# New insights into mechanisms driving carbon allocation in tropical forests

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## Summary

- The proportion of carbon allocated to wood production is an important determinant of the carbon sink strength of global forest ecosystems. Understanding the mechanisms controlling wood production and its responses to environmental drivers is essential for parameterization of global vegetation models and to accurately predict future responses of tropical forests in terms of carbon sequestration.
- Here, we synthesize data from 105 pantropical old-growth rainforests to investigate environmental controls on the partitioning of net primary production to wood production (%WP) using structural equation modeling.
- Our results reveal that %WP is governed by two independent pathways of direct and indirect environmental controls. While temperature and soil phosphorus availability indirectly affected %WP via increasing productivity, precipitation and dry season length both directly increased %WP via tradeoffs along the plant economics spectrum.
- We provide new insights into the mechanisms driving %WP, allowing us to conclude that projected climate change could enhance %WP in less productive tropical forests, thus increasing carbon sequestration in montane forests, but adversely affecting lowland forests.

## Introduction

The allocation of gross primary production (GPP) to net biomass production (NPP) as opposed to losses through respiration determines the residence time and sink strength of carbon (C) in terrestrial ecosystems (Chen *et al.*, 2013; Galbraith *et al.*, 2013). As terrestrial NPP is controlled by temperature, water, and nutrient availability, global change probably affects terrestrial C allocation and hence the terrestrial C sink strength, in turn triggering feedback mechanisms on climate (Clark *et al.*, 2001b). Tropical forests contribute substantially to the terrestrial C sink (Stephens *et al.*, 2007) and thereby play important roles in global climate regulation, but they also respond sensitively to global changes (Clark *et al.*, 2003). Understanding the mechanisms of tropical forest C allocation and its response to environmental drivers is therefore of paramount importance for parameterization of global vegetation models and to accurately predict future responses of tropical C sequestration to global changes (Litton *et al.*, 2007; Chen *et al.*, 2013; McMurtrie & Dewar, 2013).

The available empirical data have so far not resulted in an unequivocal pattern of forest C allocation at larger scales. A recent synthesis of carbon allocation across global forest ecosystems could not identify priorities for the products of photosynthesis, as fluxes to all components of GPP increased with productivity (Litton *et al.*, 2007). However, the authors reported that increased resource supply resulted in increased productivity,

followed by increased allocation to above-ground wood production, while the allocation to foliage and autotrophic respiration was more conservative and that to roots decreased with productivity (Litton *et al.*, 2007). In agreement with this, Vicca *et al.* (2012) demonstrated that fertile forests exert higher biomass production efficiency, such that the fraction of C allocated to above-ground wood production increased with nutrient availability.

However, knowledge of the mechanisms controlling C allocation remains especially scarce for tropical forests, as GPP and NPP data are available for only a few sites, causing these ecosystems to be underrepresented in global syntheses (Malhi *et al.*, 2011; Chen *et al.*, 2013; Clark *et al.*, 2013; Zhou *et al.*, 2013; Zuidema *et al.*, 2013). This is even more valid for environmental controls on tropical forest C allocation.

Across the tropical forest biome, temperature was reported as the strongest predictor of tropical forest NPP, such that all components of NPP increased in response to temperature with no effect on wood relative to canopy production (Raich *et al.*, 2006), athough, globally, allocation to wood production increased with productivity (Litton *et al.*, 2007). However, just recently, Cleveland *et al.* (2011) found that the strong positive relationship between temperature and tropical forest productivity was driven by distinct differences in NPP between cool montane and warm lowland forests, caused by differences in proximal drivers of NPP in these forest types. By contrast, for lowland tropical rainforests, small increases in night-time temperature associated with El Niño

phenomena were shown to strongly depress wood production while canopy production was relatively unaffected (Clark *et al.*, 2013), indicating that these forests thrive close to their thermal optimum (Corlett, 2011). Moreover, the productivity of tropical rainforests was reported to decline at the highest amounts of mean annual precipitation, caused by reduced decomposition and nutrient availability in the long term (Schuur, 2003; Powers *et al.*, 2009). However, this negative effect could also result from indirect effects of reduced light availability as a result of increased cloud cover during precipitation events (Graham, 2003; Pau *et al.*, 2013), rather than being a direct consequence of water availability (Wagner *et al.*, 2012, 2014). On the other hand, wood production was found to respond more sensitively to drought in throughfall exclusion experiments than canopy production and litterfall (Brando *et al.*, 2008; Moser *et al.*, 2014), suggesting that allocation tradeoffs among NPP components dominate the response of tropical forest growth to seasonal and interannual drought (Doughty *et al.*, 2014). Overall, these opposing trends therefore point to strong differences in spatial (montane vs lowland) as well as temporal (long-term vs short-term) responses of tropical NPP components, forest C allocation and eventually C sequestration to environmental drivers, such as changing climate and atmospheric deposition.

Short-term and long-term responses may differ markedly, as short-term environmental changes act on the present tree community, whereas long-term responses affect species turnover, triggering changes in tropical forest community composition. Alterations in the composition of tropical tree communities in response to environmental change could trigger community-wide shifts in plant functional traits that affect the performance and life-history strategy of tropical trees (Poorter *et al.*, 2009).

Many important plant functional traits covary or are negatively related as a result of opposing investment strategies along the plant economics spectrum (Baraloto *et al.*, 2010). For instance, opportunistic species are characterized by fast growth and high hydraulic conductivity, whereas drought-tolerant species grow more slowly but maximize plant hydraulic safety (Poorter & Bongers, 2006). Hence, plant functional traits such as those associated with slow vs fast plant growth (Reich, 2014) can determine the resistance and resilience of trees to periodic disturbances and cause drought-induced shifts in the functional composition of tropical rainforest trees in the long term (Fauset *et al.*, 2012). Concomitant shifts along the plant economics spectrum resulting from species turnover could thus lead to changes in stand-level measures of C allocation, as, for instance, a shift towards greater plant hydraulic safety associated with higher wood density and lower leaf area : sapwood area ratios could result in increased C allocation to wood production and decreased allocation to canopy production.

The current knowledge suggests that projected changes in environmental drivers such as elevated temperature, increasing length of drought periods and increasing nutrient deposition could result in alterations of long-term woody biomass C sequestration in tropical old-growth forests (Phillips *et al.*, 2010; Fauset *et al.*, 2012; Doughty *et al.*, 2014). So far, however, the relationships and interactions among multiple environmental drivers and

tropical forest wood allocation remain poorly resolved. Hence, in this study we aimed to elucidate the underlying mechanisms and pathways among environmental drivers of C allocation to wood production in tropical rainforests. To that end, we compiled a pantropical database of > 100 old-growth forests for which data on wood and canopy (and fine root) production were reported. We applied structural equation modeling to resolve the relative importance of environmental controls (i.e. mean annual temperature (MAT), mean annual precipitation (MAP), dry season length (DSL) and cloud cover (CLD), as well as leaf, litter and soil N : P ratios) on the partitioning of NPP to wood production (%WP).

We hypothesized that %WP increases with environmental factors that promote overall forest productivity, and thus cause light limitation and enhanced stem height growth; that %WP increases as a result of drought-induced changes in investment strategies along the plant economics spectrum, causing coordinated tradeoffs among plant functional traits which promote %WP; and, finally, that projected global changes might affect the C sequestration potential of tropical tree species in montane and lowland regions differently, based on shifts in major environmental constraints on NPP and %WP across altitudinal gradients.

## Materials and Methods

### Study design and site characterization

To identify relationships between environmental factors and mechanisms driving C allocation in tropical forests, we compiled a database of 105 pantropical forest sites using the ISI Web of Knowledge search engine and other online resources, searching for the following terms and combinations thereof: tropical, forest, litterfall, canopy production, tree increment, wood production, root production, root turnover, net primary production, gross primary production and carbon allocation (see Supporting Information Table S1 for database). Annual fluxes of dry mass as presented by some studies were converted to mass C by assuming that C concentration of vegetation was, on average, 50% (Clark *et al.*, 2001b). We incorporated only data from old-growth wet and moist evergreen tropical forests without recent disturbance for which both plot-based litterfall (as surrogate for canopy production) and above-ground biomass increment (as surrogate for wood production) were reported. Mangrove forests, dry tropical forests, tropical deciduous forests and secondary tropical forests, which together comprise *c.* 50% of total tropical forest land area (Silver *et al.*, 2000; http://www.fao.org/docrep/k0050e/k0050e03.htm), were excluded from this analysis.

Litterfall comprises the largest portion of canopy production, which is sampled by litterfall traps and transects; only studies extending over at least 1 yr with at least monthly collection intervals were included in our database. Large leaves (> 50 cm in length) and branches (coarse litterfall > 2 cm in diameter) are rarely measured and therefore were not included here. Fine litterfall (< 2 cm in diameter) generally comprises leaves, reproductive structures, small twigs and other fine materials (Clark *et al.*, 2001a). Other components of canopy production are rarely

studied, including branch production, losses to herbivores, volatile organic compounds and decomposition of litter trapped in the canopy or in litterfall traps. The contribution of these components is usually small, with the exception of branch production and branchfall, but given the scarcity of branchfall data, we did not correct for this.

Wood production is assessed as tree girth increment at breast height (c. 1.3 m) measured over intervals ranging from monthly to 5-yearly using tree girth tapes or with dendrometer bands. Allometric equations were applied to relate the increment in diameter at breast height (DBH), tree height (H) and wood density (WD) to above-ground biomass increment. A range of different allometric equations were used by the compiled studies, based on $DBH^2$, $DBH^2 \times H$, $DBH^2 \times WD$ or $DBH^2 \times H \times WD$. We did not correct for these differences in allometric equations used for the 105 study sites, as raw data for individual trees (species, DBH, H, WD) are commonly not reported or available.

The final dataset comprised 43 montane and 62 lowland forests (Fig. 1; Table S1) according to a threshold elevation of 1000 m above sea level (a.s.l.) (sensu Holdridge et al., 1971). The geographical coverage by continent was highest for South and Central America (62 sites), and decreased towards South and East Asia (26), Hawaii (12), Africa (3) and Australia (2). Climate data (i.e., MAT, MAP, DSL) were derived from the respective papers or, if not presented, from online resources such as the Climatic Research Unit databases (http://www.cru.uea.ac.uk) and WorldClim global climate data (http://www.worldclim.org). DSL is defined as the number of months during which rainfall is > 100 mm. CLD was retrieved from the IPCC-data distribution center using 0.5° resolution datasets during the period 1961–1990 (CRU TS2.1) provided by the Climatic Research Unit (CRU; http://www.cru.uea.ac.uk/).

Moreover, we searched for site-matched data on soil total N and P, litter N and P and foliar N and P to compute respective N : P ratios for soil (soil N : P), litter (litter N : P) and leaves (foliar N : P). Stand-level data on litter and leaf N : P were either reported, or we calculated this as the mean of species-specific values (usually > 5 to up to > 50 species were reported). Soil data were derived from soil samples taken between 0 and 30 cm excluding surface litter, and where necessary were calculated as a weighted mean for 0–30 cm soil depth. Soil types comprised many organic soils in montane tropical forests and mainly mineral soils in lowland sites (Table S1). Soil total N and P are much higher in organic soils than in mineral soils, and the contribution

of organic horizons to topsoil increases with elevation as a result of decreasing decomposition rates. We therefore refrained from using soil total N or soil P as proxies for N or P availability. Instead, we used soil N : P (litter N : P, foliar N : P) as an indicator of soil P relative to N availability as soil N : P ratios are relatively independent of soil N or P concentration (Xu et al., 2012). High soil N : P ratios as found in highly weathered soils might therefore be used as indicators of P limitation in such environments (Yang & Post, 2011). Final site coverages for climate data were 100% for MAT, MAP and DSL, 96% for CLD, 82% for soil N : P, 68% for litter N : P, and 51% for foliar N : P. Root production data were only available for 40 out of 105 sites.

## Statistical design and data analysis

All statistical analyses were performed using R (R Development Core Team, 2012). Data distributions were analyzed for normality and nonnormal data were log-transformed or rank-transformed to attain normality. Before further analysis, we removed outliers, defined as data that were beyond three SD of the mean, from the dataset. Residuals of linear regression analyses were analyzed for normality, and data with leverage and influence inconsistent with the full dataset were identified and removed. To describe patterns in the available data and discern potentially responsible drivers, we used three complementary statistical approaches. To investigate drivers of NPP partitioning to WP we used linear regressions as well as partial linear regressions and their residuals. Classification and regression tree (CART) analyses were conducted to indicate the relative importance among environmental controls on %WP. Finally, we computed structural equation models (SEMs) to investigate pathways of interrelated environmental controls on %WP.

Linear regressions were computed to test for dependencies between NPP components (Fig. S1) as well as above-ground NPP (ANPP) components (Fig. 2), that is, canopy production (CP), wood production (WP), root production (RP) and partitioning to WP (%WP). We moreover used linear regression models to investigate the effects of climatic variables, that is MAT, MAP, DSL and CLD (Fig. 3), as well as the various N : P ratios (Fig. 4), on tropical ANPP, CP, WP and %WP. Climate variables were standardized to allow direct comparison of respective effects on ANPP components and %WP. The standardized variables are dimensionless with a mean of zero and an SD of one. Thus, coefficients in simple and multiple regressions with
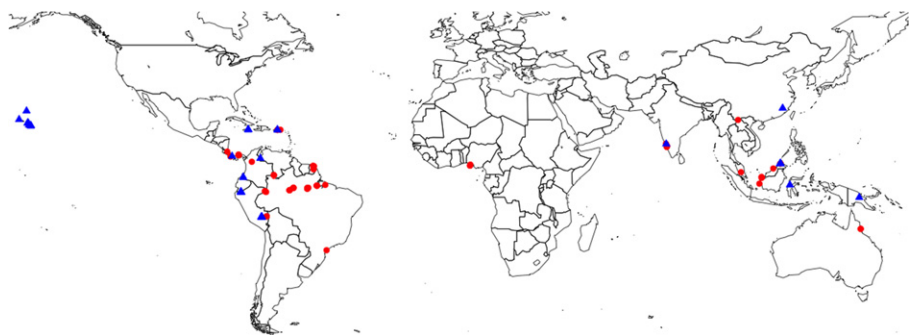


Fig. 1 Geographic locations of tropical study sites (fully described in Table S1). Blue triangles, montane tropical rainforests (> 1000 m above sea level (a.s.l.)); red circles, lowland tropical rainforests (< 1000 m a.s.l.).
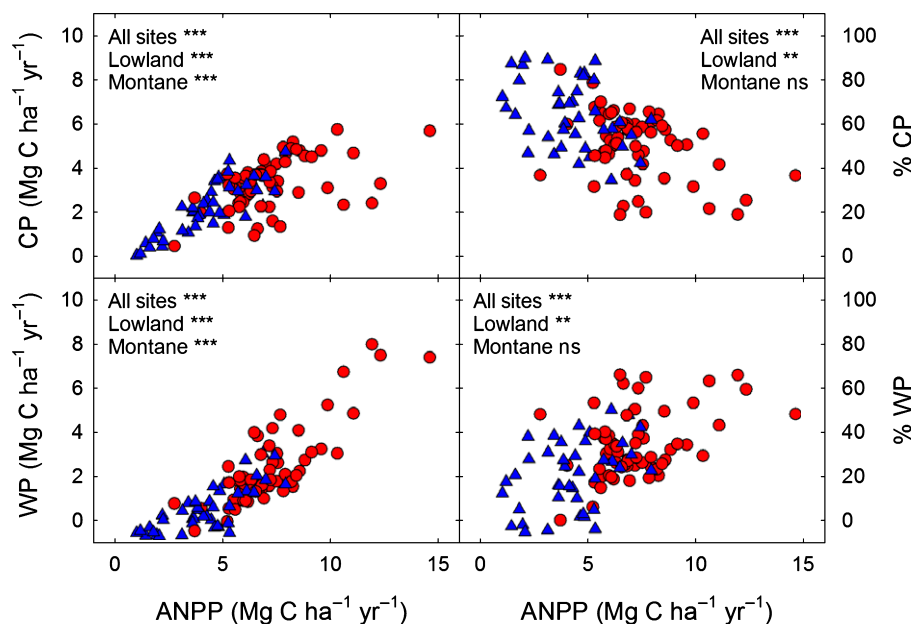
**Fig. 2** Relationship of canopy production (CP; in Mg ha$^{-1}$ yr$^{-1}$) and wood production (WP; in Mg ha$^{-1}$ yr$^{-1}$), as well as respective partitioning of above-ground net primary production (ANPP; in Mg C ha$^{-1}$ yr$^{-1}$) to canopy production (%CP) and wood production (%WP) in relation to ANPP. Blue triangles, montane tropical rainforests (> 1000 m above sea level (a.s.l.)); red circles, lowland tropical rainforests (< 1000 m a.s.l.). Corresponding regression significance levels are indicated by asterisks (***, $P < 0.001$; **, $P < 0.01$; ns, not significant).

standardized variables indicate the respective contributions to the variation in ANPP and %WP in terms of a relative unit change. Residuals of the most significant predictor in multiple regressions were used to test for independent effects of interrelated significant variables on %WP (Table S2).

Classification and regression tree (CART) analysis was used to determine the relative importance of predictors in explaining variation in the response variable. This method is especially suited for handling unbalanced data, including missing values (De'ath & Fabricius, 2000). Moreover, CART is capable of handling higher-order interactions among variables such as effects of nutrient–climate interactions (Townsend *et al.*, 2011). Based on the assumptions by Cleveland *et al.* (2011) and given that across the whole data set MAT had the strongest effect on tropical forest production, we used CART to dissect the pantropical data set into lowland and montane forest sites and investigated the environmental factors controlling ANPP and %WP in both forest types (Fig. 5).

Structural equation modeling is a multivariate statistical tool using the covariance among variables to build and test models with specific multistep pathways of influence on one or more final response variables. This technique goes beyond standard multiple regression approaches by elucidating the interaction of variables related to the process of interest (Fox, 2006). As a first step, we developed a conceptual base model (Fig. S2) involving all variables that might be causally related to one another and to the response variables. For this, we included the climate variables MAT, MAP, DSL and CLD as exogenous factors, as well as ratios of soil N : P, litter N : P and foliar N : P as endogenous factors; both sets of variables were reasoned to directly and indirectly affect the response variables ANPP and %WP. To cope with missing values and thus changing total numbers of observations in the full pantropical data set (Table S1), we had to evaluate different base models. The full model, including all environmental variables, had the lowest number of observations ($n = 38$). The

climate-only model, including the variables MAP, MAT, DSL and CLD, was based on the largest data set ($n = 101$). The graphical model representations show the respective variables (boxes), with respective causal and directional connections between variables (arrows). Arrow length does not indicate the strength of the connection, but each path has a (standardized) path coefficient, which represents the slope of that relationship in a multivariate context. The overall goodness of fit is indicated by a $\chi^2$ statistic and corresponding *P*-values, where a high *P*-value represents a good fit between the model and the data. Model optimization was an iterative process analogous to stepwise multiple regression. Insignificant paths were removed from the base model in a stepwise manner, aiming at improvement of the overall model fit (see Colman & Schimel, 2013). To compare alternative models and determine the most parsimonious model, we used Akaike's information criterion (AIC; Burnham *et al.*, 2011), arriving at a final model including the variables MAP, MAT, DSL, and soil N : P ratio ($n = 86$; Fig. 6).

## Uncertainty and robustness of the environment–ANPP relationships

We expect relatively low uncertainty in the litterfall data, as very similar methodology was used at all sites (litter traps had 0.25– 1 m$^2$ area, were replicated five to 20 times in each forest type/site, with collection intervals of 2–4 wk over at least 1 yr). Measurements of tree girth and increment are also not expected to cause large uncertainty; however, the use of different allometric models (most studies used DBH-only based models, some DBH × WD, the fewest DBH × *H* × WD) adds the highest degree of bias and uncertainty in studies of forest biomass and wood production (see Chave *et al.*, 2005). The use of a recently published pantropical allometric model (Chave *et al.*, 2014) could greatly narrow this uncertainty, but inaccessibility of the raw data on species affiliations, DBH, *H* and WD, obviated this approach. Another
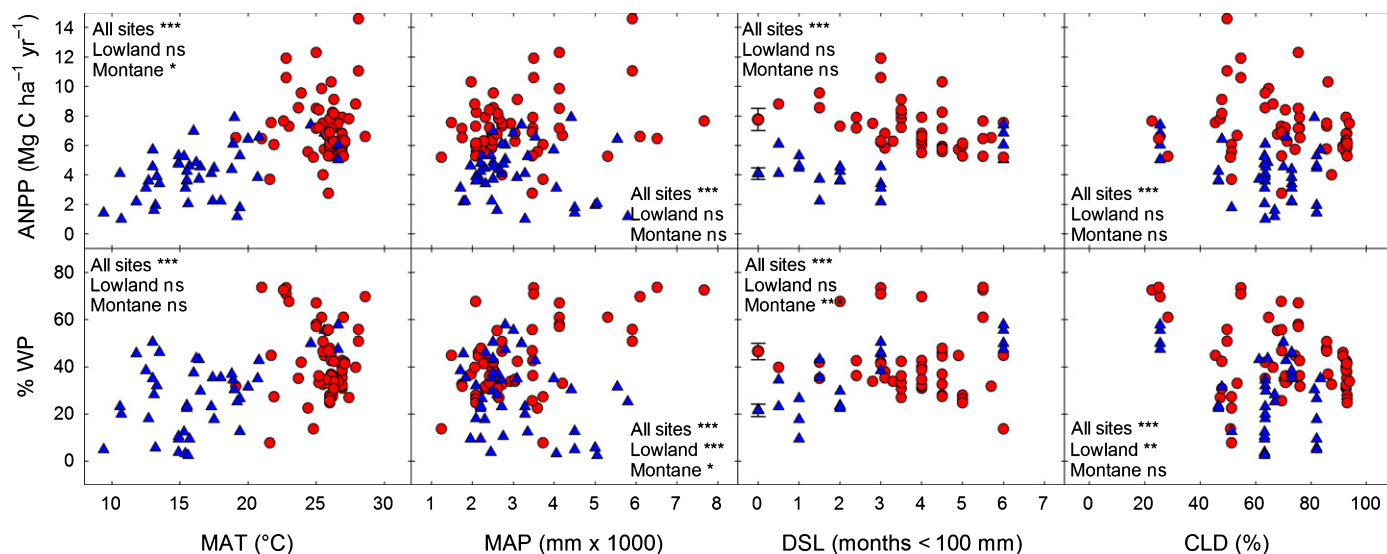
**Fig. 3** Relationships of above-ground net primary production (ANPP) and ANPP partitioning to wood production (%WP, as a percentage of ANPP) to major climatic drivers, that is, mean annual temperature (MAT), mean annual precipitation (MAP), dry season length (DSL) and cloud cover (CLD). Blue triangles, montane tropical rainforests (> 1000 m above sea level (a.s.l.)); red circles, lowland tropical rainforests (< 1000 m a.s.l.). Corresponding regression significance levels are indicated by asterisks (***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; ns, not significant). See Table S1 for details on respective study sites.
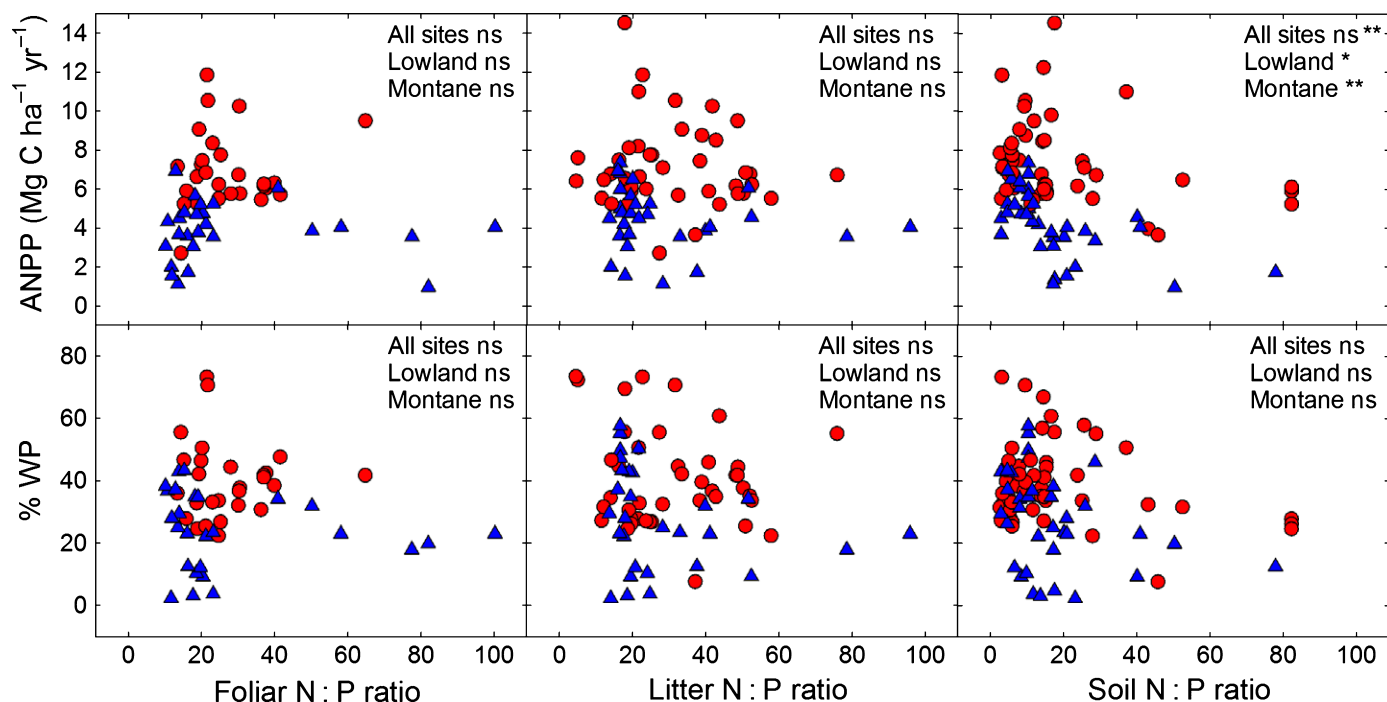


**Fig. 4** Relationships of above-ground net primary production (ANPP) and ANPP partitioning to wood production (%WP, as a percentage of ANPP) to nitrogen : phosphorus (N : P) ratios of leaves (foliar N : P), litter (litter N : P), and soil (soil N : P). Blue triangles, montane tropical rainforests (> 1000 m above sea level (a.s.l.)); red circles, lowland tropical rainforests (< 1000 m a.s.l.). Corresponding regression significance levels are indicated by asterisks (**, $P < 0.01$; *, $P < 0.05$; ns, not significant). See Table S1 for details on respective study sites.

uncertainty in the pantropical dataset derives from the fact that in some tropical forests litterfall and wood increment were not measured over the same period of time, and for some sites measurements differed by up to 10 yr. Taken together, these errors cause a substantial increase in the uncertainty of data on wood increment relative to litterfall data; we suggest therefore that any uncovered significant environment–productivity relationship

across tropical forest sites can be considered robust. Moreover, we want to point out that environment–ANPP and environment–%WP relationships as reported here, based on sites where both litterfall and wood increment were reported, can be expected to be more reliable compared with the many studies where only one component of ANPP was measured and missing components were extrapolated from mathematical
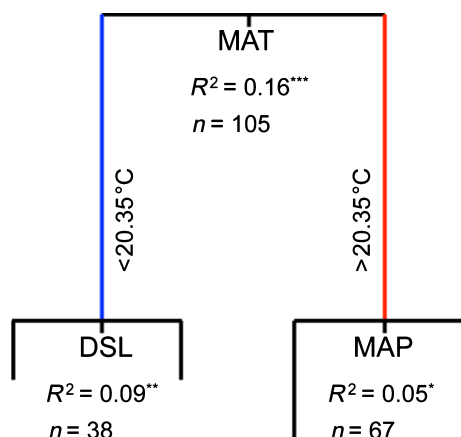
**Fig. 5** Classification and regression tree (CART) analysis indicating how the major environmental controls, mean annual temperature (MAT), mean annual precipitation (MAP), and dry season length (DSL), explain variance in above-ground net primary production partitioning to wood production (%WP) in tropical rainforests. Predictor variables are depicted at each branch and coefficients of determination and corresponding significance levels are indicated by asterisks (***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; ns, not significant) as well as the number of observations reported below. MAT was the most important predictor of %WP, followed by DSL in montane sites (MAT < 20.4°C, $n = 38$; blue branch) and MAP in lowland sites (MAT > 20.4°C; $n = 67$; red branch). See Table S1 for details of respective study site.
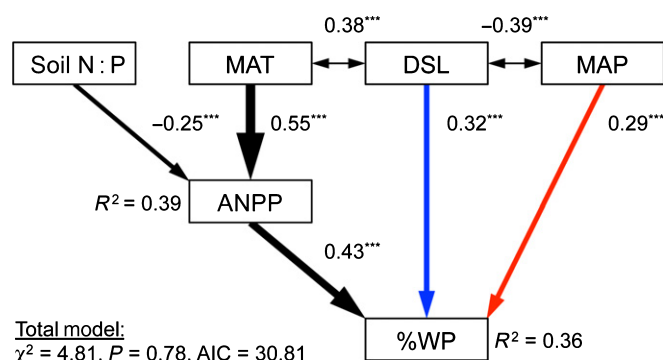


**Fig. 6** Structural equation model (SEM) indicating pathways of influence among environmental drivers (mean annual temperature (MAT), mean annual precipitation (MAP), dry season length (DSL) and soil nitrogen : phosphorus (N : P) ratio) on above-ground net primary production (ANPP) and ANPP partitioning to wood production (%WP) in tropical rainforests. Arrow width indicates effect strength, and numbers are standardized path coefficients with corresponding significance levels indicated by asterisks (***, $P < 0.001$). The overall goodness of fit of the model is indicated by the $\chi^2$ statistic and corresponding $P$-values, where a high $P$-value ($P > 0.05$) represents little difference between the model and the data. Akaike's information criterion (AIC) was used to compare alternative models and determine the most parsimonious model.

relationships to the measured component (see Shoo & VanDerWal, 2008).

## Results

We found that in the full dataset ($n = 105$) both components of ANPP (i.e., CP and WP) increased with ANPP (Fig. 2). However, compared with CP, WP showed a steeper increase with

ANPP, such that ANPP partitioning to WP (%WP) increased while that to CP (%CP) decreased with productivity (Fig. 2).

We further analyzed a subset ($n = 40$) of tropical forest sites, where data on ANPP and root production (RP) were available, to evaluate the partitioning of NPP to canopy, wood and root production, and similarly found that all components of NPP (i.e., CP, WP, and RP) increased with productivity (Fig. S1). However, NPP partitioning to CP (%CP), WP (%WP) and RP (% RP) showed no significant relationship with productivity; that is, we found no evidence of changes in NPP partitioning with increasing productivity in the smaller dataset (Fig. S1). In the smaller dataset, we also did not observe the increase in %WP with ANPP that we found in the large dataset (data not shown).

### Mechanisms driving ANPP partitioning to WP in tropical forests

Testing predictors of ANPP revealed that MAT most strongly affected ANPP ($R^2 = 0.35$, $P < 0.001$) followed by soil N : P ($R^2 = 0.11$, $P < 0.01$) and DSL ($R^2 = 0.04$, $P < 0.05$) (Table S2). Testing predictors of ANPP partitioning showed that %WP was affected by ANPP ($R^2 = 0.28$, $P < 0.001$), as well as by MAT ($R^2 = 0.16$, $P < 0.001$), DSL ($R^2 = 0.09$, $P < 0.01$), MAP ($R^2 = 0.05$, $P < 0.05$) and nearly so by soil N : P ($R^2 = 0.04$, $P = 0.052$). Furthermore, we found significant effects of MAP ($R^2 = 0.05$, $P < 0.05$) and DSL ($R^2 = 0.05$, $P < 0.05$) on the residuals of the ANPP–%WP relationship, which are therefore independent of ANPP effects on %WP. In turn, we found significant effects of ANPP on the residuals of the environment–%WP relationships ($R^2 = 0.10$–$0.32$, $P < 0.001$), including MAT, MAP, DSL and soil N : P, which are therefore independent of environmental effects on %WP (Table S2). Overall, this indicated that there must exist multiple independent but parallel pathways of control on the partitioning of ANPP to WP.

We therefore computed a CART analysis to determine the relative importance of the predictors (MAT, MAP, DSL, CLD and soil N : P ratio) in explaining the variation in the response variable (%WP; Fig. 5). We found that MAT was the most important predictor ($R^2 = 0.16$, $P < 0.001$), followed by DSL ($R^2 = 0.09$, $P < 0.01$) in tropical rainforests with MAT < 20.4°C, and MAP ($R^2 = 0.05$, $P < 0.05$) in tropical rainforests with MAT > 20.4°C. CART therefore dissected the data set into cool (< 20.4°C) and warm (> 20.4°C) tropical forest sites. This dissection is in good agreement with the classification threshold of lowland forests (< 1000 m a.s.l., $n = 62$) and montane forests (> 1000 m a.s.l., $n = 43$), with a misclassification of only five out of 105 (< 5%) tropical forest sites (Table S1). Furthermore, this indicated that % WP was affected by MAT, MAP and DSL (Fig. 3; Table S2). While MAT increased %WP across all forest sites, MAP increased %WP in lowland but not montane sites, and DSL increased % WP in montane but not lowland sites (Fig. 5).

Computation of a series of SEMs finally provided an insight into the effects of simultaneous and interactive environmental drivers on the partitioning of ANPP to WP (Fig. 6). The most parsimonious model (AIC = 30.81, $\chi^2 = 4.81$, $P = 0.78$) revealed two pathways of control on %WP ($R^2 = 0.36$, $P < 0.001$). First,

MAT and soil N : P positively affected %WP but indirectly through stimulating ANPP ($r = 0.43$, $P < 0.001$), such that % WP increased with productivity. MAT most strongly increased ANPP ($r = 0.55$, $P < 0.001$), while soil N : P negatively affected ANPP ($r = -0.25$, $P < 0.001$), indicating a positive effect of soil phosphorus relative to nitrogen content on forest productivity and %WP. Secondly, DSL and MAP did not affect ANPP but showed a direct positive effect on the partitioning of ANPP to WP ($r = 0.29$–0.32, $P < 0.001$), indicating an independent and direct pathway driving %WP in response to DSL and MAP. The fact that the coefficients of determination were almost identical for the indirect ($R^2 = 0.19$, $P < 0.001$) as well as the direct pathway ($R^2 = 0.19$, $P < 0.001$) furthermore highlights that both mechanisms contribute similarly (Fig. 6).

## Discussion

Based on an SEM investigating 105 pantropical old-growth forests, we show that carbon allocation is controlled by two independent pathways involving multiple environmental variables. While in our model, the first pathway represents indirect environmental controls on the partitioning of ANPP to WP (%WP), the second pathway represents direct environmental controls on %WP. Our results for tropical forests are in line with theoretical C allocation strategies (Franklin *et al.*, 2012) and a recently proposed C allocation scheme for global forests (Chen *et al.*, 2013). The novelty of our approach, however, is that it clearly differentiates between direct and indirect environmental controls on %WP. In the following sections we therefore differentiate between these independent mechanisms, discuss each with regard to respective environmental drivers and conclude with implications of our findings for tropical C sequestration.

### Environmental controls on wood partitioning in tropical forests

Given the few data available on tropical forest GPP ($n = 10$; Chen *et al.*, 2013) and the limited number of tropical forest sites for which data on ANPP and below-ground production are available, we investigated the environmental controls on %WP at two levels: on the basis of NPP data ($n = 40$) as well as ANPP data ($n = 105$).

In the smaller data set on tropical forest NPP, we found strong allometric constraints on component NPP fluxes (i.e. CP, WP, and RP increased with NPP). However, we did not find tradeoffs in the partitioning among NPP components; that is, %WP, %CP and %RP did not change with NPP and %WP did not increase with ANPP in this dataset (Fig. S1).

In the larger dataset on tropical ANPP, we did identify a tradeoff between ANPP components, such that along the pantropical gradient of productivity, the partitioning to wood biomass (%WP) increased with ANPP (Fig. 2), similar to what was shown for global forests (Litton *et al.*, 2007). In agreement with this, a recent study investigating the biomass production efficiency of global forests reported that the fraction of carbon allocated to wood production increased threefold with increasing nutrient

availability, while foliage and root production remained unchanged (Vicca *et al.*, 2012). This suggests that in more productive forests with high nutrient and water availability and high MAT, a greater proportion of NPP (and ANPP) is allocated to wood production, reflecting our findings of increased %WP in lowland than in montane forests (Fig. 2).

This result was mirrored by the first pathway of the SEM that indicated indirect environmental controls of MAT and soil N : P on %WP by promoting ANPP (Fig. 6). While MAT was reported as the strongest predictor of NPP across tropical rainforests (Raich *et al.*, 2006), a recent synthesis indicated that this relationship was driven by distinct temperature differences between low productive montane and high productive lowland forests (Cleveland *et al.*, 2011). However, within tropical lowland forests, soil-based measures of phosphorus were the only variables explaining a significant proportion of the variation in ANPP (Cleveland *et al.*, 2011). In agreement with this, the SEM in this study indicated positive effects of MAT and relative soil P availability (i.e. the inverse of soil N : P ratio) on ANPP along the pantropical gradient in forest productivity (Fig. 6). It is, however, likely that increased vegetation density in high productive forests triggers increased competition for limiting resources. For instance, it was shown that crowded plants adapt their growth strategy by allocating a greater proportion of biomass to competitive structures such as stems as a consequence of light limitation (Weiner, 2004). This has also been termed the 'race for light' in forests (Wolf *et al.*, 2011), driving NPP allocation towards stem height growth (instead of leaf area production) to maximize exposure of the leaf area to more favorable light conditions. Moreover, limitations by soil water and/or nutrient availability were reported to be lower in highly productive forests, stocking on soils rich in nutrients and moisture, thus essentially decreasing relative investments into roots to capture below-ground resources (McMurtrie & Dewar, 2013). As a result of the fact that plants will allocate relatively more biomass in response to the most limiting factor for growth, this would be seen as increased relative investment into above-ground structures, mainly woody biomass (Poorter *et al.*, 2011). Hence, we suggest that the pattern of indirect controls on %WP identified in the SEM could result from the observation that increasing forest productivity simultaneously increases competition for light, causing tree height and tree diameter growth and therefore %WP to increase (Lewis & Tanner, 2000).

The second, direct pathway of environmental controls on % WP, through MAP and DSL, points to direct tradeoffs between WP and CP (or between WP and RP) in response to proximate environmental drivers, independent of constraints by forest productivity (Fig. 6). Although both MAP and DSL represent measures of forest water availability, which are commonly inversely related, our model indicated that both MAP and DSL had a positive effect on %WP (see SEM analysis in Fig. 6). This was because, in lowland forests, %WP increased with MAP, while in montane forests, %WP increased with DSL (see CART analysis in Fig. 5; Table S2), explaining that DSL and MAP, though acting adversely on forest water relations, both had positive effects on %WP across all forest sites in the SEM analysis. We suggest

that this direct pathway of environmental controls on %WP could be associated with tradeoffs along the plant economics spectrum and thus relates to the cost-effectiveness of investments into stem, leaf and root tissues, independent of productivity.

Leaf investment strategies were shown to vary from cheap, short-lived to well protected, long-lived leaves, trading off carbon gain against leaf persistence (Poorter & Bongers, 2006). In general, increasing MAP should increase stand-level leaf longevity as a result of decreasing prominence of deciduous tree species, in turn promoting evergreen broadleaved tropical trees. Furthermore, it was shown that increasing MAP triggered coordinated changes in physiological traits of tropical canopy trees, such that the longevity of leaves increased in lowland tropical rainforests (Santiago et al., 2004). Given that the leaf area index of tropical lowland rainforests does not change significantly with MAP (Asner et al., 2003), greater leaf longevity translates into smaller investments into canopy production relative to wood production and therefore into an increase in %WP, although this might be offset by greater leaf mass per area in long-lived leaves. Our finding of increasing %WP with MAP in lowland forests therefore points to a tradeoff between CP and WP mediated by concerted changes along community-wide means of the leaf economics spectrum.

Wood investment strategies are also expected to change along the plant economics spectrum in order to maximize plant hydraulic safety with increasing drought frequency and intensity. Wood traits affect the hydraulic conductance and thus represent important components affecting the performance and life-history strategy of tropical trees (Poorter et al., 2009). For instance, opportunistic species are characterized by low wood density, reduced leaf dry mass per area, and high hydraulic conductivity in order to maintain high photosynthetic rates that enhance carbon gain and boost vertical growth (Poorter & Bongers, 2006). However, such cheap volumetric stem construction represents less structural support, and thus low wood density is often associated with higher mortality rates (Chave et al., 2009). As a result, drought-intolerant species, because of high hydraulic efficiency but low hydraulic safety, are restricted to habitats that have high water availability, whereas drought-tolerant species, because of high hydraulic safety, are better competitors in drier habitats (Markesteijn et al., 2011). In reverse, increased hydraulic safety is associated with higher wood density, lower hydraulic conductivity and therefore less leaf area per area of stem conducting tissue (Markesteijn et al., 2011). All these trends cause %WP to increase and %CP to decrease when increasing DSL enhances community-wide degrees of hydraulic safety. A recent synthesis of an African long-term forest inventory indicated the importance of species composition in determining the response of tropical forests to long-term droughts (Fauset et al., 2012). In the two decades of drought, species increasing in abundance showed significant differences in traits compared with those decreasing in abundance, such that a shift in community composition in favor of drought-tolerant species was in conjunction with an increase in forest biomass, pointing to increased C allocation to wood production. Our finding of increasing %WP with DSL in montane forests therefore points to a tradeoff between plant traits that maximize water conservation and hydraulic safety along community-wide means of the stem (plant) economics spectrum. Overall, the effects of MAP and DSL on %WP, driving changes in the relative investments into leaves, stems or roots, may therefore be reconciled on the basis of community-wide shifts along the plant (leaf, stem, and root) economics spectrum in the long run.

## Implications for tropical biogeochemistry and ecosystem functioning

Our analysis provided new insights into patterns and mechanisms driving C allocation in tropical rainforests by identifying independent pathways of environmental controls on %WP. The expression of the different pathways will, however, strongly depend on the functional plasticity of the present species in the short term as well as on species turnover, depending on species migration and dispersal abilities in the long term. Understanding the patterns and mechanisms driving C allocation are key for the parameterization of global vegetation models in order to accurately predict changes in C sequestration of tropical and global forests in response to environmental change.

The pattern of enhanced %WP along tropical gradients in forest productivity that we found in this study supports the global relationship reported by Litton et al. (2007) and suggests greater C sequestration in wood biomass in more productive lowland than in montane tropical rainforests. Our results further imply that predicted increases in temperature and dry season length could potentially increase %WP and thus C sequestration in montane tropical forests. By contrast, in lowland tropical forests that were reported to thrive close to their thermal optimum (Doughty & Goulden, 2008; Corlett, 2011; Clark et al., 2013), %WP is more likely to respond neutrally or negatively to increasing temperatures. Decreases in annual precipitation (or increases in heavy precipitation with prolonged intermittent dry periods) could therefore decrease %WP in lowland rainforests, causing C sequestration to decrease. However, this effect could be partially alleviated by drought-induced shifts in the functional composition of tropical rainforest trees, favoring drought-tolerant species over less competitive opportunistic species in conjunction with a shift in community-wide functional traits that promote %WP and thus C sequestration.

In conclusion, our analysis demonstrated the complex interplay of direct and indirect environmental drivers controlling tropical C allocation that eventually determine the potential responses of tropical forest C sequestration to environmental changes. Albeit that further long-term and local measurements of forest productivity as well as manipulative experiments are urgently needed to allow implementation of the right causalities (Fatichi et al., 2013), our study provides a novel framework to disentangle interrelated pathways among environmental drivers controlling the C sink strength of tropical forest ecosystems.

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## Supporting Information

Additional supporting information may be found in the online version of this article.

**Fig. S1** Relationships of canopy production (CP), wood production (WP) and root production (RP), as well as respective relative partitioning to net primary production (NPP).

**Fig. S2** Structural equation base model indicating pathways of influence among environmental drivers on ANPP partitioning to wood production (%WP).

**Table S1** Literature compilation of pantropical study sites ($n = 105$)

**Table S2** Results of partial linear regressions indicating the relative importance of direct and indirect environmental controls on ANPP partitioning to wood production (%WP)

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