RESEARCH ARTICLE

Key Points:
- Carbon allocation was measured in two contrasting Amazon forests
- Differences in carbon allocation components where not proportional between forests
- Soils control a trade-off between allocation to fine roots versus aboveground parts

Supporting Information:
- Readme
- Table S1

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Edaphic controls on ecosystem-level carbon allocation in two contrasting Amazon forests

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Abstract Studies of carbon allocation in forests provide essential information for understanding spatial and temporal differences in carbon cycling that can inform models and predict possible responses to changes in climate. Amazon forests play a particularly significant role in the global carbon balance, but there are still large uncertainties regarding abiotic controls on the rates of net primary production (NPP) and the allocation of photosynthetic products to different ecosystem components. We evaluated three different aspects of stand-level carbon allocation (biomass, NPP, and its partitioning) in two amazon forests on different soils (nutrient-rich clay soils versus nutrient-poor sandy soils) but otherwise growing under similar conditions. We found differences in carbon allocation patterns between these two forests, showing that the forest on clay soil had a higher aboveground and total biomass as well as a higher aboveground NPP than the sandy forest. However, differences between the two forest types in terms of total NPP were smaller, as a consequence of different patterns in the carbon allocation of aboveground and belowground components. The proportional allocation of NPP to new foliage was relatively similar between them. Our results of aboveground biomass increments and fine-root production suggest a possible trade-off between carbon allocation to fine roots versus aboveground compartments, as opposed to the most commonly assumed trade-off between total aboveground and belowground production. Despite these differences among forests in terms of carbon allocation, the leaf area index showed only small differences, suggesting that this index is more indicative of total NPP than its aboveground or belowground components.

1. Introduction

Three different aspects of the forest carbon cycle—biomass, flux, and partitioning—are key to understanding forest ecosystem metabolism and accurately predicting the effects of global change on forest carbon cycling [*Chapin et al.*, 2011]. Terrestrial ecosystem models require information on the partitioning of carbon among different forest compartments, but there are few studies that have actually measured all components of the forest carbon budget that allow accurate estimation of these partitioning coefficients [*Litton et al.*, 2007]. Even in the world's most extensive tropical forest ecosystem, the Amazon forest, most previous studies have focused on quantifying biomass or net primary production with very few attempts at a more comprehensive analysis of carbon allocation [*Girardin et al.*, 2010; *Malhi et al.*, 2009].

Amazon forests are highly heterogeneous in terms of their structure and resource environment. Most soil groups are represented within the Amazon Basin with considerable variations in soil fertility and potential physical limitations to plant growth, even within the same soil order [*Quesada et al.*, 2011]. Therefore, belowground resource availability may vary considerably across the basin, with potential consequences for resource acquisition, carbon allocation, and consequently ecosystem carbon balances. There have been important attempts to understand basin-wide patterns of biomass and net primary production controlled by the soil environment [*Aragão et al.*, 2009; *Malhi et al.*, 2009, 2004], but given that not only soils but also climate, plant community composition, and levels of human influence covary at the basin scale, it is difficult to discern patterns of carbon allocation as controlled by the soil environment alone.

Although the allocation of net primary production (NPP) to different aboveground and belowground components might be expected to show systematic patterns that vary with soil resource availability, reports for Amazon forests on contrasting soils (measured as soil available phosphorus $[P]_a$) can display surprisingly similar NPP allocation strategies. For example, *Aragão et al.* [2009] showed that in both a phosphorus-rich fertile site (an anthroposol *terra preta* forest) and a nutrient-depleted site (a white-sand forest) NPP partitioning was ~0.5 to aboveground and belowground components. Traditionally, it has been assumed that carbon allocation belowground is higher in nutrient-poor or dry soils where plants need to invest more resources for nutrient and water uptake [*Bloom et al.*, 1985; *Cannell and Dewar*, 1994]. However, it is unclear weather the similar pattern of carbon allocation observed in these two sites is driven by soil characteristics alone or whether other confounding environmental variables are involved.

Despite a lack of clear patterns and large uncertainties, *Malhi et al.* [2011] suggest a roughly equal three-way split of NPP for tropical forests as a whole, with $34 \pm 6\%$ for foliage, $39 \pm 10\%$ for wood, and $27 \pm 11\%$ for fine roots. They suggested that the dominant allocation trade-off in Amazon forest may be a "fine root versus wood" [*Dybzinski et al.*, 2011], as opposed to the expected "root-shoot" trade-off.

Current terrestrial ecosystem models vary widely in their prescribed NPP allocation schemes. Allocation fractions for the dominant tropical plant functional types range from 10 to 45% for foliage, 16–77% for wood, and 4–39% for fine-root production [*Malhi et al.*, 2011]. Although this variation encompasses the narrower range observed for Amazon forests [*Aragão et al.*, 2009], $33.5 \pm 1.5\%$ for foliage, $21.3 \pm 2.2\%$ for wood, and $31.4 \pm 3.5\%$ for fine-root production, the NPP allocation schemes of some terrestrial ecosystem models are far removed from those actually observed [*Malhi et al.*, 2011]. In addition, biomass ratios are often used as proxies to infer NPP partitioning in some terrestrial ecosystem models [*Litton et al.*, 2007; *Malhi et al.*, 2011; *Wolf et al.*, 2011a]. In contrast, *Litton et al.* [2007] showed that biomass cannot be used to infer either flux or partitioning in forests, because trees accumulate biomass in both long- and short-lived tissues, and flux and partitioning are not proportional to retention.

To calculate NPP many ecosystem models also require estimates of leaf area index (LAI) [*Malhi et al.*, 2011]. Nevertheless, the relationship between the satellite-based indices of seasonal greenness and ecosystem productivity remains an unresolved focus of debate [*Davidson et al.*, 2012]. Thus, although time series of LAI from remote sensing products can be of significant relevance to analyze fluctuations in light absorption that translate into temporal and spatial dynamics of carbon metabolism at different scales, the fidelity of these observations and their means of extrapolation remain highly controversial [*Medlyn*, 2011; *Nemani et al.*, 2003; *Saleska et al.*, 2007; *Samanta et al.*, 2011, 2010; *Zhao and Running*, 2010]. Similarly, it is unclear whether spatial patterns of LAI can account for changes in NPP and its partitioning in tropical forests.

In this study, we aimed to assess possible soil-related impacts on the three different aspects of carbon allocation (biomass, net primary production, and its partitioning) and in the leaf area index of two Amazon forest ecosystems growing under the same climatic conditions but differing substantially in their soil resource availability (a nutrient-rich clay soil and a nutrient-poor soil on white sands). We expect that by studying adjacent forest growing under the same climatic conditions, we can better discern the effects of edaphic factors on carbon allocation. For this purpose, we hypothesize, first, that the proportions of the total biomass in different vegetation parts (aboveground and belowground) differ considerably from the proportions of total net primary production for the two forests studied, consistent with the idea that biomass cannot be used to predict the carbon flux allocated to different vegetation parts [*Litton et al.*, 2007]. Second, we hypothesize that fluxes are proportionally larger in the nutrient-rich clay site than in the nutrient-poor sandy site. This hypothesis is consistent with the idea presented by *Litton et al.* [2007] of a "rising tide lifts all boats," i.e., allocation fluxes should be proportionally higher in sites where total productivity is high. Alternatively, if fluxes are not proportionally larger for all vegetation parts in the clay soil forest, we hypothesize similar allocation to foliage in both forests consistent with the idea of a trade-off between root and wood production [*Dybzinski et al.*, 2011].

2. Materials and Methods

2.1. Site Description

The study was conducted in the northwestern Amazon (Colombia), in two types of old-growth mature terra firme forests with no signs of previous disturbance. We established two 1 ha plots in a clay soil forest located in

the Amacayacu National Natural Park (AGP-01: 3°43′10.5″S–70°18′25.8″W and AGP-02: 3°43′20.2″S–70°18′25.8″W) and a 1 ha plot in a white-sand forest at the Zafire Biological Station (ZAR-01: 4°0′20.9″S–69°53′55.2″W). There is not true plot replication within each forest type. The sites are between 105–110 and 130 m asl, respectively.

The two forest types are approximately 50 km apart and are under similar climatic conditions, typical of a perhumid lowland equatorial climate. Mean annual precipitation was 3342 mm (±320 mm) with a monthly mean of 279 mm (±73 mm) measured at the Vásquez Cobo airport in Leticia (04°11′36″S–69°56′35″W) for the period 1973–2008. This region lacks a marked dry season (defined as rainfall < 100 mm month^{-1} as in *Malhi et al.* [2004]); the driest month being July (164 mm) and the wettest April (368 mm). Mean annual temperature was 26°C (24–27°C minimum and maximum) for the same period, and with a mean annual relative humidity of 86%.

The plots were established on contrasting soils: a clay (plots AGP-01 and AGP-02, with 43% clay content) and sandy soil (plot ZAR-01, with 75% sand content). These soils are classified according to the World Reference Base as Endostagnic Plinthosol (Alumic, Hyperdystric) and Ortsteinic Podzol (Oxyaquic), respectively. A detailed soil description of these plots is provided in *Quesada et al.* [2011] (soil profiles for AGP-02 and ZAR-01 therein). Physical and chemical characteristics of these soils are also discussed in *Quesada et al.* [2010]. In general, the clay soils have higher $[P]_a$, nitrogen concentrations $[N]$, and especially a higher effective cation exchange capacity (CEC) than the sandy soils ($[P]_a$: 25.4 versus 14.4 mg kg^{-1}, $[N]$: 0.16 versus 0.11%, and CEC: 6.2 versus 0.7 mmol$_c$ kg^{-1}, respectively). In the clay soils, the plinthic layer was considered relatively permeable thus exerting only moderate constraints on drainage, but the sandy soil (hydromorphic podzol) contains a hardpan at approximately 1 m depth that causes periodic water stagnation in the layers above it. This hydromorphic podzol is in an advanced stage of soil development, with most clay, iron oxides, and cations elluviated to a Bh horizon (hardpan layer) 1 m below the surface [*Sierra et al.*, 2013].

As a result of differences in resource availability, these two soil types are associated with a distinctive flora. The forest on sandy soils is known as "white-sand forest," and it is dominated by few species that only grow on this particular soil type [*Fine et al.*, 2010, 2004, 2006; *Peñuela-Mora*, 2014; *Stropp et al.*, 2011; *Tuomisto et al.*, 2003]. Furthermore, the white-sand forests have substantially lower species richness than the forest on clay soils, even though the stem density is higher (889 stems ha^{-1} with diameter at breast height, $d \geq 10$ cm) than in the clay soil forest (618 stems ha^{-1}).

2.2. Carbon Allocation

We estimated the three different aspects of carbon allocation at the ecosystem level [*Litton et al.*, 2007]: biomass, flux (NPP), and NPP partitioning. We considered NPP partitioning as the fractional NPP allocated to the aboveground and belowground plant parts (similar as in *Aragão et al.* [2009], *Malhi et al.* [2011], and *Wolf et al.* [2011b]). This definition of partitioning differs slightly from that proposed by *Litton et al.* [2007], who propose partitioning as a proportion of total gross primary production. For clarity, we refer always as NPP partitioning in this manuscript. Methods for the estimation of these three different aspects of carbon allocation are presented in the following sections.

2.2.1. Biomass

2.2.1.1. Aboveground Biomass

Aboveground biomass (AGB) was calculated from stem diameter measurements of all trees and palms with $d \geq 10$ cm every year (2004, 2005, and 2006). During these annual censuses we also registered dead stems as well as the ingrowth of the new individuals that grew during the interval between the censuses and reached d minimum (10 cm).

Allometric biomass equations are required to estimate aboveground biomass from measurements of tree diameters and heights; however, for this study site there are no local biomass equations. Although many equations are available in the literature, it is risky to select a single one and disregard many equally likely biomass equations [*Picard et al.*, 2012]. There is uncertainty associated with the selection of a biomass equation, which should be estimated and reported [*Picard et al.*, 2012; *Zapata-Cuartas et al.*, 2012].

We developed a methodology to account for the uncertainty related to the fact that there are no local biomass equations for either of the two forest types. AGB was calculated as the median of biomass estimates from different allometric models selected from the literature. For this selection of equations we considered several criteria such as differences in biomass allometry and growth patterns of palms and trees [*Brown*, 1997; *Clark et al.*, 2001a]; palms contributed about 9 and 5% of the stems per hectare in the clay soil forest and

white-sand forest, respectively. Therefore, we estimated AGB separately for trees and palms. We selected 28 models, 25 were from harvested trees and three from palms (Table S1 in the supporting information). Other criteria used were biomass estimation from whole tree or palm, differences between height-diameter relationships by geographic regions [*Feldpausch et al.*, 2011, 2012], d minimum of harvested individuals (at least 1 cm), and the type of forest (old growth, terra firme, and dense forests). For palms, we chose equations of the same species or with similar architectural characteristics. Consequently, most of the equations selected were generated from Amazon forests although we included other models broadly used in the literature. For the models that include wood density, we used the database of *Chave et al.* [2006], and also, for the white-sand forest we used wood density values directly measured in this forest [*Agudelo*, 2005].

The advantage of this approach, as opposed to selecting one single biomass equation for the tropical biome, is that we can minimize bias and account for the uncertainty associated with selecting a biomass equation. We report this uncertainty with our biomass and NPP estimations (see error propagation section) and therefore account for possible differences in allometric patterns at the local level.

2.2.1.2. Belowground Biomass

Belowground biomass (BGB) was defined as $BGB = BGB_{fineroot} + BGB_{coarseroot}$, where $BGB_{fineroot}$ is fine-root biomass and $BGB_{coarseroot}$ the coarse-root biomass. Although the importance of belowground carbon stocks in tropical forests is well recognized [*Cairns et al.*, 1997; *Jackson et al.*, 1996], allometric models to estimate $BGB_{coarseroot}$ are rare. Similar as for AGB, there are not local allometric models to estimate $BGB_{coarseroot}$ for our sites; notwithstanding, we found five allometric equations for trees and one for palms harvested from tropical forests (Table S1). We therefore followed the same procedure used to calculate AGB, using all available models for $BGB_{coarseroot}$ and taken the median of the predictions.

The methodology to estimate $BGB_{fineroot}$ (root diameter ≤ 2 mm) is described in *Jiménez et al.* [2009], who used the sequential root coring method [*Vogt et al.*, 1998] to estimate fine-root mass at 0.2 m depth of soil samples taken every three to four months from September 2004 to December 2006. We used the average fine-root mass observed during the entire monitoring period to calculate stand-level fine-root biomass [*Jiménez et al.*, 2009, Table 3].

2.2.2. Net Primary Production

In practice, the net primary production that can be estimated is defined as the total new organic matter produced during a specified interval [*Clark et al.*, 2001a], i.e., the sum of the net increments in aboveground and belowground live biomass plus losses. We estimated net primary production as $NPP = ANPP_{total} + BNPP_{root}$, where $ANPP_{total}$ is the total aboveground and $BNPP_{root}$ the belowground net primary production in roots [*Clark et al.*, 2001a; *Litton et al.*, 2007]. We assumed dry organic matter to be 50% carbon. Other components of NPP (see section 3.1) such as herbivory, emissions of volatile organic compounds, and root exudates were not quantified here; however, their contribution to total NPP is marginal [*Clark et al.*, 2001b; *Sierra et al.*, 2007] and of minor importance for comparisons among forest types.

2.2.2.1. Total Aboveground Net Primary Production

Total aboveground net primary production ($ANPP_{total}$) was estimated as $ANPP_{total} = \Delta AGB + FLF$, where ΔAGB is the aboveground biomass increment defined as the net increase in aboveground biomass as calculated from the allometric equations. FLF is defined as fine litterfall or new foliage, i.e., small twig and flower/fruit production rate (assumed equal to the "soft litterfall") [*Clark et al.*, 2001a]. We estimated FLF using litter traps (25 traps per hectare with dimensions of 1 m × 0.5 m, 1 mm mesh with a concavity to allow enough material to accumulate, and 1 m above the forest floor). We collected fine litterfall (leaves, flowers, fruits, twigs with diameter ≤ 2 cm, and indeterminate material) every 15 days from October 2005 until December 2006. The organic matter collected was dried for 48 h at 70°C and then weighed. We calculated ΔAGB as the increments of surviving trees or palms (difference between its estimated biomass at the beginning of the year and end of the year) plus increments of ingrowth trees, calculated as the difference between its estimated biomass at the end of the year and the minimum d measured (10 cm) [*Clark et al.*, 2001a].

For the purpose of our analysis, we assumed FLF to be indicative of NPP allocation to foliage, assuming that foliage biomass is in steady state and foliage production is balanced by losses in the form of fine litterfall. Accordingly, we assumed ΔAGB as indicative of NPP partitioning to aboveground woody components.

2.2.2.2. Belowground Net Primary Production

We estimated belowground net primary production as $BNPP_{root} = BNPP_{fineroot} + BNPP_{coarseroot}$, where $BNPP_{fineroot}$ is the new fine-root production and $BNPP_{coarseroot}$ belowground coarse-wood production. In

some studies $BNPP_{coarseroot}$ is assumed as $21 \pm 3\%$ of aboveground coarse-wood productivity [*Aragão et al.*, 2009; *Malhi et al.*, 2009]. We estimate $BNPP_{coarseroot}$ as the sum of the increments in coarse-root biomass of surviving trees or palms plus increments of ingrowth—similar as for ΔAGB due to our use of coarse-root biomass equations. Ingrowth cores at 0.20 m depth were used to estimate $BNPP_{fineroot}$ [*Jiménez et al.*, 2009], being established 3 times in February and September of 2004 and in February of 2006. The ingrowth cores were left in situ for periods of 5–7 months for the first collection, and subsequent samplings were done at 2–4 months intervals. In our analysis, we calculated $BNPP_{fineroot}$ as the mean fine-root production of the three measurement intervals [*Jiménez et al.*, 2009, Table 2].

2.3. Leaf Area Index

Leaf area index (LAI) was also measured during the same regular field trips using hemispherical photographs (26 points ha^{-1}) using a digital camera (Nikon, Cool Pix 990), and a fish-eye converter (Nikon, FC-E8). Images were recorded under overcast conditions with the camera placed on a tripod 1 m above the ground following the same protocol (http://www.rainfor.org/en/manuals). Photographs were analyzed using the Hemiview Canopy Analysis Software (Version 2.1 SR1, Delta-T Devices Ltd., UK.) following the recommendations of *Keeling and Phillips* [2007] for calculating LAI.

2.4. Error Propagation and Statistical Analysis

We estimated uncertainties in estimated biomass and fluxes through error propagation. Our measure of uncertainty includes the uncertainty associated with the biomass estimates from different allometric models (allometric uncertainty, Table S1), the spatial variation within the plots [*Chave et al.*, 2001], and the interannual variability for the 3 years measured. To estimate allometric uncertainty, we determined AGB and $BGB_{coarseroot}$ for each allometric model, calculating standard errors at the individual tree level. Then we aggregated individual trees by subunits (20 m $\times$ 20 m) to calculate biomass within these subplots to obtain spatial variability. For each forest, we then calculated the mean biomass for all years propagating uncertainties, measured as standard errors, at each step. These standard errors were calculated as the square of the median absolute deviation divided by the square of sample size depending of the situation ($n = 25$ subunits per ha or $n = 3$ years per forest). Errors were propagated as the sum or average of the squared standard errors, depending on the operations performed on the means. For statistical comparisons, we used a Z or t test to compare means depending on the size or types of samples compared. We merged the two plots on clay soils (AGP-01 and AGP-02) in all analyses. All calculations were performed in the R environment for statistical computing [*R Development Core Team*, 2012].

3. Results

3.1. Biomass

We found differences between the two forests in terms of both their aboveground and belowground biomass as well as in their total biomass (Table 1). Specifically, AGB was twice as large for the clay soil forest (120.2 ± 14.5 Mg C ha^{-1}) than for the white-sand forest (60.1 ± 7.5 Mg C ha^{-1}). BGB was also higher in the clay soil forest than in the white-sand forest, estimated at 24.5 ± 4.2 and 16.4 ± 2.1 Mg C ha^{-1}, respectively. In contrast, $BGB_{fineroot}$ in the first 20 cm was 3 times larger in the white-sand forest than in the clay soil forest (5.5 ± 0.2 versus 1.7 ± 0.1 Mg C ha^{-1}, respectively).

Overall, total biomass was twice as large for the clay soil forest (144.6 ± 15.0 Mg C ha^{-1}) than for the white-sand forest (76.5 ± 7.7 Mg C ha^{-1}). Trees contributed 94 and 85% of total biomass in the clay soil forest and in the white-sand forest, respectively. Tree aboveground biomass alone accounted for 81% of total biomass in the clay soil forest and 73% in the white-sand forest. Palms accounted for 5 and 8% of total biomass in the clay soil forest and the white-sand forest, respectively. Nevertheless, uncertainties for palm biomass estimates were high, suggesting that palms should be considered an important component of total biomass that requires specific and more accurate methods for its estimation. Fine roots contributed 1 and 7% to the total biomass for the clay soil forest and the white-sand forest, respectively.

3.2. Net Primary Production

We found differences in $ANPP_{total}$ and its components, with FLF larger in the clay soil forest than in the white-sand forest (3.8 ± 0.3 versus 2.5 ± 0.3 Mg C ha^{-1} yr^{-1}; Table 2). For the clay soil forest, ΔAGB was 3 times larger

Table 1. Aboveground and Belowground Biomass (Dry Weight, Mg C ha^{-1}) of Trees and Palms in a Clay Soil and a White-Sand Forest in the Northwestern Amazon (the Average of the Biomass Medians for 2004, 2005, and 2006 Years ± Standard Error) and Their Fraction to Total Biomass (f)

		Clay Soil Forest		White-Sand Forest	
Component	Growth Form	Median ± se	f	Median ± se	f
Aboveground biomass	Trees	114.93 ± 14.29	0.79	55.70 ± 7.07	0.73
	Palms	5.21 ± 2.11	0.04	4.44 ± 2.35	0.06
	Total	120.15 ± 14.45	0.83	60.14 ± 7.45	0.79
Belowground biomass	Trees[a]	20.86 ± 4.05	0.14	9.36 ± 1.76	0.12
	Palms[a]	1.95 ± 1.00	0.01	1.55 ± 1.07	0.02
	Fine-root mass	1.67 ± 0.09	0.01	5.47 ± 0.17	0.07
	Total	24.48 ± 4.17	0.17	16.38 ± 2.07	0.21
Biomass per growth form[b]	*Trees*	135.79 ± 14.86	0.94	65.06 ± 7.29	0.85
	Palms	7.16 ± 2.33	0.05	5.99 ± 2.58	0.08
Total biomass		144.62 ± 15.04	1	76.52 ± 7.73	1

[a]Coarse root biomass.
[b]Aboveground plus belowground biomass.

than for the white-sand forest (3.0 ± 0.4 versus 0.7 ± 0.1 Mg C ha^{-1} yr^{-1}), and consequently, ANPP$_{total}$ was twice as large for the clay soil forest than for the white-sand forest (6.7 ± 0.5 versus 3.2 ± 0.3 Mg C ha^{-1} yr^{-1}; Table 2). For both forests, fine litterfall production was the major contributor to total aboveground net primary production, accounting for 60% of ANPP$_{total}$ for the clay soil forest and 80% for the white-sand forest.

We found differences in fine- and coarse-root production rates between forests (Table 2), with BNPP$_{fineroot}$ for the white-sand forest being twice that of the clay soil forest (3.0 ± 0.5 versus 1.5 ± 0.2 Mg C ha^{-1} yr^{-1} [*Jiménez et al.*, 2009]). As a consequence, BNPP$_{root}$ was higher in the white-sand forest than in the clay soil forest (3.1 ± 0.5 versus 2.1 ± 0.2 Mg C ha^{-1} yr^{-1}; Table 2). Fine-root production was the major contributor to belowground net primary production, accounting for 96% of BNPP$_{root}$ for the white-sand forest and 70% of BNPP$_{root}$ for the clay soil forest.

When adding the individual terms together, we found that NPP was 29% larger in the clay soil forest (8.9 ± 0.5 Mg C ha^{-1} yr^{-1}) than in the white-sand forest (6.3 ± 0.6 Mg C ha^{-1} yr^{-1}). Aboveground and belowground production varied largely between forests, such that ANPP$_{total}$ in the white-sand forest was less than half that in the clay soil forest, while BNPP$_{root}$ of white-sand forest was higher than in the clay soil forest. In both forests, the productivity of fine material components (viz., FLF and BNPP$_{fineroot}$) was larger than woody components (viz. ΔAGB and BNPP$_{coarseroot}$). Additionally, we found differences between most aboveground and belowground NPP subcomponents within the forests.

3.3. Net Primary Production Partitioning

The two forests exhibited different NPP partitioning between aboveground and belowground components (Table 2). For the clay soil forest they were 0.8 and 0.2 respectively; while for the white-sand forest these ratios were similar at approximately 0.5.

Table 2. Aboveground and Belowground Subcomponents of Net Primary Productivity (NPP, Mg C ha^{-1} yr^{-1}), Partitioning With Respect to NPP (p, Unitless), and Leaf Area Index (L, m^2 m^{-2}) in a Clay Soil Forest and a White-Sand Forest in the Northwestern Amazon Between the Years 2004 and 2006

	Clay Soil Forest			White-Sand Forest		
	Median ± se	%	p	Median ± se	%	p
Fine litterfall (FLF)	3.75 ± 0.30	0.6	0.42	2.48 ± 0.25	0.8	0.39
Aboveground biomass increment (ΔAGB)	2.99 ± 0.36	0.4	0.34	0.73 ± 0.08	0.2	0.12
ANPP$_{total}$	6.74 ± 0.47	1.0	0.76	3.21 ± 0.26	1.0	0.51
Fine-root production (BNPP$_{fineroot}$)	1.53 ± 0.16	0.7	0.17	2.98 ± 0.54	0.96	0.47
Coarse root production (BNPP$_{coarseroot}$)	0.58 ± 0.11	0.3	0.07	0.13 ± 0.02	0.04	0.02
Belowground NPP (BNPP$_{total}$)	2.11 ± 0.19	1.0	0.24	3.11 ± 0.54	1.0	0.49
NPP	8.85 ± 0.51			6.31 ± 0.60		
L	4.45 ± 0.06			4.25 ± 0.07		

The partitioning of NPP to foliage was similar between forests (FLF/NPP ~ 0.4), but with the partitioning to aboveground biomass increment differing, ΔAGB /NPP being much higher in the clay soil forest (~0.3) than in the white-sand forest (~0.1). However, partitioning to fine-root production showed the opposite pattern, being much higher in the white-sand forest (BNPP$_{fineroot}$/NPP ~0.5) than in the clay soil forest (BNPP$_{fineroot}$/NPP ~0.2). This same pattern applies to total belowground net primary production, with partitioning to belowground components higher in the white-sand forest (BNPP$_{root}$/NPP ~ 0.5) than in the clay soil forest (BNPP$_{root}$/NPP ~ 0.2).

3.4. Leaf Area Index

Leaf area index (LAI) was slightly higher for the clay soil forest with $4.5 \pm 0.1 \, m^2 \, m^{-2}$ than for the white-sand forest with $4.3 \pm 0.1 \, m^2 \, m^{-2}$ (Table 2) and presented significant differences between forests ($P = 0.045$, $t = 1.697$, d.f. = 726).

4. Discussion

Analyses of forest ecosystems at local scales provide the opportunity to tease apart edaphic controls versus climatic controls on the allocation of carbon. The forests studied here are under the same climate conditions, yet the different measures of carbon allocation we found varied as much as what has been observed across all sites studied to date within the Amazon Basin [*Aragão et al.*, 2009; *Chave et al.*, 2010; *Malhi et al.*, 2004; *Quesada et al.*, 2012]. Given that our study sites did not present variation in climatic factors (total precipitation and its seasonal distribution) and that carbon allocation was assessed with the same methods and over the same time interval (2004–2006), the results suggest that edaphic factors likely play a strong role in determining NPP and allocation patterns. These differences were observed for the three aspects of carbon allocation: biomass, net primary production, and NPP partitioning. These are discussed in detail in the next sections.

4.1. Differences in Aboveground and Belowground Biomass

The values of aboveground and belowground biomass of the white-sand forest studied here were among the lowest of the range of values reported for Amazon forests. The white-sand forest AGB (60 Mg C ha^{-1}) was within the lowest values previously reported for other forests on podzols [*Klinge and Herrera*, 1983]. Meanwhile, the clay soil forest AGB was close to the average for Amazon forests (143 ± 38 Mg C ha^{-1}) (average and standard deviation calculated from *Brown et al.* [1995, 1989], *Carvalho et al.* [1998], *Chambers et al.* [2001], *Chave et al.* [2001], *Fearnside et al.* [1993], *Keller et al.* [2001], *Laurance et al.* [1999], *Londoño* [2011], *Malhi et al.* [2006], *Nascimento and Laurance* [2002], *Nogueira et al.* [2008], *Overman et al.* [1990], and *Saldarriaga et al.* [1988]). The BGB range for tropical forests (average of 40 ± 28 Mg C ha^{-1}) showed a large variability in Amazon forests (compiled from *Chave et al.* [2001], *Fearnside et al.* [1993], *Keller et al.* [2001], *Klinge and Herrera* [1978], *Nogueira et al.* [2008], *Saldarriaga et al.* [1988], and *Salomão et al.* [1996]), varying from the white-sand forest studied here (16 Mg C ha^{-1}) to two forests on podzols, a Tall and Low Caatinga in San Carlos del Rio Negro, with 98 and 168 Mg C ha^{-1}, respectively. The value of BGB in the clay soil forest studied here was below the basin-scale average.

Comparing the two sites, there were large differences in total biomass between the forests (50%), with even larger differences in terms of aboveground and belowground components analyzed separately. AGB was almost a factor of 2 higher in the clay soil forest than in the white-sand forest, and conversely, fine-root mass in the white-sand forest was more than a factor of 3 higher than in the clay soil forest.

Our results suggest that differences in soils are playing an important role in the observed differences of aboveground and belowground biomass, as well as in its subcomponents, as expressed by the differences in aboveground and fine-root biomass observed between the forests. These differences also suggest that conclusions on the factors that contribute to differences in biomass allocation may be very different depending on whether the aboveground and belowground components are analyzed independently or in combination.

4.2. Differences in Aboveground and Belowground Net Primary Production

The two forests exhibited differences in net primary production (NPP). They differed more in their total biomass than in their NPP, and differences in the belowground pools mainly contributed to these differences in biomass and NPP.

Total, aboveground, and belowground net primary production were within the lowest values reported for Amazon forests [*Klinge and Herrera*, 1978, 1983]. The white-sand forest had a lower NPP than the clay soil forest, both below the average for Amazon forests (12 ± 3 Mg C ha^{-1}). Although both forests had lower total biomass and net primary production in comparison to other Amazon forests, there were differences between them, highlighting the enormous site-to-site variation within the Amazon Basin.

Consistent with our initial hypothesis, we found that biomass ratios differed considerably than NPP fluxes to similar pools. Differences in total biomass between forests were larger (50%) compared to the differences in NPP (clay soil forest 29% higher than the white-sand forest NPP). However, differences in net primary production between forests are much larger when the aboveground and belowground components are analyzed separately. For example, aboveground wood production and fine-root production exhibited the larger differences. ΔAGB was a factor of 3 larger in the clay soil forest than in the white-sand forest, and BNPP$_{fineroot}$ was twice as high in the white-sand forest than in the clay soil forest. Similar as for biomass, the observed differences in aboveground and belowground NPP between the two forests suggest that conclusions on the factors that contribute to differences in NPP may be very different when the aboveground and belowground parts are analyzed separately than in combination.

One important topic in carbon allocation analyses is to evaluate whether component fluxes are related [*Aragão et al.*, 2009; *Girardin et al.*, 2010], i.e., if the increase in the total amount of NPP involve a proportional increase in the aboveground and belowground flux components. For Amazon forests, it has been reported that larger values of NPP typically involve larger values of both aboveground and belowground NPP [*Litton et al.*, 2007]. Conversely, and in contrast with our initial hypothesis, the forests studied here showed that NPP was higher in the clay soil forest than in the white-sand forest, but above and belowground production were not both larger by the same proportions. While aboveground NPP was proportionally larger to total NPP in the clay soil forest, belowground NPP was not.

4.3. Biomass Ratios and Net Primary Production Partitioning

Biomass ratios have been used widely for total biomass estimations in the Amazon Basin, especially for root biomass. Some indirect assessments of total biomass at large spatial scales use an average of root biomass directly measured in the field, or an overall mean for forests (17% by *Brown and Lugo* [1992], 19% by *Jackson et al.* [1996], and 24% by *Cairns et al.* [1997]). *Cuevas* [2001] showed that belowground contributions for terra firme forests can vary from 9 to 25%, while *Klinge and Herrera* [1983] registered by direct measurements a wide belowground biomass range, between 18 and 59% for podzols in San Carlos de Rio Negro. The belowground contribution to total biomass for our sites was 15 and 21% for clay soil forest and white-sand forest, respectively. Taken together, our observations and reports from the literature suggest that biomass ratios are not constant in Amazon forests, and the use of basin-scale ratios to predict the contribution of belowground biomass to total biomass may lead to significant errors.

Furthermore, biomass ratios have been used to infer either flux or partitioning of NPP in forests. Our results show that despite the differences in the total amount of biomass and net primary production, both are higher in the clay soil forest than in the white-sand forest; the differences between them in the fractional distribution of biomass and the NPP partitioning of aboveground and belowground components were certainly marked. These results confirm those found by *Litton et al.* [2007] who revealed that biomass was poorly related to carbon flux and to partitioning of photosynthetically derived carbon and should not be used to infer either. Likewise, *Wolf et al.* [2011b] showed that stand biomass is weakly related to NPP partitioning, and other factors that impact NPP such as soils or climate may have a stronger influence on partitioning than does biomass per se.

Our estimations showed that the NPP fractions allocated to short-lived structures (foliage and fine roots) were the main contributors to aboveground and belowground components. Consistent with our initial hypothesis, we found that NPP partitioning to foliage was rather similar for both forests, while NPP partitioning to fine-roots and aboveground biomass was largely different (Table 2). These results are also consistent with the idea that allocation to foliage is relatively constant across different forests, but what varies most among sites is how the remaining NPP is allocated between wood and fine-root production [*Wolf et al.*, 2011b]. This trade-off in NPP partitioning between wood and belowground production (wood to fine-roots) may be associated with differences in soil resources, the main abiotic factor that strongly differs between our sites.

Although litterfall production and LAI have been also proposed as a good proxy for above and total NPP [*Litton et al.*, 2007; *Malhi et al.*, 2004, 2011; *Wolf et al.*, 2011b], FLF and LAI in the two forests studied seem to be less sensitive indicators of differences in the total NPP and its components between them. Differences in fine-root production suggest that by measuring ANPP$_{total}$ alone, total NPP can be underestimated by 20 and 50% in the clay soil forest and the white-sand forest, respectively.

5. Conclusions

We found important edaphic controls on carbon allocation of two Amazon forests under similar climatic conditions on contrasting soils. In particular, we found

1. Biomass ratios between aboveground and belowground components differed from the partitioning of total NPP to aboveground and belowground components. In general, biomass ratios for the components did not reflect the fraction of NPP allocated to them.
2. Component fluxes in these forests were not related. High values of total NPP in the clay soil forest did not correspond to high values for all NPP components. Differences in the soil environment (nutrients and water availability) are probably responsible for the large values of belowground NPP observed in the white-sand forest.
3. Our results of aboveground biomass increments support the hypothesis of a possible trade-off between carbon allocation to fine roots versus aboveground wood growth, as opposed to the most commonly assumed trade-off between total aboveground and belowground production.
4. The leaf area index showed slight differences between the two forests that could be indicative of differences in total NPP but did not reflect differences in carbon allocation components. Furthermore, our analysis may have important implications for ecosystem modeling. In particular, (1) land surface models that require parameters on NPP partitioning, but only use data on biomass fractions, may incur in important errors for predicting total NPP and component fluxes and (2) models in which NPP is proportional to LAI may miss important differences in internal ecosystem responses caused by edaphic factors.

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