnover carbon pool (Clark et al., 2001). If the overall figure of NPP around 12.8 Mg C/ha/yr is valid for Amazonian forests (Aragão et al., 2009), then, about a third of total NPP is invested into leaves, twigs and reproductive organs. The largest fraction of soft tissue allocation is invested into photosynthesis (ca. 71%). Another 9% is invested into reproduction. Following Clark et al. (2001), we reemphasize that the estimates of litterfall reported here do not include large branches. Other methods may be used to assess how much carbon is released by branch falls, and this flux ranges between 0.4 and 1.8 Mg C/ha/yr (Chambers et al., 2001; Nepstad

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Most of the NPP eventually contributing to fine litterfall is allocated to leaves. Because leaf fall was estimated around 2.8 Mg C/ha/yr in the field, the stocks of photosynthetically active material available in the ecosystem may be estimated through two independent methods. First, the stock of leaves at any one time *fB* is related to *fNPP* through the mean lifetime of leaves, denoted by τ, $\tau = fB/fNPP$. This parameter τ can be estimated directly for selected species, and it varies between 6 months for secondary moist tropical forests (n=20, Coley, 1988), and 25 months for old-growth tropical forests on poor soils (n=23, Reich et al., 2004). Taking an average value of τ=1 yr, the stock of leaf biomass is estimated at 2.8 Mg C/ha, or 280 g C/m^2. Alternatively, assuming that the leaf area index of Amazonian forests is close to 5.4 m^2/m^2 (Malhi et al., 2009; Patiño et al., 2008; it may reach up to 7 m^2/m^2, see Clark et al., 2008), and that mean leaf-mass area (LMA) is around 47 g C/m^2 (cross-site mean taken from Fyllas et al., 2009), then leaf biomass should be 254 g C/m^2. These two estimates tightly bracket the leaf biomass stocks in tropical rain forests. They also provide a consistency check for some of the lesser known variables in Amazonian rainforests (mean leaf lifetime and leaf area index).

Secondary forests showed a peculiar signal compared with old-growth forests. Although the total annual litterfall was comparable between secondary forests and old-growth forests, the former were less seasonal, and they invested less in reproduction than in photosynthesis. Since secondary tropical forests are likely to cover an ever larger area than today, and will remain in secondary status for a long time (Chazdon, 2003; Feldpausch et al., 2005, 2007), it is critical to account for this in global carbon cycle models.

There was a positive correlation between total litterfall and soil richness. This pattern may be underestimated in our analysis because herbivory is more active in the most fertile forests (Gentry and Emmons, 1987). Litterfall is already highest in forests growing on fertile soils (Fig. 5), and the amount of missed litterfall is difficult to quantify. Also, in many Amazonian forests, palms are an important fraction of the flora, and these palms also contribute to number of bias to litterfall as estimated by litter traps. Large palms tend to trap litter in their crown hence reducing the amount of litter falling to the ground (Alvarez-Sánchez and Guevara, 1999). Furthermore, many palm species have big leaves that tend to be discarded in litter trap measurements, since they are considered as coarse debris. These effects add up in western Amazonian forests, and it would therefore be important to develop different methods for litter collection in these forests. Then the positive relationship between litterfall and soil richness (see Fig. 5) may be linear rather than curvilinear.

We found a weak but significant correlation between litterfall seasonality and rainfall seasonality. This may be explained by limitations in our dataset, or by biological mechanisms. In the former class, several unpublished datasets span unusual climatic years, such as the intense 2005 drought, and they may therefore be not representative of the long-term trend in seasonality. In the latter category of explanations, it is known that leaves are not shed or flushed only in response to variation in rainfall. Recently developed methods may be used to estimate, even though indirectly, the large scale variation in leaf coverage seasonality. Myneni et al. (2007) used remote sensing imagery techniques to show how the seasonality in green leaf cover (leaf area index, or LAI) varies across the Amazon. They also sought for causal explanations for this variation. Specifically, they suggested that LAI was driven by the seasonality in solar radiation, rather than in rainfall. Indeed, solar radiation may be a foremost trigger for the flushing of new leaves during the dry season (see Wright and van Schaik, 1994), but also of leaf abscission, leading to concerted leaf fall. Phenological models (Morin and Chuine, 2005) remain poorly developed for tropical trees (Sakai, 2001), and this important challenge is ahead of us.

Finally, our results shed light on carbon allocation strategies of tropical trees. We have shown that in poor soils, and especially in phosphorus-deprived environments, forests as a whole tend to invest less into the construction of reproductive organs relative to photosynthesis. This suggests that allocation into leaves (hence photosynthesis) is the priority for plants, but when resources are well supplied the excess in resources is made available for reproduction. Also, the plants of poor-soil communities seem to converge toward a low growth rate, low mortality rate and infrequent reproduction, a classic example of habitat filtering (Weiher and Keddy, 1999). The pattern we uncovered should however be considered critically. Tropical forest reproduction is often characterized by infrequent events of mast-flowering, hence the *RL* ratio should show a high interannual variability. For instance, at the Nouragues site, one of the dominant tree families, the Chrysobalanaceae has a mast-fruiting strategy, and these species have only fruited once between 2001 and 2008 (Norden et al., 2007). Hence, it would be essential to rely on long-term monitoring programs to accurately measure *RL*. Also, the N:P ratio in litterfall is only a rough proxy of resource richness (Quesada, 2008). Finally, fruit production is clearly underestimated in palm-rich forests of western Amazon. More refined tests of this hypothesis should be based on more thorough and appropriate measurements of resources available to plants.

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References

Ågren, G. I.: Stoichiometry and nutrition of plant growth in natural communities, Ann. Rev. Ecol. Evol. Syst, 39, 153–170, 2008.

Alvarez-Sánchez, J. and Guevara, S.: Litter interception on *Astrocaryum mexicanum* Lieb. (Palmae) in a tropical rain forest, Biotropica, 31, 89–92, 1999

Aragão, L. E. O. C., Malhi, Y., Metcalfe, D. B., Espejo, J. E. S., Jiménez, E., Navarrete, D., Almeida, S., Costa A. C. L., Salinas, N., Phillips, O. L., Anderson, L. O., Baker, T. R., Dávila,

A. R., Goncalvez, P. H., Junior, J. A. S., Meir, P., Monteagudo, A., Ovalle, J. H., Prieto, A., Quesada, C. A., Rudas, A., Solórzano, M. M., and Vasquez, R.: Above- and below-ground net primary productivity across ten Amazonian forests on contrasting soils, Biogeosciences Discuss., accepted, 2009.

Barbosa, R. A. and Fearnside, P. M.: Carbon and nutrient flows in an Amazonian forest: Fine litter production and composition at Apiau, Roraima, Brazil. Trop. Ecol., 37, 115–125, 1998.

Barlow, J., Gardner, T. A., Ferreira, L. V., and Peres, C. A.: Litter fall and decomposition in primary, secondary and plantation forests in the Brazilian Amazon, For. Ecol. Manag., 247, 91–97, 2007.

Brando, P. M., Nepstad, D. C., Davidson, E. A., Trumbore, S. E., Ray, D., and Camargo, P.: Drought effects on litterfall, wood production and belowground carbon cycling in an Amazonian forest: result of a throughfall reduction experiment, Phil. Trans. Roy. Soc. B., 363, 1839–1848, 2008.

Bray, J. R. and Gorham, E.: Litter production in forests of the world, Adv. Ecol. Res., 2, 101–157, 1964.

Chambers J. Q., dos Santos J., Ribeiro R. J., and Higuchi N.: Tree damage, allometric relationships, and above-ground net primary production in central Amazon forest, For. Ecol. Manage., 152, 73–84, 2001.

Chazdon, R. L.: Tropical forest recovery: Legacies of human impact and natural disturbances, Persp. Plant Ecol. Evol. Syst., 6, 51–71, 2003.

Chuyong, G. B., Newbery, D. M., and Songwe, N. C.: Litter nutrients and retranslocation in a central African rain forest dominated by ectomycorrhizal trees, New Phytol., 148, 493–510, 2000.

Clark, D. A., Brown, S., Kicklighter, D. W., Chambers, J. Q., Thomlinson, J. R., Ni, J., and Holland, E. A.: Net primary production in tropical forests: an evaluation and synthesis of existing field data, Ecol. Applic., 11, 371–384, 2001.

Clark, D. B., Olivas, P. C., Oberbauer, S. F., Clark, D. A., and Ryan, M. G.: First direct landscape-scale measurement of tropical rain forest Leaf Area Index, a key driver of global primary productivity, Ecol. Let., 11, 163–172, 2008.

Coley, P. D.: Effects of plant growth rate and leaf lifetime of the amount and type of anti-herbivore defense, Oecologia, 74, 531–536, 1988.

Cuevas, E. and Medina, E.: Nutrient dynamics within Amazonian forest ecosystems. I. Nutrient flux in fine litterfall and efficiency in nutrient utilization, Oecologia, 68, 4466–4472, 1986.

Del Grosso, S., Parton, W., Stohlgren, T., Zheng, D. L., Bachelet, D., Prince, S., Hibbard, K., and Olson, R.: Global potential net primary production predicted from vegetation class, precipitation, and temperature, Ecology, 89, 2117–2126, 2008.
Dezzeo, N. and Chacon, N.: Litterfall and nutrient input in undisturbed and adjacent fire disturbed forests of the Gran Sabana, Southern Venezuela, Interciencia, 31, 894–899, 2006.
Dantas, M. and Phillipson, J.: Litterfall and litter nutrient content in primary and secondary Amazonian "terra firme" rain forest, J. Trop. Ecol., 5, 27–36, 1989.
Esser, G., Lieth, H. F. H., Scurlock, J. M. O., and Olson, R. J.: Worldwide Estimates and Bibliography of Net Primary Productivity Derived from pre-1982 Publications, ORNL/TM-13485, Oak Ridge National Laboratory, Oak Ridge, Tennessee, USA, 1997.
Feldpausch, T. R., Riha, S., Fernandes, E. C. M., and Wandelli, E. V.: Development of forest structure and leaf area in secondary forests regenerating on abandoned pastures in Central Amazonia, Earth Interacti., 9, 1–22, 2005.
Feldpausch, T. R., Prates-Clark, C. C., Fernandes, E. C. M., and Riha, S. J.: Secondary forest growth deviation from chronosequence predictions in central Amazonia, Glob. Change Biol., 13, 967–979, 2007.
Fittkau, E. J. and Klinge, H.: On biomass and trophic structure of the Central Amazonian rain forest ecosystem, Biotropica, 5, 2–14, 1973.
Fyllas, N. M., Patiño, S., Baker, T. R., Nardoto, G. B., Martinelli, L. A., Quesada, C. A., Paiva, R., Schwarz, M., Horna, V., Mercado, L. M., Santos, A. J. B., Arroyo, L., Jiménez, E. M., Luizão, F. J., Neill, D. A., Silva, N. M., Prieto, A., Rudas, A., Silviera, M., Viera, I., López-González, G., Malhi, Y., Phillips, O. L., and Lloyd, J.: Basin-wide variations in foliar properties of Amazon forest trees: Phylogeny, soils and climate, Biogeosciences Discuss., accepted, 2009.
Gentry, A. H. and Emmons, L. H.: Geographical variation in fertility, phenology, and composition of the understory of neotropical forests, Biotropica, 19, 216–227, 1987
Grace, J.: Understanding and managing the global carbon cycle, J. Ecol., 92, 189–202, 2004.
Keller, M., Alencar, A., Asner, G. P., Braswell, B., Bustamente, M., Davidson, E., Feldpausch, T., Fernandes, E., Goulden, M., Kabat, P., Kruijt, B., Luizão, F., Miller, S., Markewitz, D., Nobre, A. D., Nobre, C. A., Priante Filho, N., da Rocha, H., Silva Dias, P., von Randow, C., and Vourlitis, G. L.: Ecological research in the Large-Scale Biosphere-Atmosphere experiment in Amazonie: early results, Ecol. Appl., 14, S3–S16, 2004.
Klinge, H. and Rodrigues, W. A.: Litter production in an area of Amazonian terra firme forest,

Amazoniana, 1, 287–310, 1968.
Leigh Jr., E. G.: Tropical Forest Ecology. A View from Barro Colorado Island, Oxford University Press, Oxford, 245 pp., 1999.
Lips, J. M., Duivenvoorden, J. F.: Fine litter input to terrestrial humus forms in Colombian Amazonia, Oecologia, 108, 138–150, 1996.
Luizão, R. C. C., Luizão, F. J., Paiva, R. Q., Monteiro, T. F., Sousa, L. S., and Kruijt, B.: variation of carbon and nitrogen cycling processes along a topographic gradient in a central Amazonian forest, Glob. Change Biol., 10, 592–600, 2004.
Luizão, F. J.: Litter production and mineral element input to the forest floor in a Central Amazonian forest, GeoJournal, 19, 407–417, 1989.
Luyssaert, S., Inglima, I., Jung, M., Richardson, A. D., Reichstein, M., et al.: CO_2 balance of boreal, temperate, and tropical forests derived from a global database, Glob. Change Biol., 13, 2509–2537, 2007.
Malhi, Y., Phillips, O. L., Baker, T. R., et al.: An international network to understand the biomass and dynamics of Amazonian forests (RAINFOR), J. Veg. Sci., 13, 439–450, 2002.
Malhi, Y., Baker, T. R., Phillips, O. L., et al.: The above-ground coarse wood productivity of 104 Neotropical forest plots, Glob. Change. Biol., 10, 563–591, 2004.
Malhi, Y., Aragão, L. E. O. C., Metcalfe, D. B., Paiva, R., Quesada, C. A., Almeida, S., Anderson, L., Brando, P., Chambers, J. Q., da Costa, A. C. L., Hutyra, L. R., Oliveira, P., Patiño, S., Pyle, L. H., Robertson, A. L., and Teixeira, L. M.: Comprehensive assessment of carbon productivity, allocation and storage in three Amazonian forests, Glob. Change Biol., in press, 2009.
Martius, C., Höfer, H., Garcia, M. V. B., Römbke, J., and Hanagarth, W.: Litter fall, litter stocks and decomposition rates in rainforest and agroforestry sites in central Amazonia, Nutr. Cycl. Agroecosyst., 68, 137–154, 2004.
McGroddy ,M. E., Daufresne, T., and Hedin, L. O.: Scaling of C:N:P stoichiometry in forests worldwide: Implications of terrestrial Redfield-type ratios, Ecology, 85, 2390–401, 2004
Morães, R. M., Carvalho, W. B., and Struffaldy de Vuono, Y.: Litterfall and litter nutrient content in two Brazilian tropical forests, Rev. Bras. Bot. 22, 9–16, 1999.
Morin, X. and Chuine, I.: Sensitivity analysis of the tree distribution model PHENOFIT to climatic input characteristics: Implications for climate impact assessment, Glob. Change Biol., 9, 1493–1503, 2005.
Myneni, R. B., Yanga, W., Nemani, R. R., Huete, A. R., Dickinsone, R. E., Knyazikhina, Y.,

Didan, K., Fu, R., Negron Juarez, R. I., Saatchi, S. S., Hashimoto, H., Ichii K., Shabanov, N. V., Tana, B., Ratana, P., Privette, J. L., Morisette, J. T., Vermote, E. F., Roy, D. P., Wolfe, R. E., Friedl, M. A., Running, S. W., Votava, P., El-Saleous, N., Devadiga, S., Su, Y., and Salomonson, V. V.: Large seasonal swings in leaf area of Amazon rainforests, PNAS, 104, 4820–4823, 2007.

Nebel, G., Dragsted, J., and Vega, A. S.: Litter fall, biomass and net primary production in flood plain forests in the Peruvian Amazon, For. Ecol. Manage., 150, 93–102, 2001.

Nepstad, D. C., Moutinho, P., Dias-Filho, M. B., Davidson, E., Cardinot, G., Markewitz, D., Figueiredo, R., Vianna, N., Chambers, J., Ray, D., Guerreiros, J. B., Lefebvre, P., Sternberg, L., Moreira, M., Barros, L., Ishida, F. Y., Tohlver, I., Belk, E., Kalif, K., and Schwalbe, K.: The effects of partial throughfall exclusion on canopy processes, aboveground production, and biogeochemistry of an Amazon forest, J. Geophys. Res. Atm., 107, 8085, doi:10.1029/2001JD000360, 2002.

New, M., Hulme, M., and Jones, P.: Representing twentieth century space-time climate variability. Part I. Development of a 1961–1990 mean monthly terrestrial climatology, J. Climate, 12, 829–856, 1999.

Norden, N., Chave, J., Belbenoît, P., Caubère, A., Châtelet, P., Forget, P.-M., and Thébaud, C.: Mast fruiting is a frequent strategy in woody species of Eastern South America, PLoS ONE, 2, e1079, 2007.

Patiño, S., Lloyd, J., Paiva, R., Quesada, C. A., Baker, T. R., Santos, A. J. B., Mercado, L. M., Malhi, Y., Phillips, O. L., Aguilar, A., Alvarez, E., Arroyo, L., Bonal, D., Costa, A. C. L., Czimczik, C. I., Gallo, J., Herrera, R., Higuchi, N., Horna, V., Hoyos, E. J., Jimenez, E. M., Killeen, T., Leal, E., Luizão, F., Meir, P., Monteagudo, A., Neill, D., Núñez-Vargas, P., Palomino, W., Peacock, J., Peña-Cruz, A., Peñuela, M. C., Pitman, N., Priante Filho, N., Prieto, A., Panfil, S. N., Rudas, A., Salomão, R., Silva, N., Silveira, M., Soares de Almeida, S., Torres-Lezama, A., Turriago, J. D., Vásquez-Martínez, R., Schwarz, M., Sota, A., Schmerler, J., Vieira, I., Villanueva, B., and Vitzthum, P.: Branch xylem density variations across Amazonia, Biogeosciences Discuss., 5, 2003–2047, 2008, http://www.biogeosciences-discuss.net/5/2003/2008/.

Priess, J. A., Then, C., and Fölster, H.: Litter and fine-root production in three types of tropical premontane rain forest in SE Venezuela, Plant Ecol., 143, 171–187, 1999.

Proctor, J.: Tropical Forest Litterfall. I. Problems of Litter Comparison. in: Tropical Rain Forest: Ecology and Management, edited by: Sutton, S. L., Whitmore, T. C., and Chadwick. A. C.,

Blackwell, Oxford, 267–273, 1983.
Puig, H., Riéra, B., and Lescure, J.-P.: Phytomasse et productivité, Bois Forêts Trop., 220, 25–32, 1983.
Quesada, C. A.: Soil Vegetation Interactions Across Amazonia. Unpublished PhD dissertation, University of Leeds, 2008.
Quesada, C. A., Lloyd, J., Schwarz, M., Patiño, S., Baker, T. R., Czimczik, C. I., Fyllas, N. M., Martinelli, L. A., Nardoto, G. B., Schmerler, J., Santos, A. J. B., Hodnett, M. G., Herrera, R., Luizão, F. J., Arneth, A., Lloyd, G., Dezzeo, N., Hilke, I., Kuhlmann, I., Raessler, M., Moraes Filho, J., Paiva, R, Araujo Filho, R., Chaves, E., Cruz Junior, O., Pimentel, T. P., and Paiva, R.: Chemical and physical properties of Amazonian forest soils in relation to their genesis, Biogeosciences Discuss., accepted, 2009.
Reich, P. B., Uhl, C., Walters, M. B., Prugh, L., and Ellsworth, D. S.: Leaf demography and phenology in Amazonian rain forest: a census of 40 000 leaves of 23 tree species, Ecol. Monogr., 74, 3–23, 2004.
Röderstein, M., Hertel, D., and Leuschner, C.: Above- and below-ground litter production in three tropical montane forests in Southern Ecuador, J. Trop. Ecol., 21, 483–492, 2005.
Sakai, S.: Phenological diversity in tropical forests, Pop. Ecol., 43, 77–86, 2001.
Santiago, L. S., Schuur, E. A. G., and Silvera, K.: Nutrient cycling and plant-soil feedbacks along a precipitation gradient in Lowland Panama, J. Trop. Ecol., 21, 461–470, 2005.
Schessl, M., Luiz da Silva, W., and Gottsberger, G.: Effects of fragmentation on forest structure and litter dynamics in Atlantic rainforest in Pernambuco, Brazil, Flora, 203, 215–228, 2008.
Schuur, E. A. G.: Productivity and global climate revisited: the sensitivity of tropical forest growth to precipitation, Ecology, 84, 1165–1170, 2003.
Scott, D. A., Proctor, J., and Thompson, J.: Studies on a lowland evergreen rain forest on Maraca island, Roraima, Brazil. II. Litter and nutrient cycling, J. Ecol., 80, 705–717, 1992.
Selva, E. C., Couto, E. G., Johnson, M. S., and Lehmann, J.: Litterfall production and fluvial export in headwater catchments of the southern Amazon, J. Trop. Ecol., 23, 329–335, 2007.
Silva, C. J., Sanches, L., Bleich, M. E., Lobo, F. A., and Nogueira, J. S.: Produção de serrapilheira no cerrado e floresta de transição Amazônia-Cerrado do Centro-Oeste Brasileiro, Acta Amazonica, 37, 543–548, 2007.
Sizer, N. C., Tanner, E. V. J., and Kossmann Ferraz, I. D.: Edge effects on litterfall mass and nutrient concentrations in forest fragments in central Amazonia, J. Trop. Ecol., 16, 853–863, 2000.

Smith, K., Gholz, H. L., and Oliveira, F. A.: Litterfall and nitrogen-use efficiency of plantations and primary forest in the eastern Brazilian Amazon, For. Ecol. Manage., 109, 209–220, 1998.

Sombroek W. G.: Amazon land forms and soils in relation to biological diversity, Acta Amazonica, 30, 81–100, 2000.

Vasconcelos, H. L. and Luizão, F. L.: Litter production and litter nutrient concentrations in a fragmented Amazonian landscape, Ecol. Appl., 14, 884–892, 2004.

Veneklaas, E. J.: Litterfall and nutrient fluxes in two montane tropical rain forests, Colombia, J. Trop. Ecol., 7, 319–336, 1991.

Weiher, E. and Keddy, P. A.: Ecological Assembly Rules: Perspectives, Advances, Retreats, Cambridge University Press, Cambridge, 1999.

WRB: World Reference Base for Soil Resources. A framework for international classification, correlation and communication, in: World Soil Resources Report, vol. 103, FAO, Rome, 2006.

Wright, S. J. and van Schaik, C. P.: Light and the phenology of tropical trees, Am. Nat., 143, 192–199, 1994.

Zimmerman, J. K., Wright, S. J., Calderon, O., Aponte Pagan, M., and Paton, S.: Flowering and fruiting phenologies of seasonal and aseasonal neotropical forests: the role of annual changes in irradiance, J. Trop. Ecol., 23, 231–251, 2007.

Table 1. Description of the study sites. For each site, the full site name, country, conventional site code and geographical coordinates (long.-lat., in degrees) are reported. Environmental variables include a general descriptor of forest type (LOW: short-statured tropical forest, MON: montane tropical forest, SEC: secondary tropical forest, OG: old-growth tropical forest, FLO: partially flooded tropical forests), dominant soil group (World Reference Base Soil Taxonomy System), the C:N and N:P ratios in leaves, annual rainfall (in mm/yr), and the rainfall seasonality index *SR* (in %). The next column report annual litterfall (Mg/ha/yr), the litterfall seasonality index *SL*, annual leaf fall (in Mg/ha/yr), allocation into reproductive organs (fruits and flowers, in Mg/ha/yr), and the ratio of reproductive litterfall and leaf fall (index RL in %). The sampling strategy includes the duration of litterfall sampling (in yr), the dates at which litterfall was monitored, the size of litterfall traps (in m^2), and the availability of monthly data (Y for yes, N for no). Finally, the reference from which these data were extracted is reported. The C:N and N:P ratios were obtained from Fyllas et al. (2009) for the following sites: AGP1, AGP2, TAM5, TAM6, and TAP1.

Site name	Country	Site code	long.	lat.	Forest type	Dominant soil group	C:N	N:P	Rainfall	*SR*	Total litterfall	*SL*	Leaf litterfall	Reprod litterfall	*RL*	Monitoring duration	Interval	# traps	Trap size	Monthly data	Reference
Amacayacu E	Colombia	AGP1	−70.3	−3.72	OG	Plinthosol	21.8	19.70	2888	0.13	7.90	0.02	6.45	0.39	0.060	2.0	2004–2006	25	0.5	Y	This study
Amacayacu U	Colombia	AGP2	−70.3	−3.72	OG	Plinthosol	23.8	20.00	2888	0.13	7.23	0.05	5.78	0.63	0.109	2.0	2004–2006	25	0.5	Y	This study
Apiaú, Roraima	Brazil	APR	−61.3	2.57	OG	Acrisol	29.88	25.15	1902	0.47	9.17	0.08	5.57	0.28	0.050	1.0	1988–1989	6	1	Y	Barbosa and Fearnside (1996)
poachers1	Panamá	BCI1	−79.8	9.28	OG	Acrisol			2617	0.34	11.29		7.53	0.76	0.101	5.0	1988–1992	15	0.25	N	Leigh (1999)
poachers2	Panamá	BCI2	−79.8	9.28	OG	Acrisol			2617	0.34	12.13		7.69	1.63	0.212	5.0	1988–1992	15	0.25	N	Leigh (1999)
poachers3	Panamá	BCI3	−79.8	9.28	OG	Acrisol			2617	0.34	12.02		7.14	1.02	0.143	5.0	1988–1992	15	0.25	N	Leigh (1999)
poachers4	Panamá	BCI4	−79.8	9.28	OG	Acrisol			2617	0.34	11.16		6.87	1.02	0.148	4.0	1988–1991	15	0.25	N	Leigh (1999)
BDFFP Reserve	Brazil	BDF1	−60	−2.5	OG	Ferralsol	32.19	51.78	2470	0.32	8.82		6.63	0.60	0.090	3.0	1999–2002	140	0.25	N	Vasconcelos and Luizao (2004)
BDFFP Reserve	Brazil	BDF2	−60	−2.5	SEC	Ferralsol	32.03	54.04	2470	0.32	9.5		7.05	0.63	0.089	3.0	1999–2002	140	0.25	N	Vasconcelos and Luizao (2004)
Dimona fragment BDFFP	Brazil	BDF3	−60	−2.5	OG	Ferralsol	25.57	30.34	2470	0.32	7.21	0.15				3.0	1990–1994	18	1	Y	Sizer et al. (2000)
Capitao Paco, Pará	Brazil	CAP1	−47.2	−1.73	OG	Ferralsol	31.46	31.94	2471	0.49	8.04	0.11				1.0	1979–1980	16	1	Y	Dantas and Phillipson (1989)
Capitao Paco, Pará	Brazil	CAP2	−47.2	−1.73	SEC	Ferralsol	29.80	19.51	2471	0.49	5.04	0.16				1.0	1979–1980	16	1	Y	Dantas and Phillipson (1989)
Cardoso Island	Brazil	CAR1	−48	−25.1	OG				2225	0.27	6.31		4.42	0.8	0.181	1.0	1990–1991	30	0.25	Y	Moraes et al. (1999)
Cardoso Island restinga	Brazil	CAR2	−48	−25.1	LOW	Arenosol			2225	0.27	3.92		2.92	0.25	0.086	1.0	1990–1991	30	0.25	Y	Moraes et al. (1999)
Caxiuanã tower	Brazil	CAX1	−51.5	−1.72	OG	Ferralsol			2489	0.42	7.79	0.23	5.65	0.94	0.166	2.0	2005–2006	25	0.25	Y	This study
Caxiuanã terra preta	Brazil	CAX2	−51.5	−1.72	OG	Anthrosol			2489	0.42	9.17	0.31	6.85	1.20	0.175	2.0	2005–2006	25	0.25	Y	This study
Chiribiquete, Tepuy	Colombia	CHI1	−72.4	0.07	LOW	Leptosol			1996	0.13	4.17	0.28	3.29	0.30	0.091	3.0	1999–2002	24	0.5	Y	This study
Chiribiquete, TF Alta	Colombia	CHI2	−72.4	0.07	OG	Cambisol			1996	0.16	6.67	0.23	4.70	0.84	0.179	3.0	1999–2002	24	0.5	Y	This study
Chiribiquete, TF Baja	Colombia	CHI3	−72.4	0.07	OG	Acrisol			1996	0.16	8.45	0.14	6.11	0.82	0.134	3.0	1999–2002	24	0.5	Y	This study
Chiribiquete, Rebalse	Colombia	CHI4	−72.4	0.07	FLO	Gleysol			1996	0.16	8.39	0.08	5.83	0.94	0.161	2.0	2004–2006	25	0.5	Y	This study
Cordillera Central 2550 m asl	Colombia	COC1	−75	5	MON	Cambisol	38.63	13.43	2763	0.04	7.03	0.01	4.61	0.66	0.143	1.0	1986–1987	10	0.25	Y	Veneklaas (1991)
Cordillera Central 3370 m asl	Colombia	COC2	−75	5	MON	Cambisol	56.71	18.00	2763	0.04	4.31	0.10	2.82	0.27	0.096	1.0	1986–1987	20	0.25	Y	Veneklaas (1991)
Cuieiras Reserve Plateau	Brazil	CUR1	−60.1	−2.58	OG	Ferralsol	24.59	48.71	2442	0.34	8.25	0.09	5.42	0.42	0.077	3.0	1979–1982	15	0.5	Y	Luizao (1989)
Cuieiras Reserve Valley	Brazil	CUR2	−60.1	−2.58	FLO	Podzol	30.72	29.46	2442	0.34	7.44	0.07	4.69	0.43	0.092	3.0	1979–1982	15	0.5	Y	Luizao (1989)
Cuieiras Reserve Plateau	Brazil	CUR3	−60.1	−2.57	OG	Ferralsol	22.99		2442	0.34	8.9		6.94					10	0.25	N	Luizao et al. (2004)
Cuieiras Reserve Slope	Brazil	CUR4	−60.1	−2.57	OG	Acrisol	23.92		2442	0.34	7.6		6.16					10	0.25	N	Luizao et al. (2004)
Cuieiras Reserve Valley	Brazil	CUR5	−60.1	−2.58	FLO	Podzol	35.86		2442	0.34	6.6		4.88					10	0.25	N	Luizao et al. (2004)
Curuá-Una Reserve	Brazil	CUU	−54	−2	OG	Ferralsol	37.92		1714	0.42	9.7	0.15	6.87	1.36	0.198	1.0	1994–1995	45	1	Y	Smith et al. (1998)
Ducke Forest Reserve	Brazil	DUC	−59.8	−2.72	OG	Ferralsol	31.11	48.00	2250	0.33	7.3		5.60	0.35	0.063	1.0	1963–1964	10	0.25	N	Klinge and Rodrigues (1968)
Gran Sabana, Guayana	Venezuela	GRS1	−61.3	5	OG	Ferralsol	50.92	83.40	1573	0.30	5.19	0.18				1.0	1999–2000	8	0.5	Y	Dezzeo and Chacon (2006)

Table 1. Continued.

Site name	Country	Site code	long.	lat.	Forest type	Dominant soil group	C:N	N:P	Rainfall	*SR*	Total litterfall	*SL*	Leaf litterfall	Reprod litterfall	*RL*	Monitoring duration	Interval	# traps	Trap size	Monthly data	Reference
Gran Sabana, Guayana	Venezuela	GRS2	−61.3	5	OG	Ferralsol	56.21	86.83	1573	0.30	5.64	0.18				1.0	1999–2000	8	0.5	Y	Dezzeo and Chacon (2006)
Gran Sabana, Guayana	Venezuela	GRS3	−61.3	5	LOW	Ferralsol	59.19	76.62	1573	0.30	3.93	0.10				1.0	1999–2000	8	0.5	Y	Dezzeo and Chacon (2006)
Guama, Para	Brazil	GUA	−48.5	−1.37	OG	Ferralsol	28.56	38.05	2751	0.40	9.9		8.00							N	Klinge (1977)
Jari, Para primary	Brazil	JAR1	−52	−1	OG	Ferralsol			2293	0.39	10.74	0.20	7.84	1.16	0.148	1.0	2004–2005	100	0.25	Y	Barlow et al. (2007)
Jari, Para secondary	Brazil	JAR2	−52	−1	SEC	Ferralsol			2293	0.39	8.45	0.19	6.92	0.48	0.069	1.0	2004–2005	100	0.25	Y	Barlow et al. (2007)
Rio Juruena	Brazil	JUR	−58.8	−10.4	OG	Acrisol			1970	0.50	11.8	0.36	5.90			1.0	2003–2004	15		Y	Selva et al. (2007)
Maracá Island, Peltogyne-rich forest	Brazil	MAI1	−61.4	3.37	FLO	Acrisol	38.14	18.44	1572	0.49	7.93	0.12	5.44	0.71	0.131	1.0	1991–1992	33	0.32	Y	Villela and Proctor (1999)
Maracá Island, Peltogyne poor forest	Brazil	MAI2	−61.4	3.37	FLO	Acrisol	38.14	19.34	1572	0.49	9.07	0.05	6.02	0.92	0.153	1.0	1991–1992	33	0.32	Y	Villela and Proctor (1999)
Maracá Island, Forest without Peltogyne	Brazil	MAI3	−61.4	3.37	FLO	Acrisol	38.14	19.34	1572	0.49	8.58	0.07	5.92	0.93	0.157	1.0	1991–1992	33	0.32	Y	Villela and Proctor (1999)
Maracá Island	Brazil	MAI4	−61.4	3.37	FLO	Acrisol	35.42	17.60	1572	0.49	9.28	0.06	6.3	1.21	0.192	1.0	1987–1988	27	1	Y	Scott et al. (1992)
Manaus Floresta	Brazil	MAN1	−59.9	−3.13	OG	Ferralsol	31.69		2169	0.32	8.71	0.15	6.03	0.46	0.076	2.0	1997–1999	20	0.25	Y	Martius et al. (2004)
Manaus Secondary	Brazil	MAN2	−59.9	−3.13	SEC	Ferralsol	34.09		2169	0.32	7.38	0.21	6.09	0.31	0.051	2.0	1997–1999	20	0.25	Y	Martius et al. (2004)
Mata de Piedade	Brazil	MDP1	−35.2	−7.83	OG	Acrisol			1206	0.43	12.32	0.22	8.55	0.32	0.037	1.0	2003–2004	10	0.25	Y	Schessl et al. (2008)
Mata de Piedade	Brazil	MDP2	−35.2	−7.83	SEC	Acrisol			1206	0.43	14.74	0.27	11.01	0.75	0.068	1.0	2003–2004	10	0.25	Y	Schessl et al. (2008)
Medio Río Caquetá	Colombia	MRC1	−72.5	−0.42	FLO	Acrisol/Alisol	26.95	68.02	2289	0.09	10.7		7.10	0.15	0.021	1.0	1989–1990	15	0.25	N	Lips and Duivenvoorden (1996)
Medio Río Caquetá	Colombia	MRC2	−72.5	−0.42	OG	Acrisol/Alisol	29.03	103.13	2289	0.09	6.9		6.10	0.05	0.008	1.0	1989–1990	15	0.25	N	Lips and Duivenvoorden (1996)
Medio Río Caquetá	Colombia	MRC3	−72.5	−0.42	OG	Acrisol/Alisol	37.19	118.24	2289	0.09	8.6		6.77	0.47	0.069	1.0	1989–1990	15	0.25	N	Lips and Duivenvoorden (1996)
Medio Río Caquetá	Colombia	MRC4	−72.5	−0.42	OG	Acrisol/ Ferralsol	30.20	110.37	2289	0.09	6.8		5.40	0.33	0.061	1.0	1989–1990	15	0.25	N	Lips and Duivenvoorden (1996)
Medio Río Caquetá	Colombia	MRC5	−72.5	−0.42	OG	Arenosol	41.28	74.52	2289	0.09	6.23		5.36	0.19	0.035	1.0	1989–1990	15	0.25	N	Lips and Duivenvoorden (1996)
Nouragues Petit Plateau	French Guiana	NOR1	−52.7	4.08	OG	Ferralsol/leptosol association	25.4		3476	0.29	8.23	0.24	5.94	0.67	0.113	7.0	2001–2008	15	0.5	Y	This study
Nouragues Grand Plateau	French Guiana	NOR2	−52.7	4.08	OG	Ferralsol	21.6		3476	0.29	10.05	0.23	6.75	0.82	0.121	7.0	2001–2008	25	0.5	Y	This study
Nova Xavantina cerradao	Brazil	NXA1	−52.3	−14.7	LOW	Ferralsol			1501	0.55	1.046	0.27	0.49	0.17	0.347	1.0	2002–2003	10	1	Y	Silva et al. (2007)
Nova Xavantina cerrado	Brazil	NXA2	−52.3	−14.7	LOW	Ferralsol			1501	0.55	0.62	0.41	0.27	0.24	0.889	1.0	2002–2003	20	1	Y	Silva et al. (2007)
Paracou	French Guiana	PAR	−52.54	5.16	OG	Acrisol			3041	0.34	8.30	0.11	4.20	0.55	0.131	5.0	2003–2008	40	0.45	Y	This study
Podocarpus National Park	Ecuador	PNP1	−79.1	−3.97	MON	Cambisol			1084	0.10	13.26		8.62			1.0	2001–2002	12	0.16	N	Röderstein et al. (2005)
Podocarpus National Park	Ecuador	PNP2	−79.1	−3.97	MON	Cambisol			1084	0.10	6.66		4.33			1.0	2001–2002	12	0.16	N	Röderstein et al. (2005)
Podocarpus National Park	Ecuador	PNP3	−79.1	−3.97	MON	Cambisol			1084	0.10	4.05		2.63			1.0	2001–2002	12	0.16	N	Röderstein et al. (2005)
Panama Transect	Panamá	PRT1	−80	8	OG	Acrisol	46.88	11.85	1620	0.36	12.47		9.47	0.94	0.099	1.0	2001–2002	10	0.25	N	Santiago et al. (2005)
Panama Transect	Panamá	PRT2	−80	8	OG	Acrisol	33.58	28.51	1620	0.39	10.03		6.33	1.40	0.221	1.0	2001–2002	10	0.25	N	Santiago et al. (2005)
Panama Transect	Panamá	PRT3	−79.5	8	OG	Histosol	39.82	33.24	1756	0.36	10.51		6.45	1.79	0.278	1.0	2001–2002	10	0.25	N	Santiago et al. (2005)
Panama Transect	Panamá	PRT4	−79.5	8	OG	Acrisol	35.16	34.59	1756	0.29	9.79		6.74	0.64	0.095	1.0	2001–2002	10	0.25	N	Santiago et al. (2005)
Piste de Saint Elie	French Guiana	PSE	−54	5.33	OG	Ferralsol			2530	0.21	7.89	0.19	5.31	0.90	0.169	3.0	1978–1981	60	1	Y	Puig et al. (1990)
San Carlos tall forest	Venezuela	SCR1	−67.1	1.9	OG	Ferralsol	33.00	10.90	3463	0.15	10.25		7.57	0.40	0.053	1.0	1980–1981	10	0.5	N	Cuevas and Medina (1986)
San Carlos caatinga	Venezuela	SCR2	−67.1	1.9	SEC	Podzol	41.00	12.10	3463	0.15	5.61		3.99	0.21	0.053	1.0	1980–1981	10	0.5	N	Cuevas and Medina (1986)
San Carlos bana	Venezuela	SCR3	−67.1	1.9	LOW	Podzol			3463	0.15	2.43		2.07	0.12	0.058	1.0	1980–1981	10	0.5	N	Cuevas and Medina (1986)
Sinop	Brazil	SIN	−55.3	−11.4	OG	Ferralsol			2105	0.51	6.57	0.27	5.55	0.27	0.049	1.0	2002–2003	20	1	Y	Silva et al. (2007)
Tambopata	Peru	TAM5	−69.7	−12.8	FLO	Cambisol	21.1	22.80	2417	0.31	11.21	0.22	8.36	1.00	0.120	2.0	2005–2006	25	0.25	Y	This study
Tambopata	Peru	TAM6	−69.7	−12.8	OG	Cambisol	19.6	13.20	2417	0.31	9.43	0.19	7.09	1.05	0.148	2.0	2005–2006	25	0.25	Y	This study

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Table 1. Continued.

Site name	Country	Site code	long.	lat.	Forest type	Dominant soil group	C:N	N:P	Rainfall	*SR*	Total litterfall	*SL*	Leaf litterfall	Reprod litterfall	*RL*	Monitoring duration	Interval	# traps	Trap size	Monthly data	Reference
Tapajos forest	Brazil	TAP1	−55	−2.85	OG	Ferralsol	20.50	30.10	2142	0.44	6.43		4.50			6.0	2000–2005	25	0.5	N	Brando et al. (2008)
Tapajos exclusion	Brazil	TAP2	−55	−2.85	OG	Ferralsol			2142	0.44	6.4		4.48			6.0	2000–2005	25	0.5	N	Brando et al. (2008)
Tucuri	Brazil	TUC	−49.7	−3.77	OG	Ferralsol	21.96	40.09	2480	0.52	6.65		4.76							N	Silva (1984)
Río Ucayali	Perú	UCA1	−73.7	−4.92	OG	Fluvisol/Gleysol			2631	0.11	7.02	0.17	4.17	0.97	0.233	1.0	1997–1998	25	0.25	Y	Nebel et al. (2001)
Río Ucayali	Perú	UCA2	−73.7	−4.92	OG	Fluvisol/Gleysol			2631	0.11	7.14		4.30	1.15	0.267	1.0	1997–1998	25	0.25	Y	Nebel et al. (2001)
Río Ucayali	Perú	UCA3	−73.7	−4.92	OG	Fluvisol/Gleysol			2631	0.11	6.93		4.11	1.23	0.299	1.0	1997–1998	25	0.25	Y	Nebel et al. (2001)
Yuruani tall forest	Venezuela	YUR1	−61	5	OG	Ferralsol			1573	0.31	6.3	0.20	4.76	0.54	0.113	2.0	1990–1991	10	1	Y	Priess et al. (1999)
Yuruani medium forest	Venezuela	YUR2	−61	5	LOW	Ferralsol			1573	0.31	4.97	0.21	3.99	0.21	0.053	2.0	1990–1991	10	1	Y	Priess et al. (1999)
Yuruani low forest	Venezuela	YUR3	−61	5	SEC	Ferralsol			1573	0.31	5.33	0.06	4.22	0.39	0.092	2.0	1990–1991	10	1	Y	Priess et al. (1999)
Zafire varrilal	Colombia	ZAR1	−69.9	−4	LOW	Podzol			2828	0.14	5.02	0.18	3.79	0.50	0.132	2.0	2004–2006	25	0.5	Y	This study
Zafire flooded	Colombia	ZAR2	−69.9	−4	FLO	Gleysol			2828	0.14	9.72	0.09	6.66	1.22	0.183	1.5	2005–2006	25	0.5	Y	This study
Zafire TF	Colombia	ZAR3	−69.9	−4	OG	Cambisol			2828	0.14	8.82	0.18	6.71	0.63	0.094	2.0	2004–2006	25	0.5	Y	This study
Zafire Altura	Colombia	ZAR4	−69.9	−4	OG	Alisol			2828	0.14	9.51	0.17	6.96	0.90	0.129	1.5	2005–2006	25	0.5	Y	This study

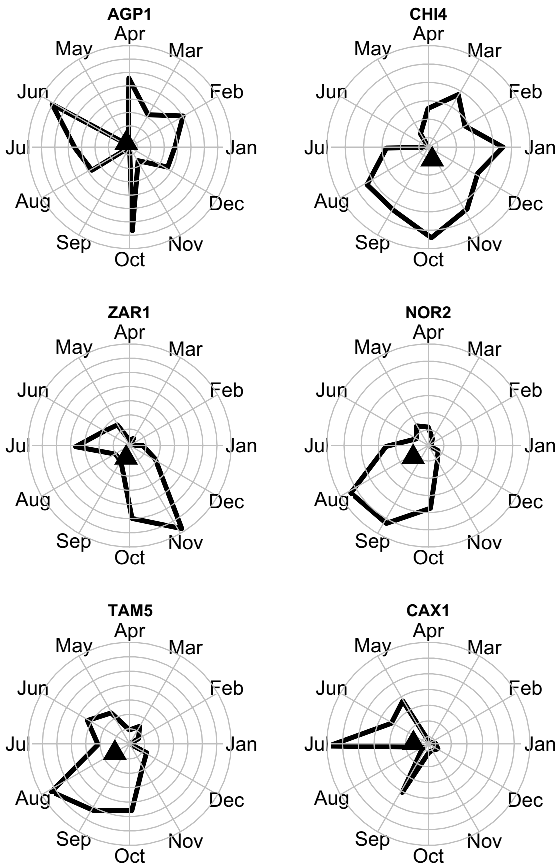

Fig. 1. Seasonality patterns for total litterfall at six sites (for site names, see Table 1). Thick lines delineate the envelope of monthly litterfall. The sites are ranked by increasing seasonality from left to right and top to bottom. Seasonality was measured using the equations reported in the Methods.

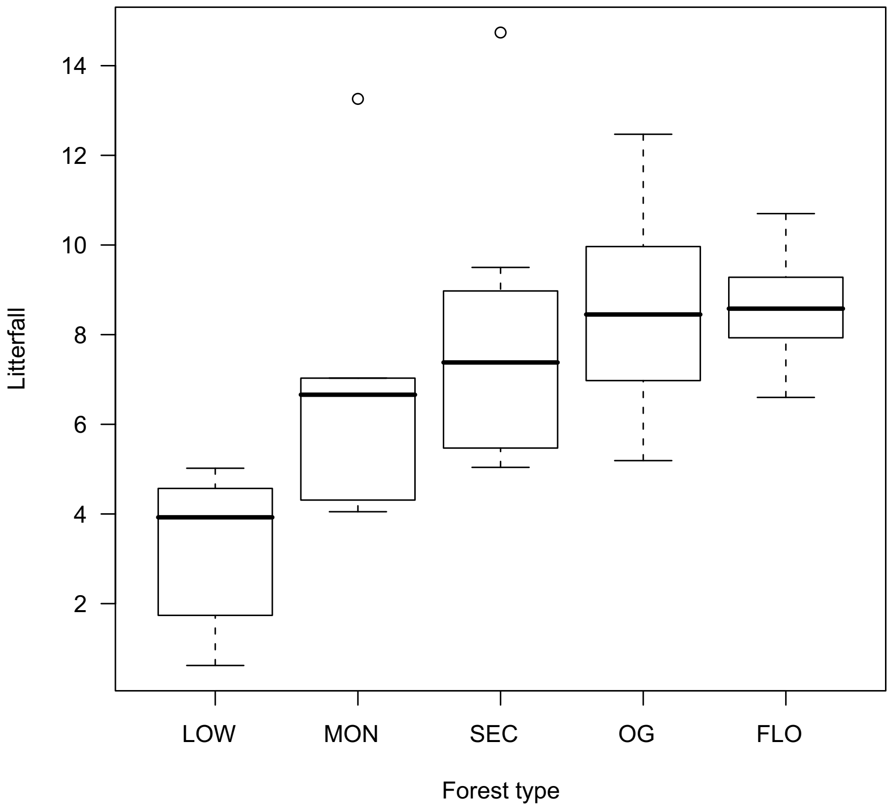

Fig. 2. Total annual litterfall (in Mg/ha/yr) in different forest types. LOW: short-statured tropical forests (see Methods for a description), MON: montane tropical forests, SEC: secondary tropical forests, OG: old-growth tropical forests, FLO: partially flooded tropical forests. For each forest type, the thick horizontal lines represents the mean, the box represents the standard deviations (possibly asymmetrical), and the dotted line represents the 95% confidence intervals. Two outliers were detected, both above 12 Mg/ha/yr (dots).

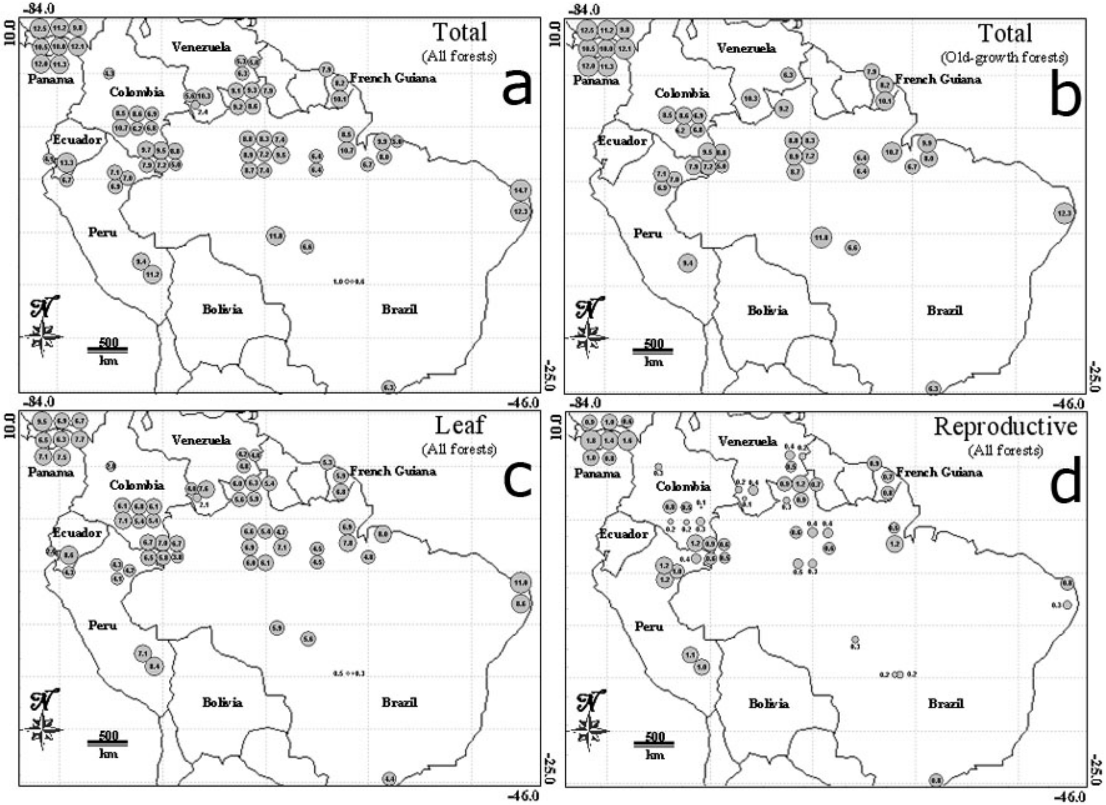

Fig. 3. Regional variation in litterfall. Variation in total litterfall across the sites **(a)**, only in old-growth forests **(b)**, variation in leaf fall **(c)** and variation in allocation into reproductive organs **(d)**. All figures are in Mg/ha/yr.

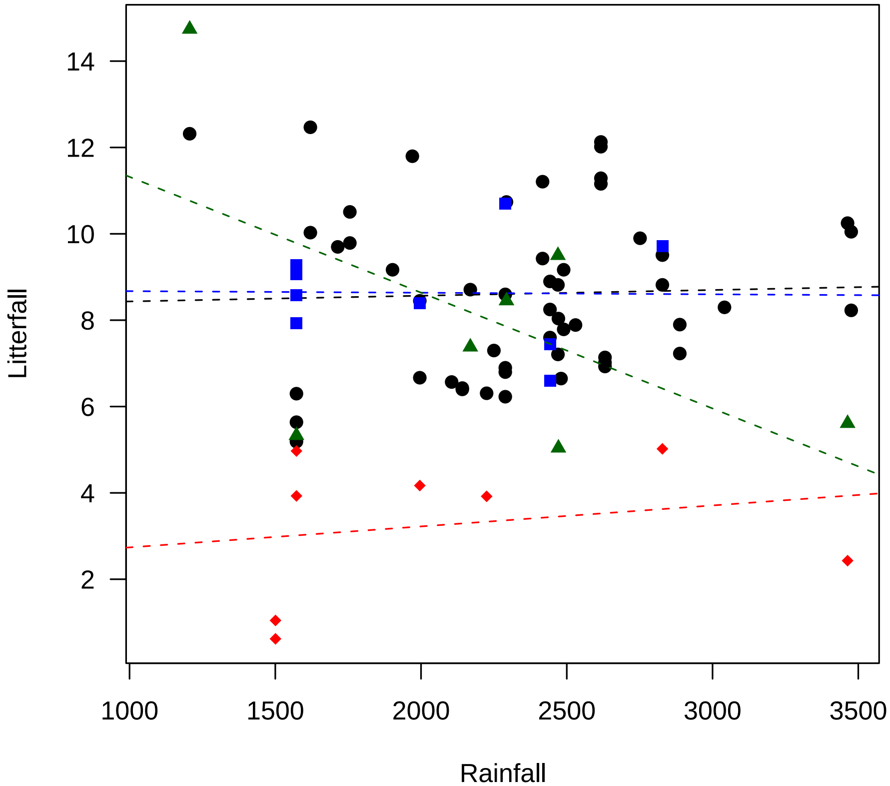

Fig. 4. Total annual litterfall (in Mg/ha/yr) versus annual rainfall (in mm/yr) for four lowland forest types. The four forest types are: old-growth tropical forests (black dots), flooded tropical forests (blue squares), secondary tropical forests (green triangles), and short-statured tropical forests (red diamonds). The dashed lines represent the least-square regression of total annual litterfall versus annual rainfall at the four forest sites. None of these regressions were significant.

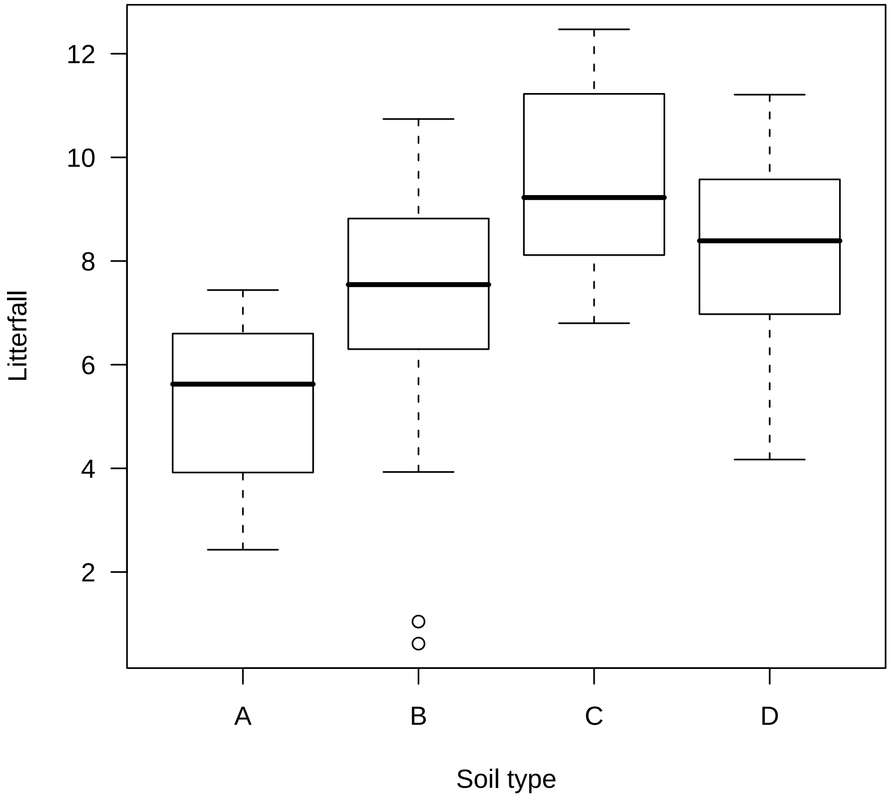

Fig. 5. Total annual litterfall (in Mg/ha/yr) on different soil types. Soil types are based on the WRB taxonomy (for more details, see Methods and Quesada 2008). Soil types are as follows. A: arenosols/podzols; B: ferrasols; C: acrisols/plinthosols/alisols; D: cambisols/leptosols/histosols/gleysols/fluvisols. The notations of this figure are the same as in Fig. 2.

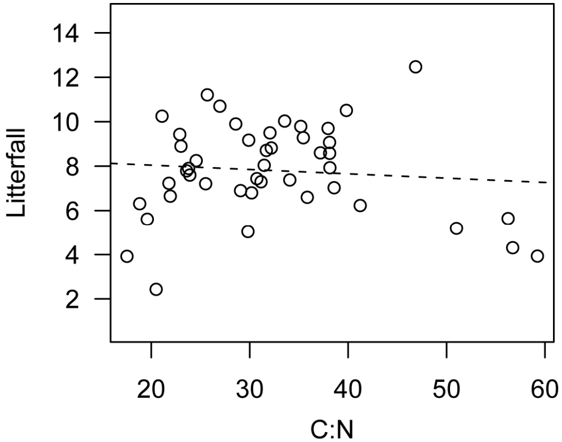

Fig. 6. Total annual litterfall (in Mg/ha/yr) versus leaf nutrient content. Left panel: litterfall versus C:N ratio. The regression was not significant (dashed line). Right panel: litterfall versus N:P ratio. A significant decline in litterfall with N:P was observed (dashed line).

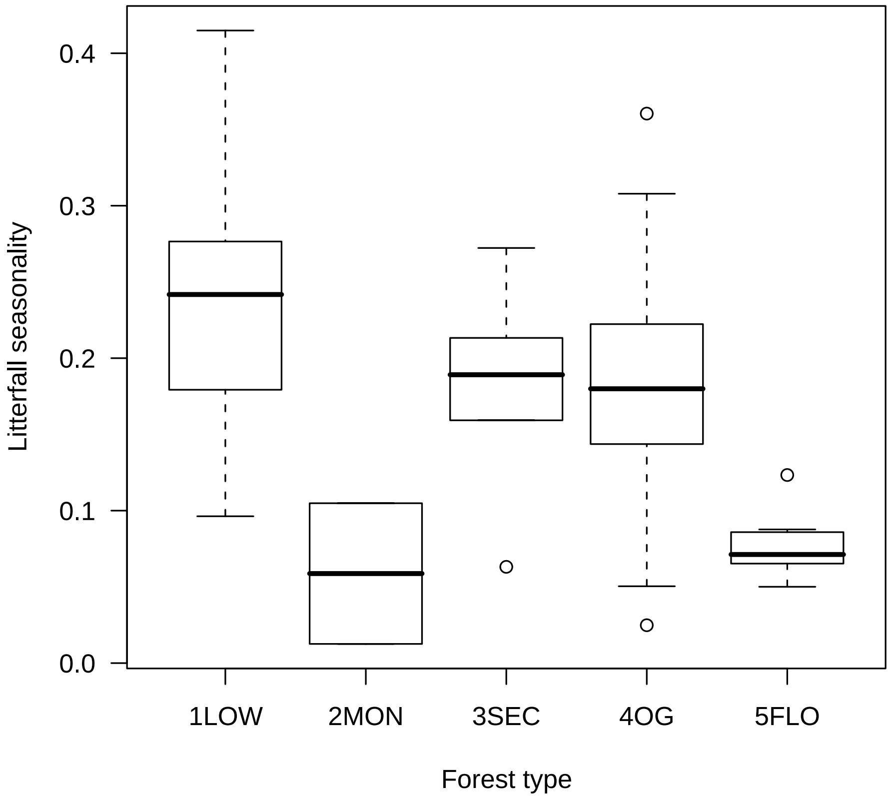

Fig. 7. Litterfall seasonality index *SL* (see Methods) in different forest types. The notations are the same as in Fig. 2.

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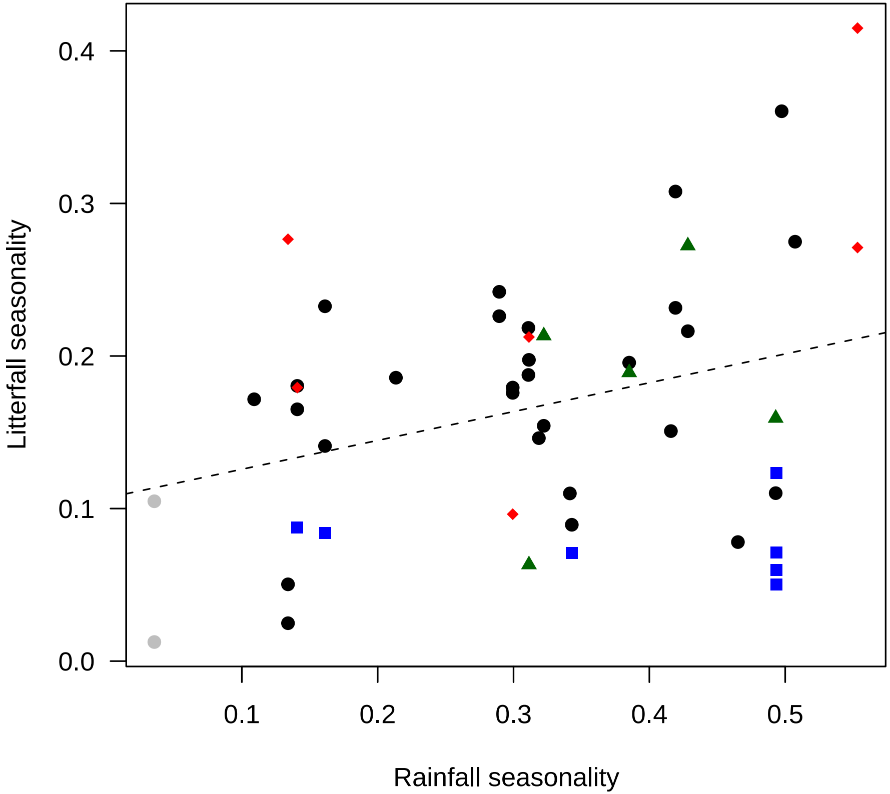

Fig. 8. Litterfall seasonality index *SL* versus rainfall seasonality index *SR*. The dashed line represents a regression across all points (r^2=0.10, p=0.02). Color codes show forest types as in Fig. 4.

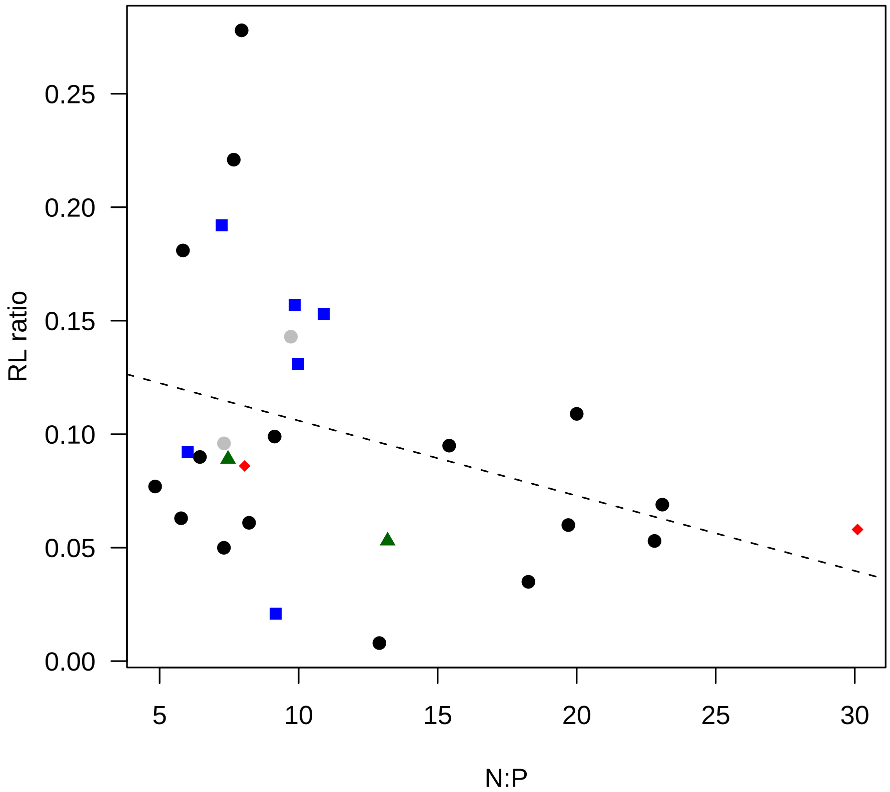

Fig. 9. Relative investment into reproduction relative to the investment into photosynthesis (*RL* ratio) versus N:P ratio. The regression line shows a declining relationship between these two variables, suggesting that plants invest relatively less into reproduction in phosphorus-deprived environments (r^2=0.12, p=0.07). Color codes show forest types as in Fig. 4.