

Allocation trade-offs dominate the response of tropical forest growth to seasonal and interannual drought

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Abstract. What determines the seasonal and interannual variation of growth rates in trees in a tropical forest? We explore this question with a novel four-year high-temporal-resolution data set of carbon allocation from two forest plots in the Bolivian Amazon. The forests show strong seasonal variation in tree wood growth rates, which are largely explained by shifts in carbon allocation, and not by shifts in total productivity. At the deeper soil plot, there was a clear seasonal trade-off between wood and canopy NPP, while the shallower soils plot showed a contrasting seasonal trade-off between wood and fine roots. Although a strong 2010 drought reduced photosynthesis, NPP remained constant and increased in the six-month period following the drought, which indicates usage of significant nonstructural carbohydrate stores. Following the drought, carbon allocation increased initially towards the canopy, and then in the following year, allocation increased towards fine-root production. Had we only measured woody growth at these sites and inferred total NPP, we would have misinterpreted both the seasonal and interannual responses. In many tropical forest ecosystems, we propose that changing tree growth rates are more likely to reflect shifts in allocation rather than changes in overall productivity. Only a whole NPP allocation perspective can correctly interpret the relationship between changes in growth and changes in productivity.

Key words: *Bolivia; deep vs. shallow soils; drought; net primary production (NPP); resource allocation; seasonally dry tropical forest.*

INTRODUCTION

The rate of woody growth in a forest is often taken as a proxy for total gross primary productivity (GPP; the total rate of photosynthesis of an ecosystem) or net primary productivity (NPP; the rate of production of biomass organic matter) (Phillips et al. 1998, Malhi and Grace 2000, Lewis et al. 2004). However, this assumption has rarely been critically examined, but is nevertheless implicit in discussions of how biomass growth rates may respond to climate change (Clark et al. 2013, Cox et al. 2013), or in understanding the climate sensitivity of forests by relating seasonal or interannual variations in growth rates to climate (Brienen and Zuidema 2005, Clark et al. 2013), and in interpreting past climates with the use of dendrochronology (Briffa 2000). The critical flaw in this assumption is that woody biomass production typically accounts for, on average,

only ~15–40% of NPP in forests, and ~5–10% of GPP (Malhi et al. 1999, Malhi 2012). Hence temporal or spatial variation in the fractional use of photosynthate in plant respiration, or in the allocation of NPP between wood, canopy, and fine roots has the potential to be more important than variation in GPP in explaining variations in woody biomass production. This may be particularly important in tropical forests, where there are year-round growing seasons and seasonal patterns of productivity, respiration, and allocation may be out of synchrony. To our knowledge, the seasonal and interannual variation of above- and belowground NPP allocation has never been explored for a tropical forest. In this paper, we present results and insights from the first such study, utilizing a high-temporal-resolution four-year time series of NPP allocation from two forest plots in Bolivia, situated close together in the same climate but on soils of similar properties but contrasting depths, which appears to lead to very different species compositions.

There has recently been discussion as to the best way to model carbon allocation in forests (Franklin et al.

Manuscript received 2 August 2013; revised 16 December 2013; accepted 21 January 2014; final version received 14 February 2014. Corresponding Editor: J. B. Yavitt.

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2012). Modeling approaches have been broadly divided between simple approaches such as fixed fraction, allometric scaling (relationships vary with size but not with the environment [West et al. 2009]) or functional balance approaches (preferential allocation towards the organ responsible for the acquisition of the most limited resource [Reynolds and Chen 1996]) and more complicated (and computationally intensive) eco-evolutionary approaches such as optimal response (optimize a strategy to maximize fitness [growth] under given abiotic conditions [Franklin et al. 2009]), game theory optimization (maximizing growth under abiotic conditions and biotic competition between individuals [King 1993]), and adaptive dynamics (optimize a strategy to maximize long-term reproductive success [Dybzinski et al. 2011]). For tropical forests, allocation patterns from 13 individual models were compared to a large data set of measured allocation values and the averages of all models were within the standard deviation of the data estimates, but there was huge variation between individual models, which demonstrates the need for more accurate representation of allocation in climate models (Malhi et al. 2011).

Biomass allocation is typically measured in the field by summing the production rates of wood, canopy components (leaves, flowers, fruit, twigs), and fine roots. These field studies provide a valuable opportunity to test and constrain different model allocation schemes. There is a large data set in the tropics now on canopy and woody growth, but fine-root production is rarely measured in parallel with the aboveground terms (Malhi et al. 2011). Plot-averaged allocation patterns seem fairly consistent across sites, with little variance in canopy allocation but shifting allocation between fine roots and woody tissue NPP (Malhi et al. 2011). This finding corresponds most closely with an “adaptive dynamics” model where, in mature forests, competition is most intense between investment in fine roots vs. investment in wood because self-shading limits returns on foliage investment (Dybzinski et al. 2011). However, few of these data sets explore seasonal allocation patterns, and none explore seasonality for all components over long periods of time.

How do allocation rates change under changing environmental conditions? There are very limited data from previous studies showing changing carbon allocation under manipulation, such as under increased atmospheric CO₂ concentrations at Duke’s FACE site, or drought manipulation (Franklin et al. 2009, Metcalfe et al. 2010). In tropical forests, increased drought may have the greatest impact on forest growth (Phillips et al. 2009), and so it remains a scientific priority to understand changing allocation patterns under drought stress. Climate change is predicted to affect the hydrologic cycle in large regions of the globe (IPCC 2007), and some changes may have already begun in the Amazon basin. For instance, in 2005 and 2010, the Amazon basin experienced two of the worst droughts in

its recorded history (Lewis et al. 2011). There has been recent evidence of such a shift taking place in the hydrological cycle of the Amazon basin and other tropical forest regions, with more frequent intense droughts and extreme wet periods (Feng et al. 2013, Gloor et al. 2013).

If changes in the hydrological cycle lead to changes in vegetation in Amazonia, we might expect the largest changes to take place in the dry forest transition zone of southern Amazonia. The humid forests of eastern Bolivia have been expanding southward over the past 3000 years, and their present-day location may be the southernmost extent of Amazonian rain forest over the past 50 000 years (Mayle et al. 2000). Long sediment cores from Lake Titicaca indicate that this region experienced a dry period 8000–5500 years ago during a time of low summer insolation (Baker et al. 2001). Precipitation changes leading to changes in vegetation are cyclical and associated with cycles in Earth’s orbital parameters, which affect the degree of summer insolation and thereby the southerly penetration of the Intertropical Convergence Zone (ITCZ) in South America (Cruz et al. 2005). As such, the dry–humid forest transition zone of southern Amazonia is an ideal place to test the response of seasonal allocation rates in response to drought. Since the region has seen large changes to vegetation and precipitation in the recent past, these forests might have inherent mechanisms for dealing with periodic drought conditions that provide insights into some of the different theoretical carbon allocation strategies (Franklin et al. 2012). However, these data are also relevant for the broader Amazon forest biome and tropical forests in general because there are no similar data sets in other regions of the tropics.

Here we present data on multiple aspects of NPP from two 1-ha plots from a transition zone of the Bolivian Amazon at the Hacienda Kenia in Guarayos Province, Santa Cruz, Bolivia, monitored from January 2009 to December 2012. These two plots straddle the humid forest–dry forest ecotone, with tree species in one plot (Kenia-deep) typical of humid Amazonian regions such as genera like *Cariniana*, *Pseudolmedia*, and *Swietenia*, and species in the other plot (Kenia-shallow) more typical of a dry deciduous *chiquitano* forest such as genera like *Anadenanthera*, *Piptadenia*, and *Sweetia* (Araujo-Murakami et al. 2013). The plots were 2 km apart, and were situated on inceptisols with similar soil physical and chemical properties and identical climate. However, one plot was located on a shallow soil (<1 m depth) over pre-Cambrian bedrock, leading to lower available water (we term this plot Kenia-shallow). The second plot was located on deeper soils in a slight topographic depression (henceforth termed Kenia-deep). The climate, soils, and carbon budget of these sites have been described in Araujo-Murakami et al. (2013). This paper compares the patterns of carbon allocation in these two plots and asks: (1) How does

seasonal and interannual variation in water stress drought affect the seasonal and annual allocation patterns in tropical forests over a four-year period? (2) What might the results mean for our current understanding of tropical forest responses to environmental variation, based in large part upon measurements of woody growth rates?

MATERIALS AND METHODS

Site characteristics

The protocols used to estimate ecosystem C flux components within the 1-ha plot (divided into 25, 20 × 20 m subplots) were largely based on those developed by the RAINFOR–GEM network.⁶ In both 1-ha Bolivian plots (latitude, 16.0158 W; longitude, 62.7301 S), we measured dendrometer bands on all trees >10 cm every month, measured monthly litterfall in canopy traps, took hemispherical photos for monthly leaf area index (LAI) estimates and estimated fine-root growth every three months using ingrowth cores, which we divided by three to estimate monthly root growth. To estimate leaf flush we add the monthly change in LAI multiplied by an average specific leaf area (SLA) value to the litterfall data, following Doughty and Goulden (2008).

Soil texture and type is similar (sandy loam) between the two plots, but Kenia-deep is slightly more fertile than Kenia-shallow (Appendix: Table A4). Both plots are relatively fertile by wider Amazonian standards (Quesada et al. 2010). The major edaphic difference between the two plots was that Kenia-deep was located on deeper soils in a slight topographic depression. These edaphic differences led to different species compositions, with Kenia-deep having species typical of humid Amazonian regions and Kenia-shallow having species more typical of a dry deciduous *chiquitano* forest with more seasonal leaf area index (variation between an LAI of >3 m²/m² and 1 m²/m² during the dry season [Araujo-Murakami et al. 2013]).

Measurements were distributed evenly through the plot, approximately one per subplot (except for ingrowth cores, which at $N = 16$, were at the corners of subplots). A detailed description is available online for download (see footnote 6) and measurements for these sites are presented in Araujo-Murakami et al. (2013). Summaries of the different components are quantified, and the field methods and data processing techniques used are presented in the Appendix: Tables A1 and A2, respectively.

We calculated total NPP using Eq. 1. This differs from our previous calculation of total NPP because it does not include herbivory, $NPP_{\text{small trees}}$, $NPP_{\text{branch fall}}$, and $NPP_{\text{coarse root}}$, as we do not have a good seasonal time series for these terms

$$NPP_{\text{total}} = NPP_{\text{woody}} + NPP_{\text{leaf flush}} + NPP_{\text{fine root}} \quad (1)$$

To examine what factors (changes in allocation vs. changes in total NPP) dominate seasonal changes in woody growth, we employ the mathematical identity

$$\frac{NPP_{\text{wood-dry}}}{NPP_{\text{wood-wet}}} = \frac{NPP_{\text{wood-dry}}}{NPP_{\text{dry}}} \times \frac{NPP_{\text{dry}}}{NPP_{\text{wet}}} \quad (2)$$

This enables us to decompose changes in NPP_{wood} between seasons into changes in allocation (the first term) and changes in total NPP (the second term).

RESULTS

Both plots typically experienced a five-month dry season (defined as the number of months with <100 mm rainfall) and strong seasonality in rainfall, ranging from >200 mm/month at the peak of the rainy season (December to February) to <100 mm/month between April and September. There was a bimodal peak in solar radiation, with a minimum caused by wet-season cloudiness in December–February, and a minimum between May and September caused by low sun angles and shorter days during the austral winter (the sites are 16° from the equator). The mean annual air temperature was ~23.4°C. The mean annual rainfall over the period 2005–2011 was ~1310 mm. There was a significant drought in late 2010 and early 2011, a local manifestation of a wider-scale drought across southern and western Amazonia in that period (Lewis et al. 2011). The drought period is identified as a gray bar in the Appendix: Fig. A1. During this drought, there were anomalously low values of volumetric soil water content and precipitation, but fewer anomalies in temperatures, solar radiation, and water vapor pressure deficit (VPD)(Appendix: Fig. A1).

Carbon allocation trade-offs

There was substantial seasonal variation in the major components of NPP (Appendix: Fig. A3). In both sites, woody NPP varied between about 0.5–0.6 Mg C·ha⁻¹·month⁻¹ in the wet season, and 0–0.1 Mg C·ha⁻¹·month⁻¹ in the dry season (corrected for potential moisture expansion). In the deep-soil site, canopy NPP ranged between ~1.0 Mg C·ha⁻¹·month⁻¹ in the dry season and ~0.2 Mg C·ha⁻¹·month⁻¹ in the wet season, but fine-root NPP showed less seasonal range (0.2–0.6 Mg C·ha⁻¹·month⁻¹) and also tended to peak in the wet season. In the shallow-soil site, both canopy and fine-root NPP showed less consistent seasonal variation. At the deep-soil site total NPP averaged 1.24 ± 0.26 Mg C·ha⁻¹·month⁻¹ (mean ± SE) in the wet season and 0.86 ± 0.38 Mg C·ha⁻¹·month⁻¹ in the dry season, but there was substantial seasonal variation, with some years (e.g., 2012) showing no seasonality in total NPP (Fig. 1). At the shallow-soil site there was a more regular seasonal decline in NPP from 1.04 ± 0.16 Mg C·ha⁻¹·month⁻¹ in the wet season to 0.52 ± 0.20 Mg C·ha⁻¹·month⁻¹ in the dry season, but

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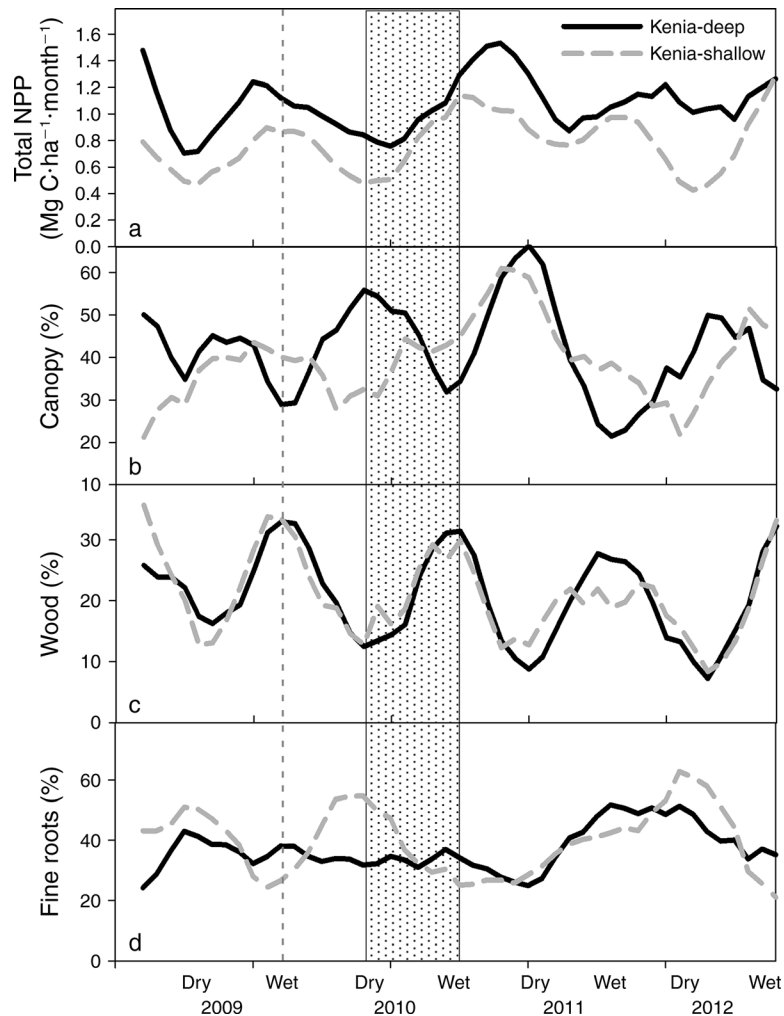


FIG. 1. (a) Total net primary production (NPP; fine-root, canopy, and wood) over a four-year period for Kenia-deep (black) and Kenia-shallow (gray) near Santa Cruz, Bolivia. (b) Percentage allocated to canopy (canopy NPP divided by total NPP). (c) Percentage allocated to wood, and (d) the percentage allocated to fine-root growth. The dotted bar highlights the approximate period of the 2010 drought. The vertical gray dashed line (2009) is in the wet season and can be used to highlight seasonal variation.

also substantial interannual variation in this seasonal pattern.

Seasonal variations in woody production in the deep-soil plot were largely explained by allocation trade-offs rather than changes in total NPP. For instance, in both plots allocation of NPP to wood varied from accounting for between $\sim 25\%$ and 35% of total NPP during the wet season to $\sim 10\text{--}15\%$ of total NPP in the dry season (Fig. 1c and Appendix: Fig. A1). Total NPP also decreased during the dry season but by a much smaller amount; the decrease in total NPP did not drive decreased dry-season woody NPP. At Kenia-deep the dry-season NPP was $69\% \pm 7\%$ of wet-season NPP, but dry-season allocation to wood was only $34\% \pm 6\%$ of wet-season allocation; these two factors combined to result in dry-season woody NPP being $20\% \pm 3\%$ of wet-season NPP (Eq. 2 and Table 1). Therefore, allocation changes are twice as important as changes in NPP in driving

seasonality of woody growth. At the deep-soil site, allocation of NPP to the canopy (including leaves, reproductive material, and twigs) showed a strong seasonal cycle that was anti-correlated with wood growth (Fig. 1: solid black line). This reflected leaf flush and not leaf fall, which we calculated as the combination of changing total LAI and litterfall (Doughty and Goulden 2008). At the shallow-soil site, there was greater seasonal decline in NPP, but less seasonality in fine-root production (Appendix: Fig. A3); hence overall allocation to wood production decreased in the dry season. The shallow-soil dry-season NPP was $50\% \pm 7\%$ of wet-season NPP, but dry-season allocation to wood was only $38\% \pm 8\%$ of wet-season allocation; these two factors combined to result in dry-season woody NPP being $21\% \pm 3\%$ of wet-season NPP (Eq. 2 and Table 1). Therefore, at the shallow-soil site, allocation changes are $\sim 33\%$ more important than changes in total NPP in

TABLE 1. Following Eq. 2, the table shows the seasonal shift (dry-season value divided by wet-season value) in woody NPP and its decomposition into a seasonal shift into the allocation of NPP and the seasonal shift in total NPP.

Plot	Seasonal shift in woody NPP ($\text{NPP}_{\text{wood-dry}}/\text{NPP}_{\text{wood-wet}}$)	Seasonal shift in NPP allocation ($\text{NPP}_{\text{wood-dry}}(\%)/\text{NPP}_{\text{wood-wet}}(\%)$)	Seasonal shift in total NPP ($\text{NPP}_{\text{dry}}/\text{NPP}_{\text{wet}}$)
Kenia-deep	0.20 ± 0.03	0.34 ± 0.06	0.69 ± 0.07
Kenia-shallow	0.21 ± 0.03	0.38 ± 0.08	0.50 ± 0.07

Notes: The large seasonal shift in woody growth is largely explained by the seasonal shift in allocation, with seasonality in NPP playing a smaller role. The role of allocation is more important in the deeper-soil plot.

driving seasonality of woody growth. At this plot, allocation of NPP to the fine roots showed a strong seasonal cycle that was anti-correlated with wood growth (Fig. 1: dashed gray line).

Direct impact of drought

Remarkably, we saw little response of NPP to the 2010 drought, despite strong declines in photosynthesis observed in the field. Leaf-level gas exchange decreased by a significant amount ($P < 0.05$ at Kenia-deep and $P < 0.001$ at Kenia-shallow) between the drought period (November 2010) and the non-drought period (June 2011; Table 2). Leaf level gas exchange dropped by approximately half at Kenia-deep and to below zero at Kenia-shallow, indicating that total canopy photosynthesis had decreased substantially during the drought period. However, total NPP did not drop during the drought period at either site, indicating a temporal decoupling between total photosynthesis and growth (Fig. 2a). This suggests that, during the drought period, the forests used nonstructural carbohydrates (or other carbon stores) to support growth, which may have been built up during the non-drought periods.

Multiyear impact of drought

There was a multiyear response in the allocation of NPP following drought, with increases in allocation to canopy NPP over the first year following the drought (2011), and then in allocation to fine-root NPP over the second year after drought (Fig. 3). Remarkably, this multiyear pattern was repeated in both plots.

Total NPP increased in both plots by $\sim 20\%$ in the six-month period following the drought period (Figs. 2 and 3). This increase in NPP does not seem to directly correspond to any simultaneous climate anomaly (Appendix: Fig. A1), suggesting that it is driven by exploitation of nonstructural carbohydrate reserves rather than an increase in gross primary production.

In both plots the increase in NPP was largely for increased canopy productivity, with little change in wood or fine-root production. Contrary to certain theoretical expectations (Bloom et al. 1985), root growth did not increase either during or the year following the drought when canopy NPP had increased, but in the year after (Fig. 2d). The year following the drought, fine-root NPP was about 20% of total NPP, and it then increased to $\sim 50\%$ of NPP the year after that. The increase in fine-root production coincided with a decline in canopy and wood production, with little overall change in total NPP.

There was a gradual declining trend in the allocation of NPP towards woody biomass over the four-year period (Fig. 2c), declining from $\sim 40\%$ during the first-year peak to $\sim 30\%$ in the peak of the fourth year. There was also a large change in allocation patterns following the drought period. We put this seasonal information into a ternary diagram to show both the axis of variation between the wet and dry season at both plots (Fig. 3, top) and the yearly variation following the drought (Fig. 3, bottom). Seasonal variation at the deep-soil site had a clear axis of variation where reduced (increased) woody NPP was offset by greater (less) canopy NPP, with minimal changes in root growth. In contrast, at the shallow-soil site, the main axis of variation in NPP allocation was between woody growth in the wet season and fine-root growth in the dry season. When we averaged yearly values for the years immediately before and including the drought (2009–2010), both sites had similar carbon allocation values. Immediately following the drought, NPP allocation shifted towards the canopy and away from wood and roots in 2011 (Fig. 3, bottom: arrow 1–2). NPP allocation then shifted towards roots in 2012 and away from the canopy (Fig. 3, bottom: arrow 2–3). A small, longer-term shift away from wood allocation remained following the drought period.

TABLE 2. The table shows mean light-saturated ($1000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ irradiance, 25°C , ambient CO_2) leaf gas exchange ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; mean \pm SE; $N = 20$ trees per plot) for a drought period (November 2010) and a non-drought period (June 2011) for sunlit branches (cut and rehydrated) on 20 trees distributed evenly through the two (Kenia-deep and Kenia-shallow) 1-ha plots.

Plot	June 2011	November 2010	Change
Kenia-deep	$6.0 \pm 0.98^*$	2.92 ± 0.85	3.08
Kenia-shallow	$3.1 \pm 0.67^{***}$	-0.29 ± 0.09	3.39

Significant differences: * $P < 0.05$; *** $P < 0.001$.

TABLE 3. The table shows key carbon cycling parameters as taken from a previous paper on our two study plots in the Hacienda Kenia in Guarayos Province, Santa Cruz, Bolivia, for averaged data over an approximately two-year period (2009–2010) (Araujo-Murakami et al. 2013).

Plot	NPP (Mg C·ha ⁻¹ ·yr ⁻¹)	GPP (Mg C·ha ⁻¹ ·yr ⁻¹)	NPP canopy (%)	NPP wood (%)	NPP fine roots (%)	Biomass (Mg C/ha)	Residence time (yr)
Kenia-deep	15.50 ± 0.89	34.1 ± 2.92	40 ± 7	34 ± 2	26 ± 3	66.2	22
Kenia-shallow	11.27 ± 0.68	26.9 ± 2.70	41 ± 8	32 ± 2	27 ± 3	68.4	26

DISCUSSION

This study highlights the importance of changes in allocation of NPP over time, on both a seasonal and interannual basis, and also the contrasting allocation trade-offs in two plots with contrasting soil depth. The differences between the two plots would have been masked if we showed only annual mean NPP allocation for several years of data, because the long-term mean values are the same for both plots (Araujo-Murakami et

al. 2013; see also Table 3). It is noteworthy that the mean annual allocation to roots is the same in both plots despite the slightly higher fertility and deep soils in Kenia-deep.

The first notable pattern is the seasonality of allocation at both plots. Seasonality in woody NPP was similar at both sites, decreasing strongly during the dry season. Dry-season declines in woody NPP have been demonstrated at many other tropical forests, and

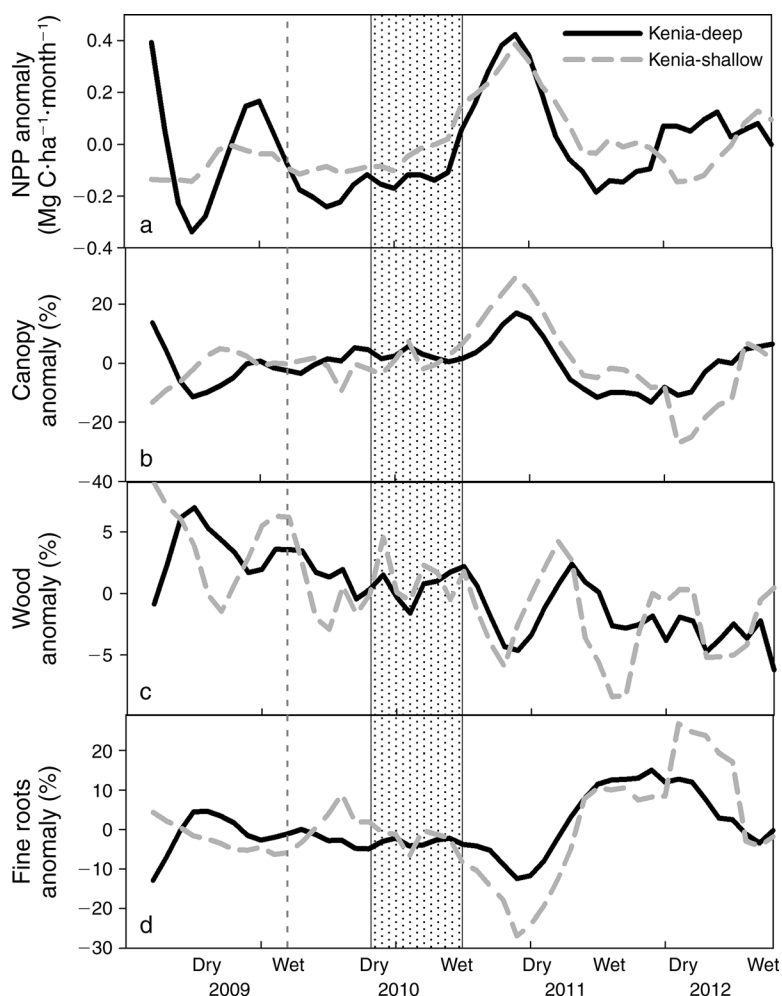


FIG. 2. (a) Total net primary production (NPP; root, canopy, and wood) seasonal anomaly (difference between measurement and average seasonal cycle) over a four-year period for Kenia-deep (black) and Kenia-shallow (gray) near Santa Cruz, Bolivia. (b) Percentage canopy anomaly. (c) Percentage wood growth anomaly, and (d) percentage fine-root growth anomaly. The dotted bar highlights the approximate period of the 2010 drought. The vertical gray dashed line (2009) is in the wet season and can be used to highlight seasonal variation.

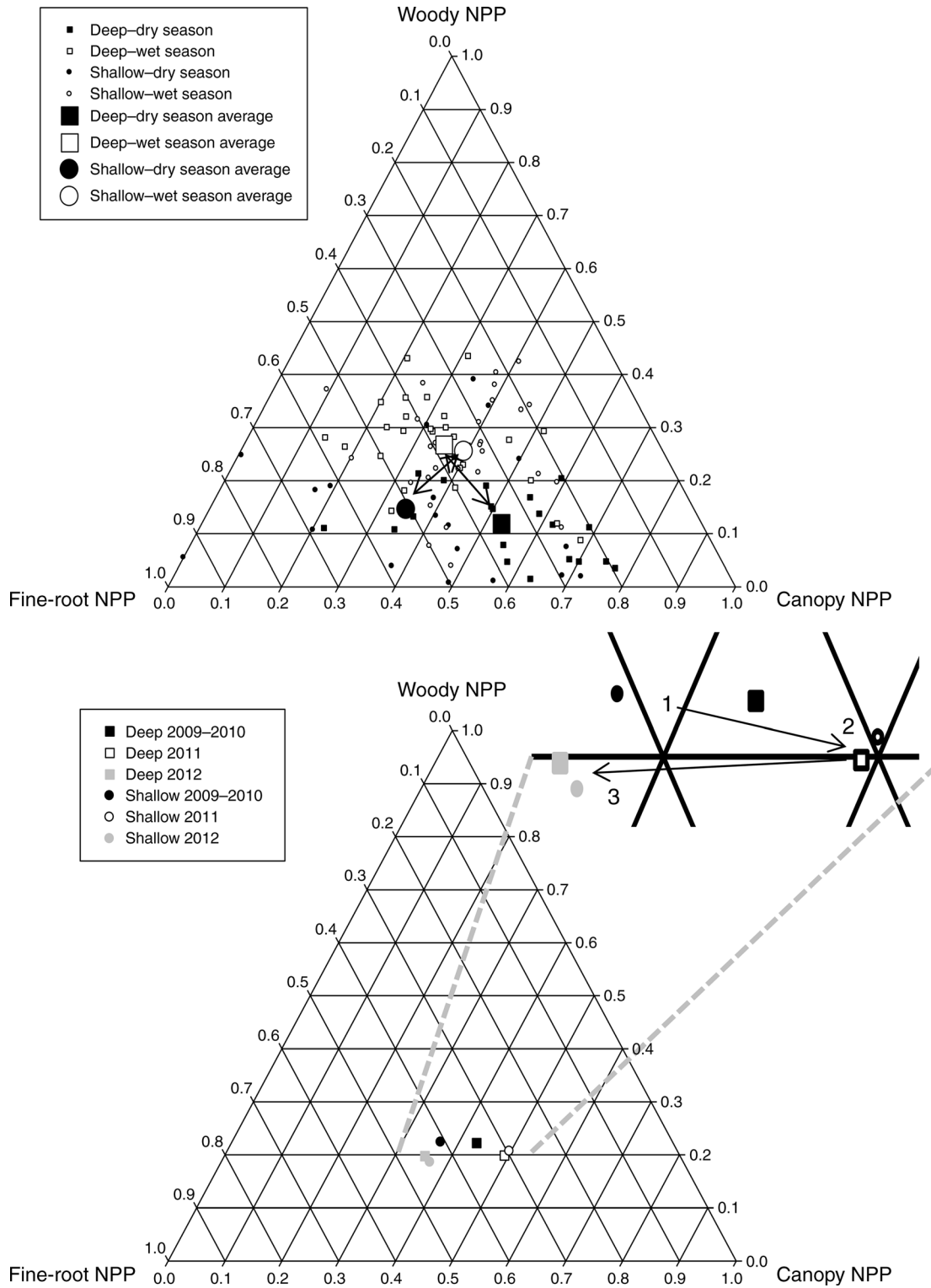


FIG. 3. (Top) A ternary diagram for Kenia-deep (squares) and Kenia-shallow (circles) for the dry season (April–September) (black symbols) and the wet season (the rest of the year) (open symbols). Seasonal averages are shown with larger symbols and monthly points with smaller symbols. (Bottom) A ternary diagram showing the different axis of variation between carbon allocation in the two 1-ha plots for Kenia-deep (squares) and Kenia-shallow (circles) for 2009–2010 (black), 2011 (open), and 2012 (gray). There was a multiyear response in the allocation of NPP following drought, with increases in allocation to canopy NPP over the first year following the drought (2011), and then in allocation to fine-root NPP over the second year after drought. The inset is

are usually interpreted as evidence that water limitation affects overall photosynthesis and productivity, which results in slower growth rates (Doughty et al. 2013). Our data suggest a reinterpretation of this body of work by showing that a decline in tree growth reflects more a shift in NPP allocation to canopy and leaves, rather than a decline in NPP. Hence trees grow wood more slowly in the dry season because they are prioritizing building new leaves or roots, not because their net primary productivity has declined. This is particularly the case for the more humid forest (the deeper-soil plot), which may be more representative in composition and function of the wider Amazon forest biome. Because of the low biomass and rapid tree turnover rates, wood allocation may be important for such forests to better compete for limited light resources (Table 2). This might explain why woody growth plays a pivotal role in the allocation rates in both plots.

A second notable feature in our data is that the axis between the seasonal trade-off differs between two plots. As soil depth decreases, game theory optimization (GTO) models would predict increased root growth competition and increased allocation of carbon towards roots (Franklin et al. 2012). Our data show that the forest on shallow soils has a dominant seasonal trade-off in carbon allocation between wood and fine roots, while the forest on deeper soils has a dominant carbon allocation trade-off between wood and canopy growth (Fig. 3, top). GTO models predict that shallow soils increase root competition as each individual increases root growth to deprive competitors of limited nutrients and water (Franklin et al. 2012). In these scenarios, root allocation is increased beyond the “collective optimum,” and stand productivity is not optimized (Franklin et al. 2012). Total GPP and NPP are lower at Kenia-shallow (GPP is $26.9 \pm 2.70 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ vs. $34.1 \pm 2.92 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) (Table 3; Araujo-Murakami et al. 2013) suggesting that restricted water access does lower leaf level photosynthesis and reduce leaf area in the dry season. Therefore, the shallow soils may drive root competition between trees, reducing available carbon for leaves and giving the drought-deciduous tree species an advantage in the shallow-soil system. In the site with deeper soils, root competition is reduced, allowing more carbon to be allocated to increased canopy growth. However, Kenia-deep has more fertile soils (Appendix: Table A4) which could serve as an alternate explanation for the difference in seasonal root allocation trade-offs between the sites. The trees in the humid plot seem to prioritize building new canopies in the dry season, probably because this is a period of low herbivory and pathogen pressure (because of the dry conditions) and high light availability (Givnish 1999). The carbon

required for this canopy building is utilized at the expense of investment in woody growth.

A third remarkable feature is relatively moderate variation in NPP during the drought event, despite clear evidence of a strong decline in leaf-level photosynthesis during dry events. This suggests that significant non-structural carbohydrate (NSC) stores may exist within the biomass of these forests (Wurth et al. 2005), providing reserves of energy and carbon that enable the forest to maintain NPP despite declines in photosynthate supply. This may reflect an adaptation of species to both regular dry seasons and occasional exceptionally severe drought events. Following the end of the 2010 drought, NPP increased, indicating that growth may still have been dependent on the NSC stores, since total stand photosynthesis likely decreased. However, because this extra NPP was allocated towards increased leaf growth, these depleted stores of carbon may have been replenished in 2011. This region likely experienced drought in 2005 in addition to 2010 (Phillips et al. 2009), and it is unclear how much of our measured effect was impacted by the previous drought. Multiple droughts could weaken the forest hydrologically. However, the period between droughts was long enough to have likely completely refilled NSC stores.

A fourth noteworthy feature is the shift in carbon allocation across years. Both plots showed consistent shifts in allocation patterns following the 2010 drought (Fig. 3). Both plots initially shifted allocation towards the canopy. At the shallow-soil site, this allocation towards the canopy came at the expense of the normal seasonal allocation towards roots. This is surprising because it has been theorized that forests may allocate more carbon towards roots during a drought (Bloom et al. 1985) and our plots did not, and in fact only increased root growth two years following the drought. This demonstrates that the allocation patterns of these trees are not predetermined or fixed, but instead are relatively plastic and adaptable to environmental pressures. This is consistent with adaptive dynamics theory (Dybzinski et al. 2011), which predicts that plant communities will modify allocation strategies to increase their success against other strategies, thus maximizing long-term productivity and reproductive fitness instead of growth.

Following the drought, both plots shifted NPP towards canopy growth likely to replace leaves damaged or fallen during the drought. This would lead to more exposed branches during the drought (Anderson et al. 2010), which could affect the forests EVI (enhanced vegetation index) signal (Saleska et al. 2007, Samanta et al. 2010). Our data suggest that changes in canopy growth (and possibly their corresponding changing EVI

an expanded version of the center of the bottom diagram; arrows indicate allocation shifts. Immediately following the drought (2009–2010), NPP allocation shifted towards the canopy and away from wood and roots in 2011 (arrow 1–2). NPP allocation then shifted towards roots in 2012 and away from the canopy (arrow 2–3). Mean values \pm SE are presented in the Appendix: Table A3.

signal) due to drought are not necessarily correlated with changing total NPP or GPP. However, our data also show that canopy growth (and possibly EVI) is anti-correlated with either root growth or woody growth on a seasonal basis, which could potentially be used by optical remote sensing to estimate wood or root growth in tropical forests.

The increased carbon allocated towards roots under conditions of water stress is a strategy which may have developed over an extended period of evolutionary time, since the region is prone to regular rainfall shifts. The vegetation in this region is in a constant state of flux as solar insolation-driven shifts in the ITCZ modify rainfall in this region on centennial and millennial timescales (Cruz et al. 2005). Therefore, it is not surprising that trees in this region can shift allocation patterns towards roots to obtain more water and acclimate to the potentially drier conditions. This allocation shift would not maximize short-term growth, but instead would maximize long-term productivity, as increased root growth would capture more rainfall and reduce drought-related mortality. Following the drought, there is a steady decline in carbon allocation towards wood (Fig. 3). It is unclear whether the shift in allocation from wood to roots is a longer-term trend or whether the plot will return to the previous allocation patterns in future years. If it does not return, this would have interesting climate implications for a region that may experience more droughts in the future, since less carbon locked in the woody biomass would reduce ecosystem-level C sequestration rates.

Had we just measured woody NPP following the drought and interpolated to total NPP or GPP, we would have inferred that total productivity decreased during the drought and showed a long-term decline following the drought. However, our total NPP perspective shows that this was not the case, and that the decrease in woody NPP was instead a shift first to canopy and then to roots, and that total NPP did not actually decrease either in the short term or the long term. At the deeper soil site there is no correlation between woody growth and total NPP on a monthly or seasonal basis ($P > 0.05$, $r^2 = 0.01$) (Appendix: Fig. A4). At the more water-stressed shallow-soil site there was a significant correlation ($P < 0.005$) between woody growth and NPP, but with low explanatory power ($r^2 = 0.19$). This has important implications both for interpreting the influence of environmental perturbations on woody biomass production rates in tropical forest plot monitoring networks (Phillips et al. 1998), and for the application and interpretation of dendrochronology (Brienen and Zuidema 2005). In both cases, decreased tree growth rates following a drought primarily represent a shift in allocation towards roots or leaves, rather than a change in total NPP or GPP. The extent to which our plots can serve as proxies for the wider Amazon basin is still unclear, but in the absence of similar data sets, we interpret the potential

broader implications as if the results of our study were common. Even if the exact patterns are not the same at other sites, the principle that a full allocation perspective can completely change our view of what is going on is important. In humid and moist tropical forest biomes, it is possible that tree growth rate data have zero predictive power in determining the relationship between weather conditions and productivity. Conversely, if we are to understand how tree growth rates are responding to changing climate and atmospheric CO₂ concentrations, we need to build and improve our understanding of carbon allocation as much as (or perhaps even more than) we need to understand the direct impacts on photosynthesis. It is incorrect to infer climate–productivity relationships from tree growth data alone.

Our study demonstrates the importance and complexity of carbon allocation strategies in tropical forests both on seasonal and interannual timescales, and provides empirical support for the predictions of eco-evolutionary carbon allocation theory (Franklin et al. 2012). We show how interpretation of seasonal and interannual variation in tree growth rates in a tropical forest will be confounded if allocation to other pools is not considered. In some humid tropical biomes, we do not therefore expect seasonal or annual woody growth data from plot networks or dendrochronology to closely match environmental changes, because forest carbon allocation priorities and NSC storage mean there is no simple, direct link between photosynthesis, net primary productivity, and tree growth. The details of the linkage and its seasonal variation may vary from site to site, but our key point in this study is that without a whole carbon budget and allocation perspective, it is difficult to infer with confidence how changes in productivity relate to changes in woody growth, and vice versa.

ACKNOWLEDGMENTS

This work is a product of the Amazon Forest Inventory Network (RAINFOR) consortium, and the Global Ecosystems Monitoring (GEM) network, and was funded by a grant from the Gordon and Betty Moore Foundation. We thank R. Castedo (owner), R. Melgar (logistic coordinator), P. Tomicha (foreman), and J. Surubi (cowboy) of the Hacienda Kenia. We also thank D. E. Guari of the Hacienda Jorochito and the Museo Noel Kempff Mercado for logistical support for the research. We declare no conflict of interest in this manuscript. Statement of authorship: C. E. Doughty, Y. Malhi, D. B. Metcalfe, A. Araujo-Murakami, and J. E. Silva-Espejo conceived and set up the study; C. E. Doughty, A. Araujo-Murakami, D. B. Metcalfe, L. Arroyo, J. Heredia, E. Pardo-Toledo, L. M. Mendizabal, V. D. Rojas-Landivar, M. Martinez, M. Valencia, R. Rivero, and L. Vare collected the data; C. E. Doughty led the writing of the paper with contributions from Y. Malhi and D. B. Metcalfe. Y. Malhi received funding for the study.

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SUPPLEMENTAL MATERIAL

Appendix

Additional site descriptions, two method tables, two data tables, and four additional figures (*Ecological Archives* E095-194-A1).