

# Forest biomass, productivity and carbon cycling along a rainfall gradient in West Africa

Sam Moore<sup>1</sup>  | Stephen Adu-Bredu<sup>2</sup> | Akwasi Duah-Gyamfi<sup>2,3</sup> | Shalom D. Addo-Danso<sup>2,4</sup> | Forzia Ibrahim<sup>2</sup> | Armel T. Mbou<sup>5</sup> | Agnès de Grandcourt<sup>5</sup> | Riccardo Valentini<sup>5,6</sup> | Giacomo Nicolini<sup>5,7</sup> | Gloria Djagbletey<sup>2</sup> | Kennedy Owusu-Afriye<sup>2</sup> | Agne Gvozdevaite<sup>1</sup> | Imma Oliveras<sup>1</sup>  | Maria C. Ruiz-Jaen<sup>8</sup> | Yadvinder Malhi<sup>1</sup>

<sup>1</sup>Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford, UK

<sup>2</sup>Forestry Research Institute of Ghana, Council for Scientific and Industrial Research, Kumasi, Ghana

<sup>3</sup>Michigan Technological University, School of Forest Resources and Environmental Science, Houghton, MI, USA

<sup>4</sup>Faculty of Forestry, University of British Columbia, Vancouver, BC, Canada

<sup>5</sup>Centro Euro-Mediterraneo sui Cambiamenti Climatici, Lecce, Italy

<sup>6</sup>Far Eastern Federal University, Vladivostok, Russia

<sup>7</sup>Department for Innovation in Biological Agro-food and Forest Systems, University of Tuscia, Viterbo, Italy

<sup>8</sup>Subregional Office for Mesoamerica, Food and Agriculture Organization of the United Nations, Panama City, Panama

## Correspondence

Sam Moore, Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford, UK.  
Email: sam.moore@ouce.ox.ac.uk

## Funding information

H2020 European Research Council; Natural Environment Research Council, Grant/Award Number: NE/1014705/1; Jackson Foundation

## Abstract

Net Primary Productivity (NPP) is one of the most important parameters in describing the functioning of any ecosystem and yet it arguably remains a poorly quantified and understood component of carbon cycling in tropical forests, especially outside of the Americas. We provide the first comprehensive analysis of NPP and its carbon allocation to woody, canopy and root growth components at contrasting lowland West African forests spanning a rainfall gradient. Using a standardized methodology to study evergreen (EF), semi-deciduous (SDF), dry forests (DF) and woody savanna (WS), we find that (i) climate is more closely related with above and belowground C stocks than with NPP (ii) total NPP is highest in the SDF site, then the EF followed by the DF and WS and that (iii) different forest types have distinct carbon allocation patterns whereby SDF allocate in excess of 50% to canopy production and the DF and WS sites allocate 40%–50% to woody production. Furthermore, we find that (iv) compared with canopy and root growth rates the woody growth rate of these forests is a poor proxy for their overall productivity and that (v) residence time is the primary driver in the productivity-allocation-turnover chain for the observed spatial differences in woody, leaf and root biomass across the rainfall gradient. Through a systematic assessment of forest productivity we demonstrate the importance of directly measuring the main components of above and belowground NPP and encourage the establishment of more permanent carbon intensive monitoring plots across the tropics.

## KEYWORDS

Africa, allocation, biomass, carbon cycle, net primary productivity, rainfall gradient, residence time, tropical forests

## 1 | INTRODUCTION

Tropical forests are among the most productive ecosystems on Earth accounting for over 60% of global terrestrial photosynthesis and

about one-third of global net primary production (NPP), which equates to approximately 18–24 Pg C yr<sup>-1</sup> (Field, Behrenfeld, Randerson, & Falkowski, 1998; Roy & Saugier, 2001; Malhi et al., 2015). NPP is the rate of formation of biomass such as woody, leaf and

root tissues and is thus one of the most fundamental attributes of an ecosystem at the base of its food web. As such, NPP is a highly important parameter in describing the functioning of any ecosystem. Due to their importance in the global carbon cycle, tropical forests have received increasing amounts of research attention in the last few decades. However, NPP of tropical forests is one of the most important and least quantified components of the global carbon cycle (Anderson-Teixeira, Wang, McGarvey, & LeBauer, 2016). This is primarily because directly measuring the NPP of forests in the field is labour-intensive. Historically, it was more commonly inferred from single components of NPP such as leaf litterfall (Bray & Gorham, 1964; Murphy, 1975), the methods of which are described in more detail in Clark et al. (2001a) or from woody growth, with belowground productivity rarely considered. In recent decades however, an increasing dataset of tropical forest total NPP measurements has been building up. The vast majority of these datasets focus on Amazonia (Clark et al., 2001b; Aragão et al., 2009; Malhi et al., 2009a, 2015, 2017; Girardin et al., 2010), the most comprehensive of which were published in a special issue on 'Ecosystem dynamics of Amazonian and Andean forests' (Galbraith et al., 2013). There are a handful of studies from SE Asia (Paoli & Curran, 2007; Riutta et al., in review) and only very recently one from tropical montane forests in Africa (Nyirambangutse et al., 2016). Despite being the world's second largest tropical forest block, African tropical forests have drawn little attention in terms of carbon cycling and global change research compared to their counterparts in South America and Southeast Asia (Baker et al., 2004; Slik et al., 2010; Malhi, Adu-Bredu, Asare, Lewis, & Mayaux, 2013).

Rainfall gradients are useful natural field laboratories that enable us to explore some of the possible effects of future climate change scenarios. For example, many climate change models predict an increase in frequency of severe droughts (Dai, 2013; Sheffield & Wood, 2008) as well as intensification of the El Niño Southern Oscillation (Cai et al., 2014) and it has been suggested that tropical forests are the most sensitive biome to climate change and most prone to species extinction (Deutsch et al., 2008). In a study along wet-dry gradients of tropical forest productivity monitoring plots in Amazonia, Malhi et al. (2015) found that the decline in Gross Primary Production (GPP) from wet to dry forest plots was not tracked by a decline in NPP. Instead, NPP stayed relatively high in the dry plots due to an increase in Carbon Use Efficiency (CUE), which was the result of a relatively greater reduction in autotrophic respiration. They also found that carbon allocation shifted more to woody components and biomass turnover increased in the drier forest plots. Whilst this study provides new insights into carbon cycling across wet-dry gradients in the Amazon, it would be valuable to replicate this on another continent to establish its generality.

West Africa is an interesting and contrasting study site to Amazonia for a number of reasons; (i) soils here are generally more fertile than in Amazonia, (ii) West Africa has a multi-decadal drying trend (Malhi & Wright, 2004) and (iii) a strong history of climate variability that has shaped present-day ecosystems (Malhi et al., 2013), resulting in (iv) species diversity that is generally lower than

Amazonia (Parmentier et al., 2011) with more ubiquitous, wide-spread species. Indeed rainfall is the single most important parameter determining the vegetation gradient for the Upper Guinean forests in West Africa (Bongers, Poorter, & Hawthorne, 2004), but until now, no network of plots along a rainfall gradient has existed in which to test key hypotheses relating to the productivity of these forests. Here, we present the first directly measured NPP dataset from lowland African tropical forests. As part of the Global Ecosystems Monitoring network (GEM: gem.tropicalforests.ox.ac.uk), the number of one-hectare carbon-intensive monitoring study plots in Africa increased from zero in 2011 to over twenty, at present. It is the first plot network in Africa that monitors carbon fluxes as opposed to other, more spatially extensive plot networks such as Afritrion (African Tropical Rainforest Observation Network, afritrion.org) and CTFS (Center for Tropical Forest Science, forestgeo.si.edu) that focus their efforts on forest inventories of woody biomass, structure and species composition. By monitoring every major component of NPP, we have assembled a new dataset that enables us to ask the following research questions in the context of African tropical forests for the first time:

1. To what extent can key plot-level characteristics such as biomass, NPP and carbon allocation to woody, canopy and root growth be predicted from rainfall patterns?
2. Is woody growth of a tropical forest a useful proxy for stand-level NPP? If not, is any other component of carbon allocation a better indicator?
3. Which aspects of NPP, carbon allocation and carbon residence time are the primary drivers for the patterns in biomass we observe?

More specifically, the objectives of this research are to:

1. Quantify above and belowground C stocks at eight-one-hectare forest plots at three sites across a rainfall gradient in Ghana.
2. Calculate total annual NPP values for all plots and quantify this NPP allocation into woody, canopy and root components.
3. Define the main drivers for the observed changes in woody, leaf and root biomass across the gradient.

## 2 | MATERIALS AND METHODS

### 2.1 | Field sites

As part of the GEM network, 14 one-hectare plots were established within three study sites along a rainfall gradient in Ghana, West Africa. The gradient contains three wet evergreen forest plots in Ankasa Conservation Area (ACA) in the extreme southwest of Ghana, close to the Côte d'Ivoire border. Two hundred kilometres to the north-east, six semi-deciduous forest plots are located within Bobiri Forest Reserve (BFR) close to the second largest city in Ghana, Kumasi, and a further one hundred kilometres to the north-east, five plots are located within the Kogyae Strict Nature Reserve (KSNR) which encompasses the dry forest to savanna transition

zone. For the purposes of this study, we refer to these 14 plots as the extended plot network and include these in the biomass and productivity analyses. For the NPP regression analysis and the productivity-allocation-turnover analysis, we include only the core plot network in the analyses which consists of two lowland, non-inundated plots with low or no logging impact within each of the four vegetation types; evergreen forest (EF), semi-deciduous forest (SDF), dry forest (DF) and woody savanna (WS), totalling eight study plots in a paired-plot sampling methodology. This core plot network excludes plots with features such as seasonal flooding and recent logging which have clear and unwanted biases on components such as stem NPP, and also excludes a forest-savanna transition where we have only one plot.

The core EF plots in ACA (ANK-01 & ANK-02) are both located on a small hill within the footprint of an eddy covariance tower. The core SDF plots (BOB-01 & BOB-02) are located within 5 km from each other in the most undisturbed part of BFR. BOB-01 is located within the Strict Nature Reserve with no record of logging. However, perhaps due to its location close to the edge of the reserve and possible wind effects, it may be quite dynamic. Forestry Commission (FC) records state that BOB-02 was last logged (very lightly) more than 60 years ago. It is important to note that this reserve is only ever very lightly logged (1–2 stems per hectare) and this is rigorously enforced by the FC. The DF and WS plots are all located within the KSNR which is made of two sub-communities; transitional forest towards the true forest zone in the south-east of the reserve and transitional forest towards Guinean woody savanna, covering about a third of the reserve (Ghana Wildlife Department, 1994). The core DF plots (KOG-02 & KOG-03) are located in the most forest-dominated region of KSNR which is sometimes comprised of isolated forest patches. Following a transition zone of several kilometres (the location of KOG-04), the core WS plots (KOG-05 & KOG-06) are located in the Guinean woody savanna-dominated region of KSNR.

## 2.2 | Rainfall gradient

The four study sites have contrasting rainfall and soil regimes, the key characteristics of which are outlined in Table 1. Ankasa, the EF site has the highest mean annual precipitation (MAP) of around 2,000 mm, mainly concentrated from March to mid-July and from September to November, and relative humidity is high throughout the year. Further north at the Bobiri and Kogyae sites, the MAP reduces to 1500 and 1200 mm, respectively. Rainfall occurs at the same time of year at all sites, but the seasonality is enhanced with increasing distance north, resulting in greater mean Maximum Climatological Water Deficits (MCWD; see Malhi et al., 2009b). Like many other tropical forest soils, the soils in Ankasa are deeply weathered, high in aluminium and acidic (pH 4.0–4.5) but are fairly rich in phosphorus compared with many Amazonian soils. Bobiri and Kogyae are unusually rich in base cations and less acidic than in Ankasa (pH 6.0). The reason for this is unclear as the bed rock is probably metamorphic or igneous (African shield). There may be local depositional features, or other possibilities include heavy cation deposition from

Saharan dust, transported from the Bodele Depression (the basin of Lake Chad in the southern edge of the Sahara Desert) during the Harmattan winds in January and February (Lyngsie, Olsen, Awadzi, Fensholt, & Breuning-Madsen, 2013; Tiessen, Hauffe, & Mermut, 1991; Washington, Bouet, & Cautenet, 2009). The soil texture at the DF and WS sites is very sandy with low water and nutrient retention capacity, whereas the SDF and EF sites have loamy soils.

## 2.3 | Field methods

All field methods employed follow the GEM protocols manual (Marthews et al., 2014; gem.tropicalforests.ox.ac.uk) where they are described in detail as well as in a number of papers in the special issue on 'Ecosystem dynamics of Amazonian and Andean forests' (Galbraith et al., 2013). To summarise, the protocol measures and sums all major components of NPP on monthly or seasonal time-scales in each 1 ha forest plot (Tables 2 and 3). This includes canopy litterfall from litterfall traps at bimonthly intervals, estimates of leaf loss to herbivory, aboveground coarse woody productivity of all large trees ( $\geq 10$  cm dbh) in the plot and small trees (2–10 cm dbh) in subplots via yearly plot censuses, the turnover of branches on live trees by conducting branch fall transects every 3 months, fine root productivity from ingrowth cores installed and harvested every 3 months, and estimation of coarse root productivity by applying a multiplying factor to aboveground woody productivity (Table 2).

## 2.4 | Statistical analysis and error calculation

We assume that most NPP terms were sampled without large biases and hence uncertainty in these terms is dominated by sampling uncertainty. We estimate sampling uncertainty by assuming each sample collection point is independent and assuming a normal distribution (see Table 3). The uncertainty of individual measurement components is propagated by standard rules of quadrature (Hughes & Hase, 2010; see also Malhi et al. (2015) for similar application to Amazonian forests). Where measurement uncertainties are dominated by systematic uncertainties, such as the allometric equations in biomass calculations (Chave et al., 2014), large systematic errors which are consistent with previous analyses (Malhi et al., 2009a, 2015; 2016; Girardin et al., 2010; Galbraith et al., 2013) were assigned to reflect the relative uncertainties. ANOVA was used to test for differences among forest types. ANOVA analysis was conducted after checking for normality using the Shapiro-Wilk test. The Tukey *post hoc* HSD test was used to determine differences between mean threshold values among the forest types. All statistical analyses were conducted using R (R Core Team, 2015).

## 2.5 | NPP calculations

Measurements of NPP were made in all plots spanning the period 2011 to 2015. Slight variations in length of datasets available for each plot do exist, but there is a minimum of 2 years continuous data for all NPP components in all plots (Table 2). Where annual

**TABLE 1** Meteorological and soil characteristics of the four study sites occurring along the rainfall gradient in Ghana

Site name	Ankasa	Bobiri	Kogyae	Kogyae
Vegetation type	Evergreen forest (EF)	Semi-deciduous forest (SDF)	Dry forest (DF)	Woody savanna (WS)
Core plot codes	ANK-01, ANK-02	BOB-01, BOB-02	KOG-02, KOG-03	KOG-05, KOG-06
Latitude (°)	5.2680	6.6910	7.2616	7.3012
Longitude (°)	-2.6955	-1.3389	-1.1501	-1.1649
Elevation (m asl)	114	235	229	221
Solar radiation (GJ m <sup>-2</sup> year <sup>-1</sup> )	1.7	2.0	2.4	2.4
Mean annual air temperature (°C)	25.0	25.7	26.4	26.4
Mean annual precipitation (mm)	2050	1500	1200	1200
Mean annual humidity (%)	91.0	83.9	79.2	79.2
Mean MCWD (mm)	-13	-374	-412	-412
pH	4.27	6.05	6.07	6.02
Soil N (%)	0.17	0.16	0.06	0.04
Soil C (%)	2.61	1.71	0.72	0.62
Soil C:N	14.57	10.18	11.35	15.10
P <sub>total</sub> (mg/kg)	147	258	67	82
Ca <sub>ex</sub>	1.34	32.81	18.91	11.83
Mg <sub>ex</sub>	3.45	11.00	6.22	6.73
K <sub>ex</sub>	0.83	1.25	1.09	0.73
Na <sub>ex</sub>	0.44	0.05	0.04	0.04
Al <sub>ex</sub>	18.44	0.89	0.02	0.07
Sum exchangeable bases	6.05	45.11	26.25	19.33
Soil cation exchange capacity	24.49	46.00	26.27	19.41
Base fraction	0.25	0.98	0.99	0.99
Sand (%)	63	47	83	77
Clay (%)	22	29	2	4
Silt (%)	15	24	15	19

Data for solar radiation, air temperature, precipitation, humidity and MCWD for DF and WS are from the same meteorological station in Kogyae. Average (0–30 cm) soil data for EF, SDF, DF and WS vegetation types were collected from plots ANK-01, BOB-02, KOG-02 and KOG-05, respectively. P<sub>total</sub> – total soil phosphorus pool; Ca<sub>ex</sub>, Mg<sub>ex</sub>, K<sub>ex</sub>, Na<sub>ex</sub>, Al<sub>ex</sub> – exchangeable calcium, magnesium, potassium, sodium and aluminium concentrations; sum of exchangeable bases; soil cation exchange capacity (all in mmol<sub>c</sub>/kg).

means are reported, this is the mean for all complete years (12 months) of data collected so as to avoid any potential seasonal biases. We calculated all components of NPP using the following equations:

$$\text{NPP}_{\text{total}} = \text{NPP}_{\text{coarse root}} + \text{NPP}_{\text{fine root}} + \text{NPP}_{\text{stem}} + \text{NPP}_{\text{branch}} + \text{NPP}_{\text{litter fall}} + \text{NPP}_{\text{herbivory}} + \text{NPP}_{\text{herb}} \quad (1)$$

$$\text{NPP}_{\text{canopy}} = \text{NPP}_{\text{litter fall}} + \text{NPP}_{\text{herbivory}} \quad (2)$$

$$\text{NPP}_{\text{woody}} = \text{NPP}_{\text{coarse root}} + \text{NPP}_{\text{stem}} + \text{NPP}_{\text{branch turnover}} \quad (3)$$

$$\text{NPP}_{\text{root}} = \text{NPP}_{\text{fine root}} \quad (4)$$

$$\text{NPP}_{\text{ACW}} = \text{NPP}_{\text{stem}} \quad (5)$$

Whilst our calculations above include all of the major NPP components, they do not capture several smaller NPP terms, such as NPP lost as volatile organic emissions (NPP<sub>VOC</sub>), litter that remains unmeasured through being trapped in the canopy or litter that falls from vegetation below the 1 m litter traps. However, Malhi et al. (2009a) showed NPP<sub>VOC</sub> to be a relatively minor NPP term that

accounted for  $\sim 0.1 \pm 0.05 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  in a central Amazonian forest. We consider root exudates and transfer to mycorrhizae as a portion of rhizosphere respiration rather than as NPP and are therefore not included in this study. Previous studies have shown these carbon fluxes to be modest ( $< 2 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ ; Malhi et al., 2017). Due to these small omissions, our total NPP estimates should be considered conservative. However, comparisons between bottom-up derived GPP (NPP + autotrophic respiration) and flux tower-derived GPP show very good agreement, especially in temperate and tropical forests (Campioli et al., 2016), which increases confidence that no major components of the carbon budget are missed.

## 2.6 | Analysis framework

In order to better understand what controls the variation in biomass of the three major carbon pools (canopy, woody and fine roots) in these tropical forests, we employ a systematic framework, first

**TABLE 2** Field methods for intensive monitoring of NPP components from Ankasa (ANK), Bobiri (BOB) and Kogyae (KOG) plots in Ghana (see also RAINFOR-GEM manual (Marthews et al., 2014))

	Component	Description	Sampling period	Sampling interval
Aboveground net primary productivity (NPP <sub>AG</sub> )	Aboveground coarse wood net primary productivity (NPP <sub>stem</sub> )	Forest inventory: All trees $\geq 10$ cm DBH were censused to determine growth rate of existing surviving trees and rate of recruitment of new trees. Biomass calculated using the Chave et al. (2014) allometric equation, employing diameter, height and wood density data. The $\geq 10$ cm DBH: $\leq 10$ cm DBH tree ratio from published data (Galbraith et al., 2013) was used to estimate the NPP <sub>stem</sub> fraction of smaller stemmed trees and data scaled up to 1 ha	2011–2013 (ANK) 2011–2015 (BOB & KOG)	Every year
	Branch turnover net primary productivity (NPP <sub>branch</sub> )	New branch fall $> 2$ cm diameter (excluding that associated with dead trees) was surveyed within four $1 \times 100$ m transects; small branches were cut to include only the transect-crossing component, removed and weighed. Larger branches had their dimensions taken (diameter at three points) and all were assigned a wood density value according to their decomposition class (Harmon, Whigham, Sexton, & Olmsted, 1995)	2012–2013 (ANK) 2012–2015 (BOB & KOG)	Every 3 months
	Litterfall net primary productivity (NPP <sub>litterfall</sub> )	Litterfall production of dead organic material $< 2$ cm diameter was calculated by collecting litterfall in $0.25 \text{ m}^2$ ( $50 \times 50$ cm) litter traps placed at 1 m above the ground at the centre of each of the 25 subplots in each plot. Litter separated into leaves, twigs, flowers, fruits, seeds and unidentifiable. Leaf biomass was calculated as leaf area index (LAI)/specific leaf area (SLA), where LAI is the plot mean over the study period and SLA is the basal area-weighted plot mean over the study period	2011–2013 (ANK) 2012–2015 (BOB & KOG)	Every 14 days
	Leaf Area Index (LAI)	Hemispherical photos were taken with a digital camera (Nikon Coolpix 4500) and hemispherical lens (Nikon FC-E8) near the centre of each of the 25 subplots in each plot, at a standard height of 1 m, and during overcast conditions. LAI was estimated from these images using <i>Hemisfer</i> software (licensed version 2.12; <a href="http://www.wsl.ch/dienstleistungen/produkte/software/hemisfer/index_EN">http://www.wsl.ch/dienstleistungen/produkte/software/hemisfer/index_EN</a> ).	2011–2013 (ANK) 2012–2015 (BOB & KOG)	Every month
	Loss to Leaf Herbivory (NPP <sub>herbivory</sub> )	Leaves collected in the 25 litterfall traps in each plot photographed prior to being dried. Leaf area was determined with image analysis software (ImageJ, NIH, USA) to calculate the area of each individual leaf lost to herbivory	2012–2013 (ANK) 2012–2015 (BOB & KOG)	Every 2 months
	Herbaceous net primary productivity (NPP <sub>herb</sub> )	Nine $1 \times 1$ m sampling areas were established within subplots 1,3,9,11,13,15,21,23 and 25 in each plot. All small herbs (defined in Geldenhuys, Knight, Russell, & Jarman, 1988) $< 1$ cm basal diameter (cut at ground level) were harvested for each collection	2014–2015 (KOG only)	Every 3 months

(Continues)

TABLE 2 (Continued)

	Component	Description	Sampling period	Sampling interval
Belowground net primary productivity (NPP <sub>BG</sub> )	Coarse root net primary productivity (NPP <sub>coarse root</sub> )	Not measured directly; estimated as 0.21 (at EF and SDF sites) and 0.28 (at DF and WS sites) of aboveground woody productivity, based on published values of the ratio of coarse root biomass to aboveground biomass (Cairns, Brown, Helmer, & Baumgardner, 1997; IPCC, 2006; Jackson et al., 1996)	n/a	n/a
	Fine root net primary productivity (NPP <sub>fine root</sub> )	Sixteen ingrowth cores (mesh cages 12 cm diameter, to 30 cm depth) were installed in each plot. Cores extracted and roots manually removed from the soil samples in four 10 min time steps and the pattern of cumulative extraction over time used to estimate root extraction beyond 40 min. Root-free soil was then re-inserted into the ingrowth core. Collected roots were thoroughly rinsed, oven dried at 80°C to constant mass, and weighed. This process was repeated for each measurement thereafter. Fine root biomass was calculated from harvested fine roots during the first installation of ingrowth cores	2012–2013 (ANK) 2012–2015 (BOB & KOG)	Every 3 months

developed by Malhi et al. (2015) to analyse carbon cycling along wet–dry gradients in lowland Amazonia, to decompose the biomass calculation into a productivity-allocation-turnover chain. Here, we express the productivity (NPP) of carbon pool 'x', as follows:

$$\text{NPP}_x = \text{NPP}_{\text{total}} \times \text{Allocation}_x \quad (6)$$

where 'NPP<sub>total</sub>' is the total calculated productivity and 'Allocation<sub>x</sub>' is the fraction of NPP<sub>total</sub> allocated to carbon pool 'x' (e.g. canopy, woody, fine roots). In mature, low disturbance forest stands such as those in this study, where biomass growth and mortality rates are approximately equal to one another and there is little net change in biomass, the residence time of carbon pool 'x' can be estimated as biomass divided by productivity (Galbraith et al., 2013):

$$\text{Biomass residence time}_x (\tau_x) = \text{biomass}_x / \text{NPP}_x \quad (7)$$

where 'biomass<sub>x</sub>' is the calculated biomass of carbon pool 'x' and 'NPP<sub>x</sub>' is the productivity of carbon pool 'x'. Hence, the biomass of carbon pool 'x' can be decomposed and expressed as:

$$\text{Biomass}_x = \text{NPP}_{\text{total}} \times (\text{NPP}_x / \text{NPP}_{\text{total}}) \times \tau_x \quad (8)$$

$$\text{Biomass}_x = \text{NPP}_{\text{total}} \times \text{Allocation}_x \times \tau_x$$

$$\text{e.g. Biomass}_{\text{woody}} = \text{NPP}_{\text{total}} \times \text{Allocation}_{\text{woody}} \times \tau_{\text{woody}}$$

### 3 | RESULTS

#### 3.1 | Aboveground biomass and soil C stocks

Mean aboveground biomass (AGB) values from the extended plot network were highest in the EF plots ( $142 \pm 17 \text{ Mg C ha}^{-1}$ ), intermediate in the SDF and DF plots ( $127 \pm 11$  and  $101 \pm 14$

$\text{Mg C ha}^{-1}$ , respectively) and lowest in the WS plots ( $62 \pm 8 \text{ Mg C ha}^{-1}$ , Figure 1), revealing a positive relationship with rainfall ( $r^2 = .51$ ,  $p = .04$ ; Fig. S1a). Mean AGB values were significantly higher ( $p < .01$ ) in the EF and SDF plots compared with the WS plots. Mean soil C stocks (0–30 cm depth) also showed a positive relationship with rainfall ( $r^2 = 0.64$ ,  $p < .001$ ; Fig. S1b) across the extended plot network with significantly higher ( $p < .01$ ) values in the EF plots ( $80 \pm 13 \text{ Mg C ha}^{-1}$ ) compared with the SDF, DF and WS plots ( $39 \pm 3$ ,  $25 \pm 1$  and  $26 \pm 1 \text{ Mg C ha}^{-1}$ , respectively, Figure 1).

#### 3.2 | Total NPP and NPP allocation

Mean total NPP increases from  $13.0 \pm 0.5 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  in EF plots to a peak of  $15.8 \pm 0.4 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  in SDF plots, before declining to  $12.0 \pm 0.7$  and  $10.8 \pm 0.5 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  in DF and WS plots, respectively (Figure 2, Table S1), showing no correlation with rainfall (Fig. S1c). However, the only statistically significant result was higher total NPP values in the SDF plots compared with the WS plots ( $p < .05$ ). Total NPP in BOB-01, one of the SDF plots, was  $14.0 \pm 0.8 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  which is comparable with the mean EF value, whilst the second SDF plot, BOB-02, obtained one of the highest total NPP values reported globally of  $19.5 \pm 1.1 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ . The DF plots ranged in total NPP values from  $10.9 \pm 0.9$  (KOG-02) to  $13.0 \pm 1.0$  (KOG-03)  $\text{Mg C ha}^{-1} \text{ year}^{-1}$ . Similarly, the WS plots ranged in total NPP values from  $9.2 \pm 0.6$  (KOG-05) to  $12.4 \pm 0.8$  (KOG-06)  $\text{Mg C ha}^{-1} \text{ year}^{-1}$ . Note that the herbaceous NPP component was only measured at the DF and WS plots and on average accounts for about  $1.1 \pm 0.1 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ . This component was not measured in the SDF and EF

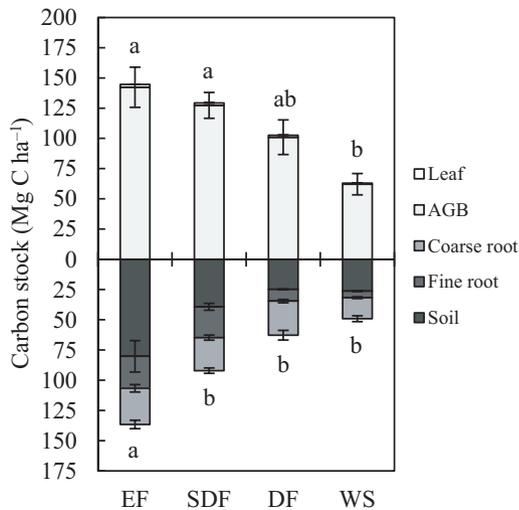
**TABLE 3** Data analysis methods for intensive monitoring of NPP components from all plots in Ghana (see also RAINFOR-GEM manual (Marthews et al., 2014))

Component		Data processing details
Aboveground net primary productivity (NPP <sub>AG</sub> )	Aboveground coarse wood net primary productivity (NPP <sub>ACW</sub> )	Biomass calculated using the Chave et al. (2014) allometric equation: $AGB = 0.0673 \times (\rho D^2 H)^{0.976}$ where AGB is aboveground biomass (kg), $\rho$ is density (g/cm <sup>3</sup> ) of wood, $D$ is dbh (cm), and $H$ is height (m). Tree height data was plot/site-specific. To convert biomass values into carbon, we assumed that dry stem biomass is 47.3% carbon (Martin & Thomas, 2011). Systematic uncertainty of $\pm 20\%$ assigned to values for error propagation
	NPP <sub>branch</sub>	See RAINFOR-GEM manual (Marthews et al., 2014; p. 74) for description of decomposition status and surface area formulas. Errors calculated as the sampling error associated with variation between the transects
	Litterfall net primary productivity (NPP <sub>litterfall</sub> )	NPP <sub>litterfall</sub> is calculated as follows: $NPP_{litterfall} = NPP_{canopy} - \text{Loss to Leaf Herbivory}$ . Litterfall was separated into different components, oven dried at 80°C to constant mass and weighed. Litter is estimated to be 49.2% carbon, based on mean Amazonian values (S. Patiño, unpublished analysis). Errors calculated as the sampling error associated with variation between the litter traps
	Leaf Area Index (LAI)	LAI was estimated from hemispherical photos using the standard Li-Cor LAI-2000 method, based on the Miller (1967) equations and correcting for non-linearity and slope effects (Schleppi, Conedera, Sedivy, & Thimonier, 2007) and canopy clumping (Chen & Cihlar, 1995). Thresholds were set to detect separately for each ring (5 rings) according to Nobis and Hunziker (2005). Errors calculated as the sampling error through variation among subplots
	Loss to Leaf Herbivory (NPP <sub>herbivory</sub> )	The fractional herbivory ( $H_f$ ) for each leaf was then calculated as: $H_f = (A_{nh} - A_h)/A_{nh}$ . Where $A_h$ is the area of each individual leaf including the damage incurred by herbivory and $A_{nh}$ is the leaf area prior to herbivory. The average value of $H_f$ of all leaves collected per litterfall trap was derived and plot level means were calculated. Errors calculated as the sampling error associated with variation between the litter traps
	Herbaceous net primary productivity (NPP <sub>herb</sub> )	A sub-sample (>100 g) of the harvested herbs from each sampling area were separated and oven dried at 80°C to constant mass and weighed. The fresh weight:dry weight ratio was applied to the total sample from each sampling area in the nine subplots and extrapolated to 1 ha. Herbs are estimated to be 49.2% carbon (S. Patiño, unpublished analysis). This protocol was only implemented in the DF and WS plots where the herbaceous layer was clearly visible. Errors calculated as the sampling error associated with variation between the sampling points
Belowground net primary productivity (NPP <sub>BG</sub> )	NPP <sub>coarse root</sub>	See RAINFOR-GEM manual (Marthews et al., 2014; p. 58) for description and range of Root:shoot ratio. Systematic uncertainty of $\pm 20\%$ and 30% assigned to values for error propagation in EF/SDF plots and DF/WS plots, respectively
	Fine root net primary productivity (NPP <sub>fine root</sub> )	Roots were manually removed from the soil samples in four 10 min time steps, according to a method that corrects for underestimation of biomass of hard-to-extract roots (Metcalfe et al., 2007) and used to predict root extraction beyond 40 min (up to 120 min); typically, there was an additional 33% correction factor for fine roots not collected within 40 min. Correction for fine root productivity below 30 cm depth (Galbraith et al., 2013) increased the value by 39%. Errors calculated as the sampling error associated with variation between the sampling points

plots, but we expect it to be an order of magnitude lower in shaded understoreys.

When NPP is separated into canopy (fine litter and herbivory), woody (stem, branch turnover and coarse root) and root (fine root, hereafter termed root) components (as per Equations 2–4), noticeable differences are observed (Figure 2). The EF plots display a near-equal division of NPP between canopy, woody and root components ( $\sim 37 \pm 1\%$ ,  $30 \pm 2\%$  and  $33 \pm 2\%$ , respectively). In contrast, NPP allocation (the process of NPP partitioning as defined in Litton, Raich, & Ryan, 2007) in the SDF plots is dominated by canopy

production, accounting for  $56 \pm 7\%$  of total NPP allocation which is significantly higher ( $p < .001$ ) than all other forest types. The remaining woody and root components account for a much more moderate allocation of  $22 \pm 2\%$  and  $22 \pm 5\%$ , respectively. By contrast, the DF and WS plots are dominated by woody allocation, which are  $39 \pm 7\%$  and  $46 \pm 9\%$ , respectively. Woody allocation was significantly higher ( $p < .05$ ) in the WS plots compared with the SDF plots and root allocation showed no significant differences between forest types. In summary, whilst the EF splits its carbon allocation evenly across the three main components, the SDF allocates more than half



**FIGURE 1** Mean aboveground biomass (all trees >10 cm DBH and leaf carbon stock  $\pm 1$  SE), belowground biomass (fine and coarse root carbon stock  $\pm 1$  SE) and soil carbon stocks (0–30 cm depth,  $\pm 1$  SE) across the extended plot network at each of the four vegetation types (EF – evergreen forest, SDF – semi-deciduous forest, DF – dry forest, WS – woody savanna) along the rainfall gradient. Letters denote significant differences (AGB:  $p < .01$ ; Soil:  $p < .01$ )

its carbon to canopy growth and the driest forest types allocate up to half of their carbon to woody growth. Hence there appear to be clear shifts in carbon allocation strategy along the rainfall gradient, but no overall patterns observed across the extended rainfall gradient plot network (Fig. S2).

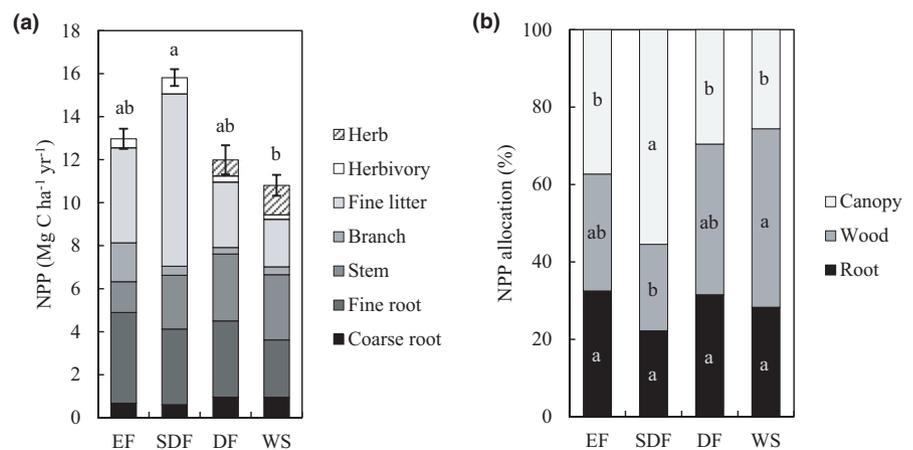
Unique NPP component allocation patterns among the four forest types enable us to ask whether woody growth, equivalent to aboveground coarse wood production ( $NPP_{ACW}$ , Equation 5) is a useful proxy for estimating stand-level NPP.  $NPP_{ACW}$  is often estimated from forest inventories (e.g. Malhi et al., 2004) and is then taken to be a proxy of total NPP, though evidence in support of this assumption is weak (Malhi, Doughty, & Galbraith, 2011). Across the core plot network,  $NPP_{ACW}$  shows no significant relationship with total NPP ( $p = .26$ ) while total canopy production ( $r^2 = 0.68$ ,  $p = .01$ )

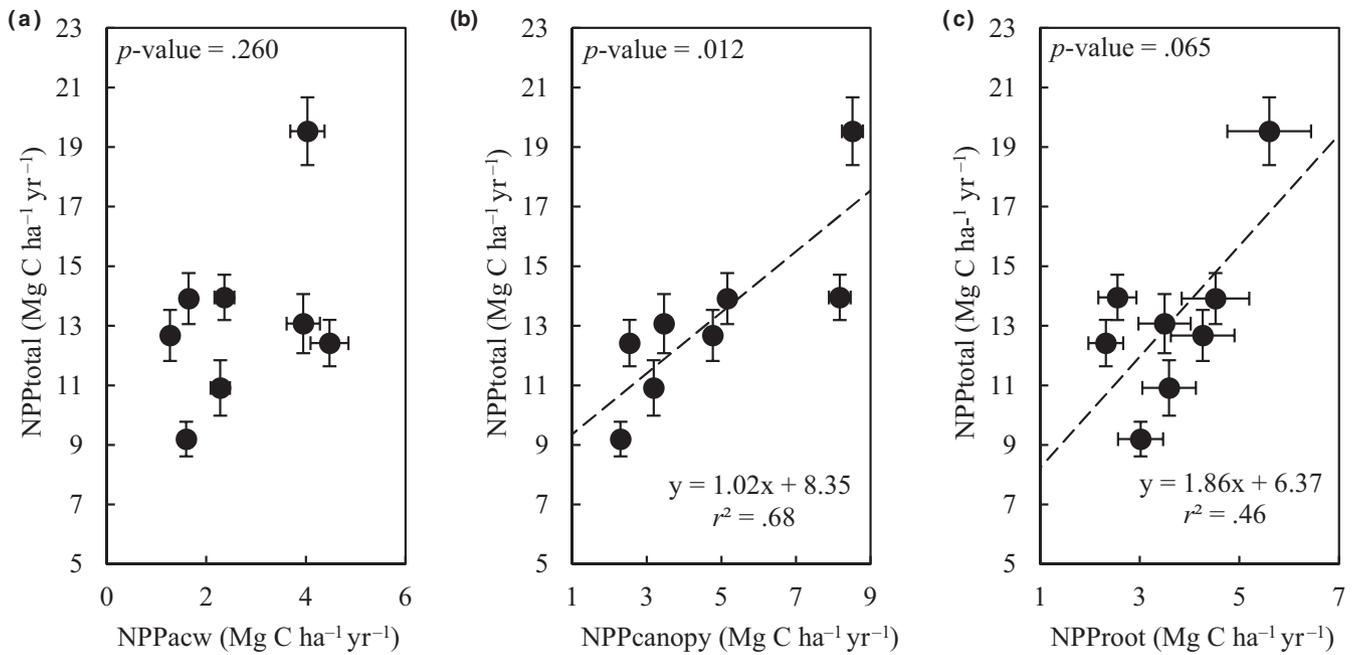
and fine root production ( $r^2 = 0.46$ ,  $p = .07$ ) have closer relationships with total NPP (Figure 3). Note that the x and y axes in these plots are not independent (as  $NPP_{ACW}$  is a component of total NPP), but this makes it even more remarkable that woody growth is not as good a proxy for total NPP. The relationship is weakened through the particularly high woody allocation in two of the drier plots (KOG-03 and KOG-06). If these two plots with very high woody allocation are excluded from the analyses, the relationship improves ( $r^2 = 0.64$ ,  $p < .05$ ). As found previously in Amazonia (Malhi et al., 2011), litterfall is a much better proxy for overall productivity (Figure 3b). Fine root productivity also shows a closer (although not statistically significant) correlation with total NPP (Figure 3c) than aboveground coarse woody NPP.

### 3.3 | Results from analysis framework for woody, canopy and root biomass

Next we apply our analysis framework to determine which of the productivity-allocation-turnover components are the primary drivers for the changes in woody biomass observed in the core plot network across the rainfall gradient (Figure 4), adopting the framework Malhi et al. (2015) applied to wet-dry transects in Amazonia. Total NPP (considering only the core plots) is highest in SDF ( $16.7 \pm 0.6$  Mg C  $ha^{-1} year^{-1}$ ), and shows declines in both the EF site ( $13.3 \pm 0.6$  Mg C  $ha^{-1} year^{-1}$ ) and the drier sites ( $12.0 \pm 0.7$  to  $10.8 \pm 0.5$  Mg C  $ha^{-1} year^{-1}$  at the DF and WS sites, respectively). Woody biomass production is lowest in the EF site, and then shows no trend along the rest of the gradient between SDF, DF and WS (Figure 4). This is despite the decline in NPP between the SDF and the WS, and occurs because the drier sites show an increased allocation to woody growth that largely offsets the reduction in NPP. Woody biomass residence times are highest in the EF site (~110 years), decrease to substantially lower values in the SDF and DF sites (25–50 years), and further decrease in the WS (15–35 years; Table 4). Hence there is an overall increase of turnover rates with increasing dryness along the gradient, and this drives the overall decline in mean biomass values along the gradient, from  $158$  Mg C  $ha^{-1}$  in the

**FIGURE 2** Mean (a) total annual NPP ( $\pm 1$  SE) split into its components and (b) annual NPP allocation into canopy, wood and root components (see Equations 2–4 for details) at each of the four vegetation types along the extended rainfall gradient plot network. Letters denote significant differences within each measurement (NPP:  $p < .05$ ; Allocation<sub>canopy</sub>:  $p < .001$ ; Allocation<sub>wood</sub>:  $p < .05$ ; Allocation<sub>root</sub>:  $p > .05$ )



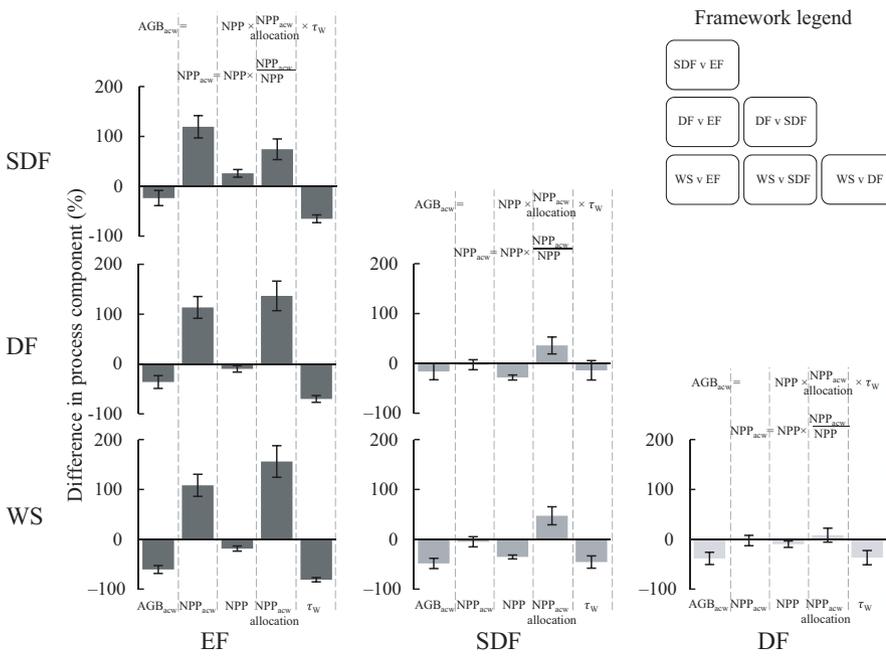


**FIGURE 3** Total NPP as a function of various components of NPP: (a) aboveground coarse woody NPP, (b) canopy NPP and (c) fine root NPP, across the core plot network. Bars indicate  $\pm 1$  SE on each axis

EF site through  $\sim 120$ ,  $\sim 100$  and  $\sim 60$  Mg C ha<sup>-1</sup> in the SDF, DF and WS sites, respectively (core plot network only). The trend in biomass is driven by variation in turnover time and mortality rate, rather than by the small trend in woody production rates.

On the other hand, the lack of trend in woody production is remarkable and is the result of substantial shifts in woody allocation, which is twice as high in the DF and WS than in the EF. Therefore, the patterns in woody biomass are ultimately influenced by the compensating roles of woody allocation against total NPP, leaving biomass turnover times to shape the overall trend in total woody biomass.

We also apply a similar framework to leaf biomass and fine root biomass (Figures 5 and 6, Table 4). Leaf biomass is highest in the EF site and decreases along the rainfall gradient. In contrast, leaf production is highest in the SDF. The trend in leaf production indicates high allocation of NPP to leaves in the SDF, and low allocation in the drier sites. Mean leaf residence times are highest in the EF (9–10 months), lowest in the SDF (4–5 months) and intermediate in the drier sites (7–10 months; Table 4). This trend likely reflects the varying mix of evergreen and deciduous species. Indeed the data indicates a biannual flush of leaves in the SDF plots, which is reflected

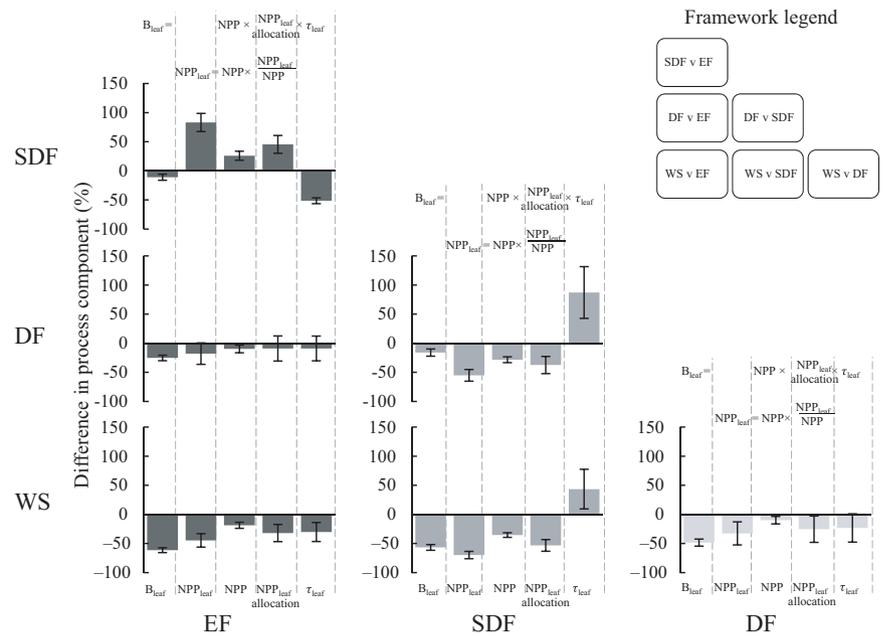


**FIGURE 4** Results from analysis framework exploring how aboveground coarse wood biomass ( $AGB_{acw}$ ) varies between EF, SDF, DF and WS. Bars indicate proportion difference ( $\pm 1$  SE) in various productivity-allocation-turnover components in the y-axis forest type relative to the x-axis forest type: aboveground coarse woody NPP ( $NPP_{acw}$ ); total NPP (NPP); allocation to  $NPP_{acw}$  ( $NPP_{acw}$  allocation); woody residence time ( $\tau_w$ )

**TABLE 4** Synthesis of woody, leaf and fine root biomass and residence time values across the core plot network

Site Plot	EF		SDF		DF		WS	
	ANK-01	ANK-02	BOB-01	BOB-02	KOG-02	KOG-03	KOG-05	KOG-06
ACW biomass (Mg C ha <sup>-1</sup> )	162.7 ± 32.5	153.3 ± 30.7	111.8 ± 22.4	129.0 ± 25.8	101.4 ± 20.3	100.5 ± 20.1	58.6 ± 11.7	65.6 ± 13.1
ACW residence time (years)	99.0 ± 22.1	120.6 ± 27.0	47.3 ± 10.6	32.0 ± 7.16	44.5 ± 9.94	25.5 ± 5.69	36.7 ± 8.21	14.7 ± 3.28
Leaf biomass (Mg C ha <sup>-1</sup> )	2.31 ± 0.10	2.25 ± 0.10	1.75 ± 0.11	2.31 ± 0.17	1.82 ± 0.15	1.59 ± 0.11	0.87 ± 0.13	0.89 ± 0.13
Leaf residence time (months)	9.22 ± 0.80	9.93 ± 1.08	4.09 ± 0.42	5.18 ± 0.58	9.61 ± 3.11	7.84 ± 2.43	6.65 ± 1.67	6.68 ± 2.47
Fine root biomass (Mg C ha <sup>-1</sup> )	31.65 ± 6.33	28.76 ± 5.75	22.87 ± 4.57	35.32 ± 7.06	8.45 ± 1.69	10.83 ± 2.17	5.93 ± 1.19	4.88 ± 0.98
Fine root residence time (months)	7.00 ± 1.75	6.74 ± 1.69	8.96 ± 2.24	6.31 ± 1.58	2.35 ± 0.59	3.09 ± 0.77	1.96 ± 0.49	2.10 ± 0.53

ACW, Aboveground coarse wood. Units as stated in brackets ±1 SE.



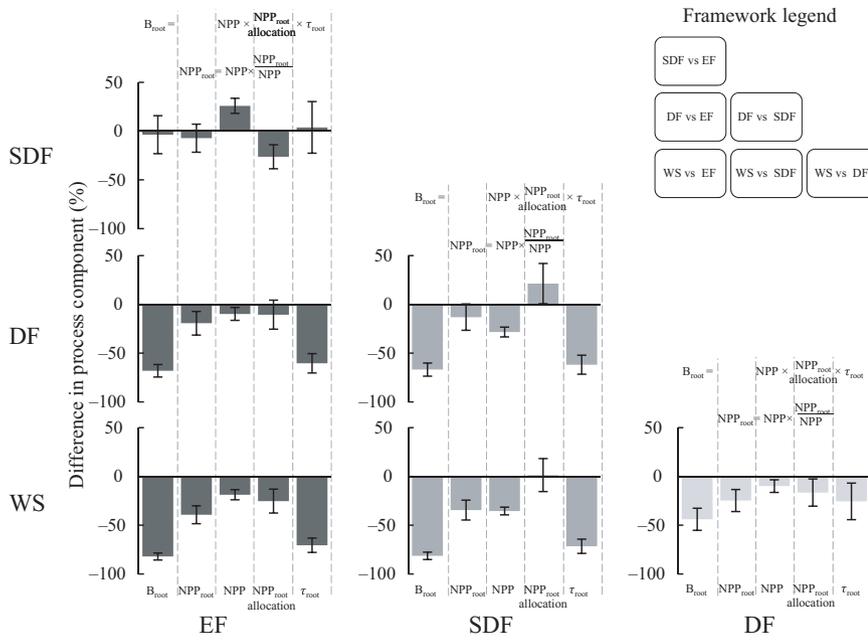
**FIGURE 5** Results from analysis framework exploring how leaf biomass ( $B_{\text{leaf}}$ ) varies between EF, SDF, DF and WS. Bars indicate proportion difference ( $\pm 1$  SE) in various productivity-allocation-turnover components in the y-axis forest type relative to the x-axis forest type: leaf NPP ( $\text{NPP}_{\text{leaf}}$ ); total NPP (NPP); allocation to  $\text{NPP}_{\text{leaf}}$  ( $\text{NPP}_{\text{leaf}}$  allocation); leaf residence time ( $\tau_{\text{leaf}}$ )

in the very high canopy NPP values and allocation of carbon to canopy components. Lower leaf productivity in the DF and WS plots becomes more important in driving down the leaf biomass values of these plots.

Fine root production does not vary much among the forest sites, but generally decreases along the rainfall gradient and is lowest in the WS plots. Therefore, the large differences in root biomass between the wetter and drier plots are caused by much higher rates of root turnover (i.e. shorter fine root lifetimes) in the drier plots (Figure 6, Table 4). Where there is little difference in root biomass between the EF and SDF plots, by decomposing the biomass calculation components we see that this is because the  $25 \pm 6\%$  higher productivity in the SDF is offset by a  $26 \pm 12\%$  lower allocation to roots. This example of root biomass illustrates the utility of this analysis framework in pinpointing what is driving observed trends. For example, here it can be clearly determined that the overall decline in

root biomass along the rainfall gradient is driven by a higher rate of root turnover in the drier plots as opposed to root productivity or carbon allocation to roots.

The results from the above analysis framework clearly indicate the importance of residence times in controlling biomass stocks of all carbon stores (wood, leaf and roots). To explore these various carbon pool residence time patterns in more detail, we create non-parametric plots of residence time against an arbitrary dry-wet gradient using the extended plot network (Figure 7). In the case of total NPP, woody and root residence times (Figures 7a,b,d), we observe a humped relationship, peaking in the SDF and EF plots whereas leaf residence times increase along the dry to wet gradient with the exception of the SDF plots which are considerably lower than even the driest of plots in the WS (Figure 7c). We take a similar approach in exploring allocation patterns along the extended rainfall gradient plot network which show no overall trends (Fig S2).



**FIGURE 6** Results from analysis framework exploring how fine root biomass ( $B_{\text{root}}$ ) varies between EF, SDF, DF and WS. Bars indicate proportion difference ( $\pm 1$  SE) in various productivity-allocation-turnover components in the y-axis forest type relative to the x-axis forest type: fine root NPP ( $\text{NPP}_{\text{root}}$ ); total NPP (NPP); allocation to  $\text{NPP}_{\text{root}}$  ( $\text{NPP}_{\text{root}}$  allocation); root residence time ( $\tau_{\text{root}}$ )

## 4 | DISCUSSION

This study presents the largest NPP dataset collected to date from tropical forests in Africa. Comparable datasets have recently emerged from South America and Southeast Asia that have explored patterns in NPP, GPP and CUE (Malhi et al., 2015; Riutta et al., in review; Slik et al., 2010), but until now carbon budget studies from African tropical forests have focused only on patterns of AGB and forest structure (e.g. Lewis et al., 2009, 2013). Therefore, we focus our discussion on the novel insights that our NPP dataset brings to our understanding of the carbon cycle along rainfall gradients in tropical African forests. We highlight three results that relate to our original research questions:

### 4.1 | To what extent can key plot-level carbon characteristics be predicted from rainfall patterns?

As previously mentioned, there are much larger, more spatially extensive datasets from Africa and other tropical forest regions that focus on the relationships between AGB, soil carbon storage, MAP and soil properties (Lewis et al., 2013). Nonetheless, in our extended network of 14 plots across EF, SDF, DF and WS vegetation types, we find positive correlations between AGB and MAP ( $r^2 = 0.51$ ,  $p = .04$ ) and soil C storage and MAP ( $r^2 = 0.64$ ,  $p < .001$ , Fig. S1a,b). As expected, the EF plots had by far the largest soil C stock of all vegetation types which, when extrapolated to 1 m depth equalled the AGB stock of  $165 \text{ Mg C ha}^{-1}$  in ANK-01, which is slightly higher than reported in Chiti, Certini, Grieco, and Valentini (2010).

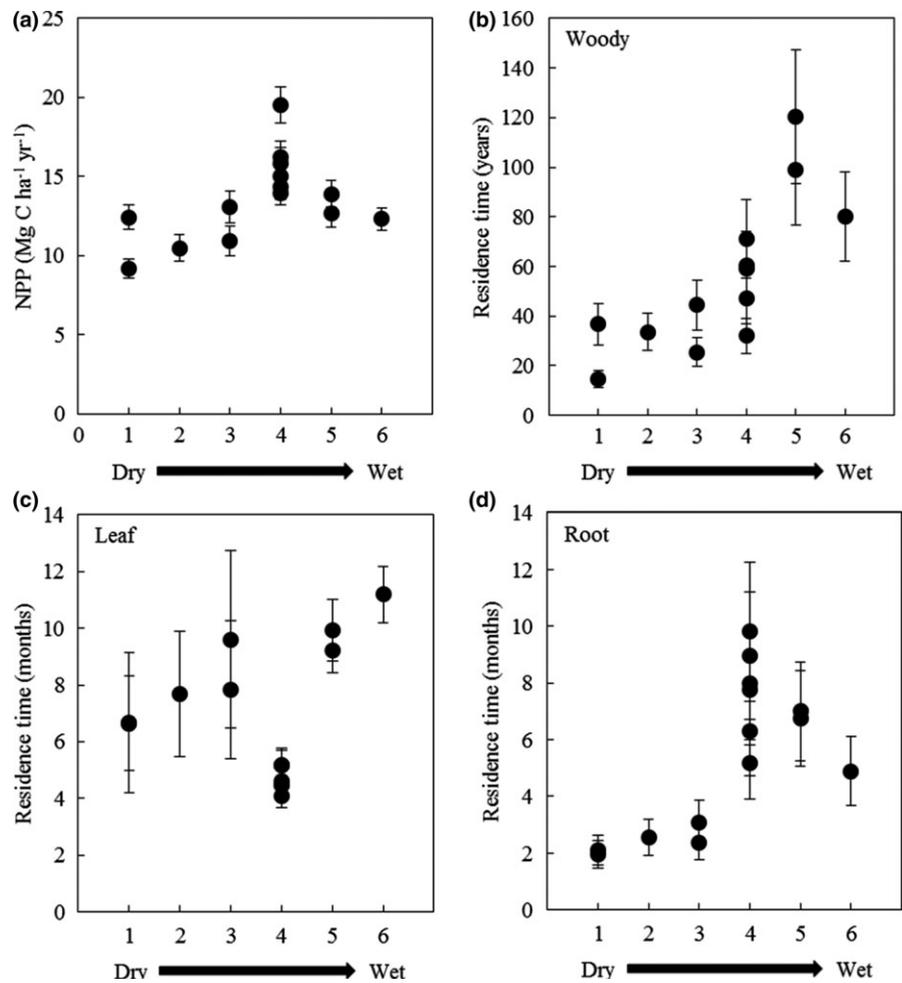
No significant relationships were found between productivity (total NPP) or carbon allocation with climate variables (Fig. S1c, S2). This may be due to the relatively narrow range of climate variables within our gradient (all plots are lowland plots), or it may provide

more support to a recent global analysis that suggests NPP is largely determined by stand age and biomass, not climate (Michaletz, Cheng, Kerkhoff, & Enquist, 2014; also see Chu et al., 2015). However, criteria for plot selection at times in this study were non-inundated with low or no logging impact (core plot network), thereby limiting variation to some extent in stand structure, so this explanation also seems unlikely.

### 4.2 | Which growth component of a tropical forest is the most useful proxy for stand-level NPP?

Our findings show that woody, canopy and root growth all have some power in predicting total NPP, but to differing extents. The woody growth component was the worst proxy in predicting total NPP which has significant implications for the widespread use of aboveground coarse woody productivity from multiple censuses of forest plots as a proxy indicator of plot-level NPP (Malhi et al., 2004). Our results indicate that prediction ability is greatest in the EF and SDF plots, but is weakened when including the DF and WS plots. This is because the drier plots allocate up to 50% of their carbon to woody components. This particularly poor predictive capacity of woody growth confirms what was found across a similar gradient of wet-dry tropical forest plots across the Amazon (Aragão et al., 2009; Malhi et al., 2015). Consistent with our study, the Amazonian study found short residence times at the dry margin which are also consistent with high stem turnover rates in other southern, dry margin Amazonian sites (Marimon et al., 2014).

Our results showed much better total NPP predictive capacity in canopy and root growth. Canopy productivity correlated well with total NPP across the rainfall gradient which includes some of the highest canopy NPP values recorded globally in the SDF plots ( $\sim 8 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ ). Litterfall is the NPP measurement that we have highest confidence in, with most possible systematic errors resulting



**FIGURE 7** Non-parametric plots of (a) total NPP, (b) woody, (c) leaf and (d) root residence times along the extended rainfall gradient plot network, where the following arbitrary x-axis values denote the dry to wet gradient; 1 = WS plots, 2 = WS-DF transition plot, 3 = DF plots, 4 = SDF plots, 5 = EF upland plots, 6 = EF lowland (seasonally flooded) plot. Bars indicate  $\pm 1$  SE

in underestimates of canopy production, thereby assuring us in our conclusion that there is a disproportionate investment in leaf growth in these SDF plots. Leaves in these highly productive SDF plots have an average lifetime of 4–5 months, with high production throughout the year possibly indicating a biannual flush of leaves. Our strong positive correlation between canopy NPP and total NPP supports the frequently applied method of estimating total NPP as 3.3 times annual litterfall which was originally based on tropical forest data in Bray and Gorham's (1964) review and since confirmed by Aragão et al. (2009) and Girardin et al. (2010) for lowland and montane Neotropical sites, respectively. Indeed, this method of estimation achieves further validation when applied to our dataset as we find a strong agreement ( $r^2 = .77$ , Fig. S3) between our directly measured total NPP and Bray and Gorham's estimated total NPP method (3.3\*annual litterfall). It is difficult to say where our finding that fine root growth has moderate power in predicting stand-level NPP sits within a broader context as very few other studies have examined this. However, in the one study that has, Malhi et al. (2015) found a very similar relationship to ours ( $r^2 = .41$  cf. 0.46) over a rainfall gradient in Amazonia. This gives us increased confidence in concluding that both canopy and root growth are more useful proxies in predicting total NPP than woody growth.

### 4.3 | Which aspects of NPP, carbon allocation and residence time are the primary drivers for the patterns in biomass variations we observe across the rainfall gradient in Ghana?

Our analyses reveal that every aspect of the productivity-allocation-turnover chain is important, but which of these is the key driver in biomass variation and why? This depends on which biomass component (woody, canopy or root) is the focus of interest, but residence time is clearly the only element which is important in all cases. Far longer woody residence times in the EF plots result in the highest woody biomass observed across the rainfall gradient. This is despite the SDF, DF and WS plots all achieving greater rates of woody productivity and carbon allocation to woody components. The high woody productivity of the drier plots is associated with high mortality rates and short turnover times. High levels of tree mortality mean there is intensified competition to attain vertical height and out-shade competitors. It is unlikely that these more dynamic DF and WS plots are recovering from some sort of previous disturbance. The KSNR is prone to fire, but census data from these plots indicates approximate biomass equilibrium (mortality rates equal recruitment rates), suggesting that they are not in a secondary, disturbance-recovery stage. The

high tree mortality rates and short woody biomass residence times are consistent with what has been reported for wet-dry gradients in Amazonia (Malhi et al., 2015). Why drier forest trees have higher turnover times requires further exploration, but is probably linked to environmental factors (drought stress and fire) having a direct effect, but also an indirect effect by favouring "live fast, die young strategies" in tree growth and reproduction.

Total leaf biomass varied nearly threefold along the rainfall gradient with very high production rates in the SDF plots. However, short leaf residence times of 4–5 months here resulted in a lower leaf biomass than in the EF plots where leaves live on average for double the length of time (9–10 months). High deciduousness in the SDF plots may be favoured by high nutrient supply which means relatively low leaf construction costs; if the resources to build new leaf organic matter are there, there are no constraints to adopting higher rates of leaf production throughout the year, which suggests a biannual leaf flush. Lower total leaf biomass in the drier plots is driven by a combination of lower overall productivity (because of a shorter growing season), lower allocation of carbon to leaves, and short leaf lifetimes. This more likely implies a different strategy employed by the more deciduous species that exist in the DF and WS plots. Where nutrients are scarcer, why allocate them to a truly deciduous canopy? This strategy is reflected in far lower allocation to canopy components not only compared with the wetter plots in this study, but compared to other values reported from tropical forests and are outside the distribution of allocation points reported by Malhi et al. (2011). This also mirrors what was observed by Malhi et al. (2015) in western Amazonia where relatively fertile soils support a more deciduous canopy compared with poorer soils in eastern Amazonia that favour an evergreen strategy.

Variation in root biomass across the rainfall gradient is clearly also driven by root life time and in particular by much higher rates of root mortality in the drier plots. To date, no studies have measured fine root production in undisturbed lowland African tropical forests (but see Ifo, Koubouana, Nganga, Bocko, and Mantota (2015) for forest grove root dynamics in the Congo basin) and only a handful of studies have reported on root productivity and turnover in tropical forests worldwide (Malhi et al., 2009a, 2015, 2016; Girardin et al., 2010, 2013; Moser, Leuschner, Hertel, Graefe, & Iost, 2011). These studies report that root production is highly seasonal and it has long been assumed that fine root growth and carbon allocation to roots is highest in water stressed environments or those experiencing drought. However our results reveal slightly lower root productivity in the drier plots but near-consistent allocation to roots across the rainfall gradient. Following the 2010 drought in Amazonia, Doughty et al. (2015) reported a surprising shift away from fine root growth, in favour of replenishing lost canopy cover, whereas data from our most water stressed plots indicate a longer-term shift in carbon allocation from roots to woody (and not canopy) components.

Data from this study represent the first comprehensive assessment of tropical forest productivity in Western Africa. Through a systematic assessment of forest productivity we have demonstrated

the value of measuring the major components of above and below-ground NPP and in turn highlighted the importance of residence time in determining the variation in woody, canopy and root biomass across a wet-dry forest gradient. Many similarities in carbon dynamics between Amazonian and West African tropical forests are apparent, but the availability of data is still insufficient to make any broader pan-tropical forest generalisations. Therefore we encourage the establishment of more permanent carbon intensive monitoring plots across the tropics, particularly in less well-studied regions such as Central Africa and Southeast Asia.

## ACKNOWLEDGEMENTS

This work is a product of the Global Ecosystems Monitoring (GEM) network ([gem.tropicalforests.ox.ac.uk](http://gem.tropicalforests.ox.ac.uk)). Fieldwork was funded by grants from the UK Natural Environment Research Council (NE/1014705/1) and Advanced Investigator Grants to YM and RV from the European Research Council (GEM-TRAIT and Africa-GHG, respectively). YM is supported by the Jackson Foundation. We also acknowledge the Wildlife Division of the Forestry Commission in Ghana as well as the many field assistants who helped with data collection from the field.

## ORCID

Sam Moore  <http://orcid.org/0000-0001-9504-5989>

Imma Oliveras  <http://orcid.org/0000-0001-5345-2236>

## REFERENCES

- Anderson-Teixeira, K. J., Wang, M. M. H., McGarvey, J. C., & LeBauer, D. S. (2016). Carbon dynamics of mature and regrowth tropical forests derived from a pantropical database (TropForC-db). *Global Change Biology*, 22, 1690–1709.
- Aragão, L. E. O. C., Malhi, Y., Metcalfe, D. B., Silva-Espejo, J. E., Jiménez, E., Navarrete, D., ... Vásquez, R. (2009). Above and belowground net primary productivity across ten Amazonian forests on contrasting soils. *Biogeosciences*, 6, 2759–2778.
- Baker, T. R., Phillips, O. L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., ... Martínez, R. V. (2004). Variation in wood density determines spatial patterns in Amazonian forest biomass. *Global Change Biology*, 10, 545–562.
- Bongers, F., Poorter, L., & Hawthorne, W. D. (2004). The forests of Upper Guinea: Gradients in large species composition. In L. Poorter, F. Bongers, F. N. Kouame, & W. D. Hawthorne (Eds.), *Biodiversity of West African forests: An ecological atlas of woody plant species* (pp. 41–52). Oxford: CABI Publishing.
- Bray, J. R., & Gorham, E. (1964). Litter production in forests of the world. *Advances in Ecological Research*, 2, 101–157.
- Cai, W., Borlace, S., Lengaigne, M., van Rensch, P., Collins, M., Vecchi, G., ... Jin, F.-F. (2014). Increasing frequency of extreme El Niño events due to greenhouse warming. *Nature Climate Change*, 4, 111–116.
- Cairns, M. A., Brown, S., Helmer, E. H., & Baumgardner, G. A. (1997). Root biomass allocation in the world's upland forests. *Oecologia*, 111, 1–11.
- Campioli, M., Malhi, Y., Vicca, S., Luyssaert, S., Papale, D., Peñuelas, J., ... Janssens, I. A. (2016). Evaluating the convergence between eddy-

- covariance and biometric methods for assessing carbon budgets of forests. *Nature Communications*, 7, 13717.
- Chave, J., Rejou-Mechain, M., Burquez, A., Chidumayo, E., Colgan, M. S., Delitti, W. B. C., ... Vieilledent, G. (2014). Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biology*, 20, 3177–3190.
- Chen, J. M., & Cihlar, J. (1995). Quantifying the effect of canopy architecture on optical measurements of leaf area index using two gap size analysis methods. *IEEE Transactions on Geoscience & Remote Sensing*, 33, 777–787.
- Chiti, T., Certini, G., Grieco, E., & Valentini, R. (2010). The role of soil in storing carbon in tropical rainforests: The case of Ankasa Park, Ghana. *Plant and Soil*, 331, 453–461.
- Chu, C., Bartlett, M., Wang, Y., He, F., Weiner, J., Chave, J., & Sack, L. (2015). Does climate directly influence NPP globally? *Global Change Biology*, 22, 12–24.
- Clark, D. A., Brown, S., Kicklighter, D. W., Chambers, J. Q., Thomlinson, J. R., Ni, J., & Holland, E. A. (2001a). Measuring net primary production in forests: Concepts and field methods. *Ecological Applications*, 11, 356–370.
- Clark, D. A., Brown, S., Kicklighter, D. W., Chambers, J. Q., Thomlinson, J. R., Ni, J., & Holland, E. A. (2001b). Net primary production in tropical forests: An evaluation and synthesis of existing field data. *Ecological Applications*, 11, 371–384.
- Dai, A. (2013). Increasing drought under global warming in observations and models. *Nature Climate Change*, 3, 52–58.
- Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C., & Martin, P. R. (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences USA*, 105, 6668–6672.
- Doughty, C. E., Metcalfe, D. B., Girardin, C. A. J., Amézquita, F. F., Cabrera, D. G., Huasco, W. H., ... Malhi, Y. (2015). Drought impact on forest carbon dynamics and fluxes in Amazonia. *Nature*, 519, 78–82.
- Field, C. B., Behrenfeld, M. J., Randerson, J. T., & Falkowski, P. (1998). Primary production of the biosphere: Integrating terrestrial and oceanic components. *Science*, 281, 237–240.
- Galbraith, D., Malhi, Y., Affum-Baffoe, K., Castanho, A. D. A., Doughty, C. E., Fisher, R. A., ... Lloyd, J. (2013). Residence times of woody biomass in tropical forests. *Plant Ecology & Diversity*, 6, 139–157.
- Geldenhuys, C. J., Knight, R. S., Russell, S., & Jarman, M. L. (1988). Dictionary of forest structural terminology. South African National Scientific Programmes Report 147, pp. 70. FRD, CSIR, Pretoria.
- Ghana Wildlife Department (1994). *Kogyae strict nature reserve: Development and management plan*. Accra: Ghana Wildlife Department.
- Girardin, C. A. J., Aragão, L. E. O. C., Malhi, Y., Huasco, W. H., Metcalfe, D. B., Durand, L., ... Whittaker, R. J. (2013). Fine root dynamics along an elevational gradient in tropical Amazonian and Andean forests. *Global Biogeochemical Cycles*, 27, 252–264.
- Girardin, C. A. J., Malhi, Y., Aragão, L. E. O. C., Mamani, M., Huasco, W. H., Durand, L., ... Whittaker, R. J. (2010). Net primary productivity allocation and cycling of carbon along a tropical forest elevational transect in the Peruvian Andes. *Global Change Biology*, 16, 3176–3192.
- Harmon, M. E., Whigham, D. F., Sexton, J., & Olmsted, I. (1995). Decomposition and mass of woody detritus in the dry tropical forests of the Northeastern Yucatan Peninsula, Mexico. *Biotropica*, 27, 305–316.
- Hughes, I. G., & Hase, T. P. A. (2010). *Measurements and their uncertainties: A practical guide to modern error analysis*. Oxford: Oxford University Press.
- Ifo, S. A., Koubouana, F., Nganga, D., Bocko, Y., & Mantota, A. (2015). Fine roots dynamics in a tropical moist forest: case of two forest Groves in the Congo Basin. *Baltic Forestry*, 21, 204–211.
- IPCC (2006). LUCF Sector Good Practice Guidance. In J. Penman, M. Gytarsky & T. Hiraishi, T. Krug, D. Kruger, R. Pipatti, ... F. Wagner (Eds.), *Good practise guidance for land use, land-use change and forestry* (pp. 338–345). Kanagawa, Japan: Intergovernmental Panel on Climate Change. Institute for Global Environmental Strategies (IGES).
- Jackson, R. B., Canadell, J., Ehleringer, J. R., Mooney, H. A., Sala, O. E., & Schulze, E. D. (1996). A global analysis of root distributions for terrestrial biomes. *Oecologia*, 108, 389–411.
- Lewis, S. L., Lopez-Gonzalez, G., Sonké, B., Affum-Baffoe, K., Baker, T. R., Ojo, L. O., ... Wöll, H. (2009). Increasing carbon storage in intact African tropical forests. *Nature*, 457, 1003–1006.
- Lewis, S. L., Sonké, B., Sunderland, T., Begne, S. K., Lopez-Gonzalez, G., van der Heijden, G. M. F., ... Zemagho, L. (2013). Aboveground biomass and structure of 260 African tropical forests. *Philosophical Transactions of the Royal Society – Biological Sciences*, 368, 20120295.
- Litton, C. M., Raich, J. W., & Ryan, M. G. (2007). Carbon allocation in forest ecosystems. *Global Change Biology*, 13, 2089–2109.
- Lyngsie, G., Olsen, J. L., Awadzi, T. W., Fensholt, R., & Breuning-Madsen, H. (2013). Influence of the inter tropical discontinuity on Harmattan dust deposition in Ghana. *Geochemistry, Geophysics, Geosystems*, 14, 3425–3435.
- Malhi, Y., Doughty, C., & Galbraith, D. (2011). The allocation of ecosystem net primary productivity in tropical forests. *Philosophical Transactions of the Royal Society B*, 366, 3225–3245.
- Malhi, Y., Adu-Bredu, S., Asare, R. A., Lewis, S. L., & Mayaux, P. (2013). The past, present and future of Africa's rainforests. *Philosophical Transactions of the Royal Society Biological Sciences*, 368, 20120293.
- Malhi, Y., Aragão, L. E. O. C., Galbraith, D., Huntingford, C., Fisher, R., Zelazowski, P., ... Meir, P. (2009b). Exploring the likelihood and mechanism of a climate-change-induced dieback of the Amazon rainforest. *Proceedings of the National Academy of Sciences USA*, 49, 20610–20615.
- Malhi, Y., Aragão, L. E. O. C., Metcalfe, D. B., Paiva, R., Quesada, C. A., Almeida, S., ... Teixeira, L. M. (2009a). Comprehensive assessment of carbon productivity, allocation and storage in three Amazonian forests. *Global Change Biology*, 15, 1255–1274.
- Malhi, Y., Baker, T. R., Phillips, O. L., Almeida, S., Alvarez, E., Arroyo, L., ... Lloyd, J. (2004). The aboveground coarse wood productivity of 104 Neotropical forest plots. *Global Change Biology*, 10, 563–591.
- Malhi, Y., Doughty, C., & Galbraith, D. (2011). The allocation of ecosystem net primary productivity in tropical forests. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366, 3225–3245.
- Malhi, Y., Doughty, C. E., Goldsmith, G. R., Metcalfe, D. B., Girardin, C. A. J., Marthews, T. R., ... Phillips, O. L. (2015). The linkages between photosynthesis, productivity, growth and biomass in lowland Amazonian forests. *Global Change Biology*, 21, 2283–2295.
- Malhi, Y., Girardin, C. A. J., Goldsmith, G. R., Doughty, C. E., Salinas, N., Metcalfe, D. B., ... Silman, M. (2017). The variation of productivity and its allocation along a tropical elevation gradient: A whole carbon budget perspective. *New Phytologist*, 214, 1019–1032.
- Malhi, Y., & Wright, J. (2004). Spatial patterns and recent trends in the climate of tropical forest regions. *Philosophical Transactions of the Royal Society – Biological Sciences*, 359, 311–329.
- Marimon, B. S., Marimon-Junior, B. H., Feldpausch, T. R., Oliveira-Santos, C., Mews, H. A., Lopez-Gonzalez, G., ... Phillips, O. L. (2014). Disequilibrium and hyperdynamic tree turnover at the forest–cerrado transition zone in southern Amazonia. *Plant Ecology & Diversity*, 7, 1–12.
- Marthews, T. R., Riutta, T., & Oliveras-Menor, I. Urrutia, R., Moore, S., Metcalfe, D., ... Cain, R. (2014). *Measuring Tropical Forest Carbon Allocation and Cycling: A RAINFOR-GEM Field Manual for Intensive Census Plots (v3.0)*. Global Ecosystems Monitoring Network, Oxford.
- Martin, A. R., & Thomas, S. C. (2011). A reassessment of carbon content in tropical trees. *PlosOne*, 6, e23533. <https://doi.org/10.1371/journal.pone.0023533>
- Metcalfe, D. B., Meir, P., Aragão, L. E. O. C., Malhi, Y., da Costa, A. C. L., Braga, A., ... Williams, M. (2007). Factors controlling spatio-temporal variation in carbon dioxide efflux from surface litter, roots, and soil organic matter at four rain forest sites in the eastern Amazon. *Journal of Geophysical Research – Biogeosciences*, 112, G04001.

- Michaletz, S. T., Cheng, D., Kerkhoff, A. J., & Enquist, B. J. (2014). Convergence of terrestrial plant production across global climate gradients. *Nature*, *512*, 39–43.
- Miller, J. B. (1967). A formula for average foliage density. *Australian Journal of Botany*, *15*, 141–144.
- Moser, G., Leuschner, C., Hertel, D., Graefe, S., & Iost, S. (2011). Elevation effects on the carbon budget of tropical mountain forests (S Ecuador): The role of the belowground compartment. *Global Change Biology*, *17*, 2211–2226.
- Murphy, P. G. (1975). Net primary productivity in tropical terrestrial ecosystems. In H. Lieth, & R. H. Whittaker (Eds.), *Primary productivity of the biosphere* (pp. 222–231). New York: Springer-Verlag.
- Nobis, M., & Hunziker, U. (2005). Automatic thresholding for hemispherical canopy-photographs based on edge detection. *Agricultural and Forest Meteorology*, *128*, 243–250.
- Nyirambangutse, B., Zibera, E., Uwizeye, F. K., Nsabimana, D., Bizuru, E., Pleijel, H., . . . Wallin, G. (2016). Carbon stocks and dynamics at different successional stages in an Afromontane tropical forest. *Biogeosciences*, *14*, 1285–1303.
- Paoli, G. D., & Curran, L. M. (2007). Soil nutrients limit fine litter production and tree growth in mature lowland forest of southwestern Borneo. *Ecosystems*, *10*, 503–518.
- Parmentier, I., Harrigan, R. J., Buermann, W., Mitchard, E. T. A., Saatchi, S., Malhi, Y., . . . Hardy, O. J. (2011). Predicting alpha diversity of African rain forests: Models based on climate and satellite-derived data do not perform better than a purely spatial model. *Journal of Biogeography*, *38*, 1164–1176.
- R Core Team (2015) *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. <http://www.R-project.org/>.
- Riutta, T. et al. Logging disturbance shifts net primary productivity and its allocation in Bornean tropical forests (in review).
- Roy, J., & Saugier, B. (2001). Terrestrial primary production: Definitions and milestones. In J. Roy, H. A. Mooney & B. Saugier (Eds.), *Terrestrial global productivity* (pp. 1–6). San Diego, CA: Academic Press.
- Schleppi, P., Conedera, M., Sedivy, I., & Thimonier, A. (2007). Correcting non-linearity and slope effects in the estimation of the leaf area index of forests from hemispherical photographs. *Agricultural and Forest Meteorology*, *144*, 236–242.
- Sheffield, J., & Wood, E. F. (2008). Projected changes in drought occurrence under future global warming from multi-model, multi-scenario, IPCC AR4 simulations. *Climate Dynamics*, *31*, 79–105.
- Slik, J. W. F., Shin-Ichiro, A., Brearley, F. Q., Cannon, C. H., Forshed, O., Kitayama, K., . . . Johan, L. C. H. (2010). Environmental correlates of tree biomass, basal area, wood specific gravity and stem density gradients in Borneo's tropical forests. *Global Ecology and Biogeography*, *19*, 50–60.
- Tiessen, H., Hauffe, H., & Mermut, A. R. (1991). Deposition of Harmattan dust and its influence on base saturation of soils in northern Ghana. *Geoderma*, *49*, 285–299.
- Washington, R., Bouet, C., & Cautenet, G. (2009). Dust as a tipping element: The Bodele Depression, Chad. *Proceedings of the National Academy of Sciences USA*, *49*, 20564–20571.

## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

**How to cite this article:** Moore S, Adu-Bredu S, Duah-Gyamfi A, et al. Forest biomass, productivity and carbon cycling along a rainfall gradient in West Africa. *Glob Change Biol*. 2018;24: e496–e510. <https://doi.org/10.1111/gcb.13907>