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Key Points:

- We study the climate sensitivity of tropical forest aboveground productivity
- Partitioning of ANPP components may shift in response to climate extremes
- Local site characteristics determine the response to climate anomalies

Supporting Information:

- Readme
- Table S1
- Table S2
- Table S3
- Table S4

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Sensitivity of tropical forest aboveground productivity to climate anomalies in SW Costa Rica

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Abstract The productivity of tropical forests is driven by climate (precipitation, temperature, and light) and soil fertility (geology and topography). While large-scale drivers of tropical productivity are well established, knowledge on the sensitivity of tropical lowland net primary production to climate anomalies remains scarce. We here analyze seven consecutive years of monthly recorded tropical forest aboveground net primary production (ANPP) in response to a recent El Niño–Southern Oscillation (ENSO) anomaly. The ENSO transition period resulted in increased temperatures and decreased precipitation during the El Niño dry period, causing a decrease in ANPP. However, the subsequent La Niña wet period caused strong increases in ANPP such that drought-induced reductions were overcompensated. Most strikingly, the climatic controls differed between canopy production (CP) and wood production (WP). Whereas CP showed strong seasonal variation but was not affected by ENSO, WP decreased significantly in response to a 3°C increase in annual maximum temperatures during the El Niño period but subsequently recovered to above predrought levels during the La Niña period. Moreover, the climate sensitivity of tropical forest ANPP components was affected by local topography (water availability) and disturbance history (species composition). Our results suggest that projected increases in temperature and dry season length could impact tropical carbon sequestration by shifting ANPP partitioning toward decreased WP, thus decreasing the carbon storage of highly productive lowland forests. We conclude that the impact of climate anomalies on tropical forest productivity is strongly related to local site characteristics and will therefore likely prevent uniform responses of tropical lowland forests to projected global changes.

1. Introduction

Tropical forests are key components of the global carbon (C) cycle because they store about 250 Gt of C in living biomass [Saatchi *et al.*, 2011], contain about 25% of the world's biomass C and account for an estimated 40% of global net primary production [Townsend *et al.*, 2011]. Moreover, tropical forests are highly relevant for Earth's climate processes [Del Grosso *et al.*, 2008], as global model simulations suggest that large-scale deforestation of the Amazon would cause a regional temperature increase (2°C) and substantial reductions (25%) of evaporation and precipitation [Malhi *et al.*, 2002]. In turn, climate and associated atmospheric conditions represent key factors driving primary productivity of tropical rainforests [Clark and Clark, 1994]. Hence, projected alterations in climatic signals and the severity of climate extremes, such as those projected by global climate change scenarios, will likely affect the productivity of tropical forest ecosystems [Intergovernmental Panel on Climate Change, 2007].

For instance, it was reported that during El Niño periods, decreased precipitation, soil moisture deficit, and increasing temperatures negatively affect the productivity of tropical rainforest ecosystems [Clark *et al.*, 2003; Phillips *et al.*, 2009; Wagner *et al.*, 2012]. In accordance, studies on tree ring chronologies [Christie *et al.*, 2009] and tree increments [Clark *et al.*, 2003] indicated that increased temperatures and drought negatively affected aboveground net primary production (ANPP) in tropical forests. However, most studies investigating the climate sensitivity of tropical forests are based on single ANPP components, particularly on wood production (WP), and thus, much less information is available on the climate sensitivity of canopy production (CP). Just recently, a long-term study evaluating 12 years of annual ANPP and its relation to climatic factors reported that increasing minimum temperatures and greater dry season water stress negatively

affected WP but not CP [Clark *et al.*, 2013]. This indicates that climate controls on tropical ANPP cannot be deduced reliably from a single component of ANPP. Both components (CP and WP) together comprise ~90% of ANPP in tropical forests [Aragao *et al.*, 2009], with average contributions of $53 \pm 14\%$ for wood and $47 \pm 8\%$ for canopy production [Malhi *et al.*, 2011]. These contributions vary between sites [Malhi *et al.*, 2011], but the environmental determinants of this variability are largely unknown. Belowground net primary production is another important contributor to total forest productivity, with aboveground: belowground production averaging 60:40 on a percentage basis [Aragao *et al.*, 2009], but very few long-term data sets are available to allow inferences on its climate sensitivity.

Despite the fact that relationships between canopy and wood production proved weak [Dybzinski *et al.*, 2011] and variable between continents [Shoo and VanDerWal, 2008; Malhi *et al.*, 2011], such relationships have often been used to extrapolate single data sets of wood production (or of canopy production) to total ANPP, in order to investigate controls on ANPP at regional or global scales [e.g., Cleveland *et al.*, 2011]. Based on such extrapolations, ANPP of tropical forests has been shown to be globally driven by mean annual temperature (MAT), mean annual precipitation (MAP), and soil phosphorous [Schuur, 2003; Raich *et al.*, 2006; Cleveland *et al.*, 2011]. However, a major weakness of simple climate metrics like MAT and MAP is that they are insufficient to capture the effects of seasonal and interannual climate variations on tropical forest productivity, which are expected to be strongly affected by future climate change [Cleveland *et al.*, 2011]. Therefore, a major challenge in exploring the causality of climate-productivity relationships in tropical forests to date is the paucity of high-resolution and long-term records on climate and primary production measured at the same site and over the same period of time [Clark *et al.*, 2001a, 2013]. So far, respective climate controls could only be assessed at large scales, comparing tropical forests across wide climate and soil gradients but rarely over seasonal and interannual time scales.

Only recently, a few studies have addressed this issue by investigating which factors control seasonal and interannual changes in tropical tree growth [Rowland *et al.*, 2013; Gliniars *et al.*, 2013; Mendivelso *et al.*, 2014]. In general, they found that precipitation and solar radiation were the main seasonal drivers of tropical tree growth [Wagner *et al.*, 2014], while maximum temperatures [Gliniars *et al.*, 2013] and increasing drought periods reduced tree growth [Mendivelso *et al.*, 2014]. Furthermore, Rowland *et al.* [2013] demonstrated significant differences between tree functional traits and the degree of seasonality of tree growth, consistent with a hypothesized trade-off between maximum potential growth rate and hydraulic safety of tropical trees. Therefore, fast-growing, low wood density, tall and broad-stemmed trees experienced greater reductions in dry season increment than slower-growing, higher wood density trees, indicating that the functional composition of tropical forests is an important determinant of annual patterns of biomass accumulation [Rowland *et al.*, 2013]. On the one hand, this suggests that long-term changes in climate variables might trigger shifts in species composition in favor of slow-growing, drought-tolerant species, which was reported in conjunction with an increase in forest biomass [Fauset *et al.*, 2012]. On the other hand, more frequent short-term disturbances such as those linked to ENSO events typically increase the mortality of large trees, as was also indicated by experimental drought experiments [Nepstad *et al.*, 2002; da Costa *et al.*, 2010] that showed that big trees tend to be the first ones to die, which may trigger a decrease in stand-level biomass [Phillips *et al.*, 2010]. Hence, projected short-term climate anomalies could possibly counteract the long-term effects of increasing biomass due to shifts in species composition and thus negatively affect the C sequestration potential of tropical lowland rainforests.

In this study we investigated the sensitivity of tropical lowland ANPP to climate anomalies triggered by a recent ENSO transition period (2009–2011) by analyzing seven consecutive years of monthly estimates of aboveground biomass increment (as a surrogate for WP) as well as total fine litterfall and leaf area index (as a surrogate for CP) at forest sites differing in topography and disturbance history in southwestern Costa Rica. We present data on the seasonal and interannual variation of CP and WP to elaborate significant relationships with interannual climate anomalies (multivariate ENSO index; MEI) and the climatic variables, bulk precipitation (BP), number of dry days (DD) as well as monthly maximum (T_{\max}), and minimum temperatures (T_{\min}). We furthermore consider local site characteristics associated to topography and disturbance history that might determine the sensitivity of tropical WP and thus might affect the C sequestration potential of tropical lowland rainforests in response to projected climate anomalies.

2. Materials and Methods

2.1. Study Area

The study area is located at the border of the Piedras Blancas National Park, encompassing 148 km² of wet lowland tropical rainforest in the southwest of Costa Rica [Weissenhofer *et al.*, 2008]. Prevailing soil types are Ultisols and Inceptisols. The dominating, highly weathered, strongly acidic Ultisols on ridges and upper slopes are replaced by younger, moderately weathered Inceptisols at ravines and lower slopes [Pamperl, 2001]. To investigate the climate sensitivity of tropical lowland net primary production, we selected three forest types differing in topography and disturbance history located in the surroundings of the Tropical Research Station La Gamba (N8°42'03", W83°12'06", 70 m above sea level (asl)). The primary ridge forest (PRi; N8°42'16", W83°12'20", 120 m asl) is tall, open, and exposed and exhibits the highest species diversity in the region. The primary ravine forest (PRa; N8°42'16", W83°12'15", 80 m asl) is species-rich and characterized by a high abundance of palms. The secondary ravine forest (SRa; N8°42'01", W83°12'09", 80 m asl) was formerly used for tree logging and thus is relatively poor in species but has remained undisturbed for over 25 years. More detailed information on vegetation structure, tree species composition, soil parameters, and nutrient contents can be found in earlier studies conducted at the same set of sites [see Wanek *et al.*, 2008; Hofhansl *et al.*, 2011, 2012].

Starting in 1997, daily records of climate data (manual readings of precipitation as well as minimum and maximum temperature) were taken at the Tropical Research Station La Gamba [Weissenhofer *et al.*, 2008; Weber *et al.*, 2001]. During the study period (2006–2013), the mean annual precipitation was 6100 ± 600 mm, the mean number of dry days was 85 ± 13 d/yr, the number of months receiving less than 100 mm of precipitation was 0.7 ± 0.4 months, and the mean annual temperature was 28.5 ± 0.4°C. The monthly mean precipitation ranged from 150 mm (February) to 870 mm (October) and was inversely related to the mean monthly number of dry days ranging from 2 days (November) to 16 days (February) per month (Figure 2). The mean monthly maximum temperature was 32.8 ± 0.7°C, ranging between 31.3°C (October) and 34.4°C (March), and the mean monthly minimum temperature was 24.2 ± 0.2°C, ranging between 23.4°C (January) and 24.9°C (April).

2.2. Study Design

In February 2005, plots (400 m²) were set up in triplicate either as squares of 20 × 20 m, separated by a distance of >10 m and divided into subplots of 10 × 10 m each or as rectangles of 10 × 40 m subdivided into subplots of 10 × 10 m and separated by 10–30 m due to spatial restriction at the ridge forest site. Hence, each forest type was covered by 0.12 ha of survey area. In each subplot, tree species above 10 cm diameter at breast height (DBH) as well as in every fourth subplot trees between 2.5 and 10 cm DBH were tagged and determined to species level. Herbarium specimens were deposited in the National Herbarium at the Museo Nacional (San Jose, Costa Rica) and at the Biologiezentrum Linz (Upper Austria, Austria).

Aboveground biomass increment was investigated by repeatedly measuring the diameters at breast height (DBH) of all trees approximately 1.30 m aboveground or above buttresses or other irregularities according to standard best practice techniques [Clark *et al.*, 2001a; Baker *et al.*, 2004]. In February 2006, trees above 10 cm DBH were equipped with dendrometer bands (D1 permanent tree girth tape measures with diameter scale and spring, made of thermally inactive Astralon, UMS, Munich, Germany). Trees below 10 cm DBH were measured (twice shifted by 90°) using sliding calipers. Measurements were performed every month for trees >10 cm DBH and every 3 months for trees <10 cm DBH throughout the study period between 2006 and 2013. Tree height was estimated for all trees of this study ($n = 349$) using inclinometers (Suunto PM-5/360 PC clinometer, Valimoti, Finland), and wood density (ρ) was measured for 13 out of 61 tree species in this study for which data were not available in the literature. For the remaining species, wood density data were retrieved from the global wood density database [Zanne *et al.*, 2009]. We used the allometric equation for wet forest stands ($AGB = \exp(-2.557 + 0.940 \ln(\rho D^2 H))$) published by Chave *et al.* [2005] to calculate aboveground biomass increment in Mg ha⁻¹ mo⁻¹ [Keeland and Sharitz, 1993; Clark and Clark, 2000].

Fine litterfall (LF) was collected in litter traps (50 × 50 cm), fixed 100 cm aboveground level. Traps were made of PVC tubing, covered by a 1 × 1 mm nylon mesh, and positioned in the center of 10 of the 12 subplots in

each of the three forest sites. Starting in February 2005, fine litter samples were collected in intervals ranging from 2–4 weeks and divided into leaf litter (consisting of leaves below 50 cm in length) and nonfoliar litter (consisting of twigs below 2 cm in diameter, reproductive material, and fine unidentifiable material), oven dried, and weighed [Drage, 2007]. The sum of these fractions was used to calculate total fine litterfall in $\text{Mg ha}^{-1} \text{ mo}^{-1}$ [but see Clark *et al.*, 2001a].

In this study we opted to investigate the seasonal variation of ANPP and therefore used aboveground biomass increment as indicator of wood production (WP), as well as total fine litterfall corrected for changes in leaf area as surrogate for canopy production (CP), at monthly time resolution. To that end, we calculated canopy production (CP in g m^{-2}) from litterfall (LF in g m^{-2}) corrected for changes in leaf area index (LAI in $\text{m}^2 \text{ m}^{-2}$) times leaf mass area (LMA in g m^{-2}) following the equation: $\text{CP} = \text{LF} + (\text{LAI}_t - \text{LAI}_{t-1}) * \text{LMA}$ [see also Doughty and Goulden, 2008] and then converted CP to $\text{Mg ha}^{-1} \text{ mo}^{-1}$ for comparison to WP. LAI was estimated from ground-based measurements taken between February 2008 and August 2011 using a SunScan probe v1.05 and Sunshine Sensor BF3 (Delta-T Ltd., U.K.), as well as from remotely sensed Moderate Resolution Imaging Spectroradiometer products available from the Land Processes Distributed Active Archive Center (https://lpdaac.usgs.gov/products/modis_products_table/mcd15a2). We subsequently removed outliers defined as data beyond 3 standard deviations, applied a 12 month moving average smoother, and then adjusted the LAI3d values obtained for each forest site to in situ measurements of LAI, taken between February 2008 and August 2011 [Hofhansl *et al.*, 2012]. Mean leaf mass area (LMA; 93.1 g m^{-2}) was calculated as average from published literature providing LMA values for nearby tropical lowland forest sites in Costa Rica [Cavaleri *et al.*, 2010] and Panama [Asner *et al.*, 2011].

2.3. Multivariate ENSO Index

Bimonthly values of the multivariate ENSO index (MEI) were obtained from the National Oceanic and Atmospheric Administration (<http://www.esrl.noaa.gov/psd/enso/mei/>). MEI is a multivariate measure of the ENSO signal that is calculated as the first principal component in an analysis of sea level pressure, surface temperature, surface air temperature, and cloudiness over the tropical Pacific Ocean [Wolter and Timlin, 1993; Wolter and Timlin, 2011]. Negative values represent the cold ENSO phase associated with heavy precipitation events (La Niña), while positive values represent the warm ENSO phase accompanied by droughts in the study region (El Niño). The ENSO cycle year typically starts in May (year X) and ends in April (year X + 1). We therefore calculated the annual sums or means of climate and productivity variables for the corresponding periods from May 2006 to April 2013.

2.4. Statistical Analysis

To test for the effects of climate on forest productivity, we linked the daily records of climate variables, i.e., bulk precipitation magnitude (BP), number of dry days (DD), maximum temperature (T_{max}), and minimum temperature (T_{min}) to the collection intervals of litterfall (2–4 weeks) and stem increment (1–3 months) using the aggregate algorithm in R (R Core Team 2012). From the period of May 2006 to April 2013, we calculated the monthly sums of canopy production (CP), wood production (WP), aboveground net primary production (ANPP), bulk precipitation (BP), and number of dry days (DD), as well as the averaged monthly mean (T_{med}), minimum (T_{min}), and maximum temperatures (T_{max}). Data distributions were analyzed for normality, and nonnormal data were log transformed to attain normality. Prior to further analysis, we removed outliers, defined as data that were beyond 3 standard deviations of the mean from the data set. Residuals of linear regression analyses were analyzed for normality, and data with leverage and influence inconsistent with the full data set were identified and removed. All statistical analyses were performed using R (R Core Team 2012).

To further explore the climate sensitivity of tropical lowland net primary production and to separate the patterns of interannual and seasonal variations, we calculated the annual sums and the monthly means of climate and productivity variables and computed complementary statistical approaches.

We calculated the annual sums or the means of climate variables recorded over the period 1997–2013 and computed linear regressions to test for significant relationships of multivariate ENSO index (MEI) with mean annual precipitation (MAP), annual number of dry days (DD), mean annual maximum temperature (MAT_{max}), number of months receiving <100 mm rainfall, mean annual minimum

temperature (MAT_{\min}), as well as the relationship between MAP and MAT_{\max} . We moreover calculated the monthly means of climate and productivity variables recorded over the period 2006–2013 and computed a canonical correlation analysis to visualize the relation of climate variables and productivity parameters with respect to the ENSO transition period (2009–2011). We furthermore computed the multiple linear regression models of that data set to investigate significant effects of multivariate ENSO index (MEI), precipitation magnitude (BP), number of dry days (DD), and maximum temperatures (T_{\max}) on canopy production (CP), wood production (WP), and aboveground net primary production (ANPP).

We applied time series analysis and performed seasonal decomposition of time series into seasonal, trend, and irregular components to test for patterns in interannual and seasonal variations of climate and productivity variables. Seasonal variation is calculated during the routine as the respective monthly mean of the study period (2006–2013), which then is subtracted from the time series to produce a seasonally detrended interannual signal. We then computed linear mixed effect models (with interannual trend as fixed factor and seasonal variation as random effect) to test for significant trends in interannual climate and productivity signals during the time series (2006–2013).

We calculated the detrended interannual and seasonal anomalies following *Clark and Clark* [1994] by subtracting the monthly means to derive the interannual anomaly and subtracting the annual means to derive the seasonal anomaly data set, respectively. We used one-way analysis of variance (ANOVA) to test for significant differences in the seasonally detrended interannual data set, as well as in the annually detrended seasonal data set, respectively. We eventually performed lagged correlation analysis to investigate maximum correlation coefficients between seasonally detrended climate and productivity variables at different time lags and plotted Spearman's R values for the correlation between climate and productivity variables to indicate the most significant drivers of tropical lowland net primary production.

3. Results

During the period of May 1997 to April 2013, the most recent ENSO transition period (2009–2011) resulted in decreased annual precipitation but increased mean maximum annual temperature (MAT_{\max}) and number of rain free dry days (DD) as indicated by significant relationships with the multivariate ENSO index (Figure 1). During the study period (2006–2013), the ENSO anomaly reduced the annual precipitation from an average of 6100 mm to 5360 mm during the 2009/2010 El Niño and subsequently reached the highest value ever recorded of 7950 mm during the 2010/2011 La Niña, whereas MAT_{\max} increased by 3°C during the 2009 drought period (Figure 1 and Figure 2). Moreover, the ENSO transition reduced ANPP by 20% in response to increased temperatures (+3°C) and decreased precipitation (−780 mm) during the El Niño period (2009/2010), whereas subsequently, ANPP recovered by 24% following the strong increases in rainfall (+1810 mm) during the La Niña period (2010/2011), such that drought-induced ANPP reductions were overcompensated (Table S1 in the supporting information).

We moreover found that the ANPP components, canopy production (CP) and wood production (WP), exhibited distinct patterns in seasonal and interannual variations (Figure 2 and Figure 3). Whereas WP showed a strong interannual pattern peaking in 2011 (Figure 2) but did not respond significantly to seasonal climate variation (Figure 3 and Table S1 in the supporting information), CP followed a strong seasonal pattern peaking in the dry season (Figure 3) but did not vary significantly between years (Figure 2 and Table S2 in the supporting information). Furthermore, we found that ENSO affected the seasonality of climate variables, such that the monthly precipitation was significantly reduced and the monthly mean maximum temperatures significantly increased during the El Niño period (Figure 3).

A canonical correlation analysis helped to visualize the distinct relations of ANPP components to climate variables (Figure 4). Whereas WP was positively related to bulk precipitation (BP) and T_{\min} and inversely to rain free days (DD) and T_{\max} , CP was positively related to DD and T_{\max} but negatively to BP and T_{\min} . Moreover, DD and T_{\max} were associated with the El Niño drought (2009/2010) and opposed to BP and T_{\min} during the La Niña wet period (2010/2011). Further investigation of multiple regression models revealed significant climatic controls on ANPP components. While DD showed no significant effect on ANPP and any of its components, BP was negatively related to CP and ANPP but not to WP. In addition,

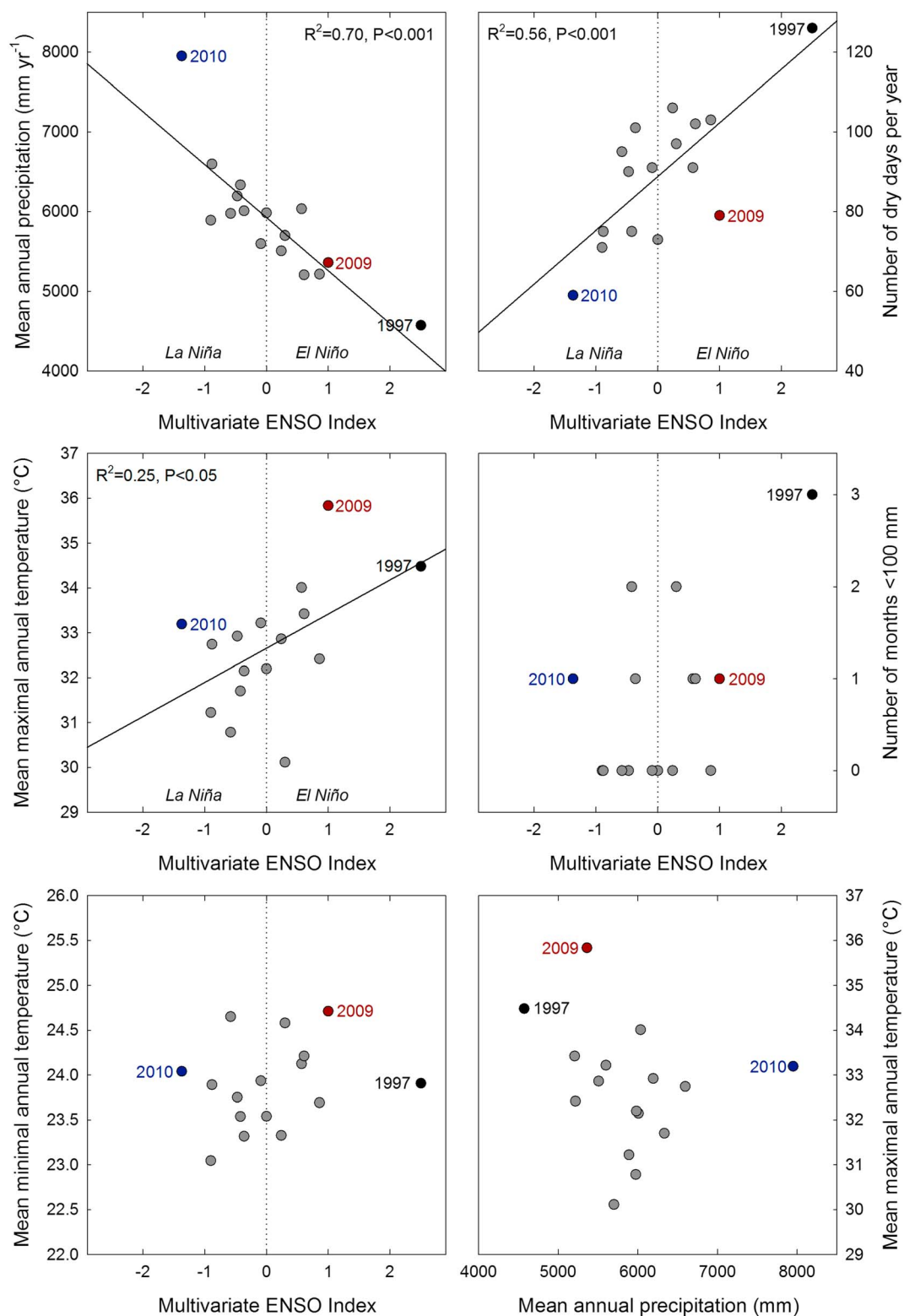


Figure 1. Relationship of multivariate ENSO index (MEI) with climate variables: mean annual precipitation (MAP), annual number of dry days (DD), mean annual maximum temperature (MAT_{max}), number of months receiving <100 mm rainfall, mean annual minimum temperature (MAT_{min}), as well as the relationship between MAP and MAT_{max} recorded over the period 1997–2013 at the Tropical Research Station La Gamba, Costa Rica. Significant relationships are indicated by respective R^2 and P values.

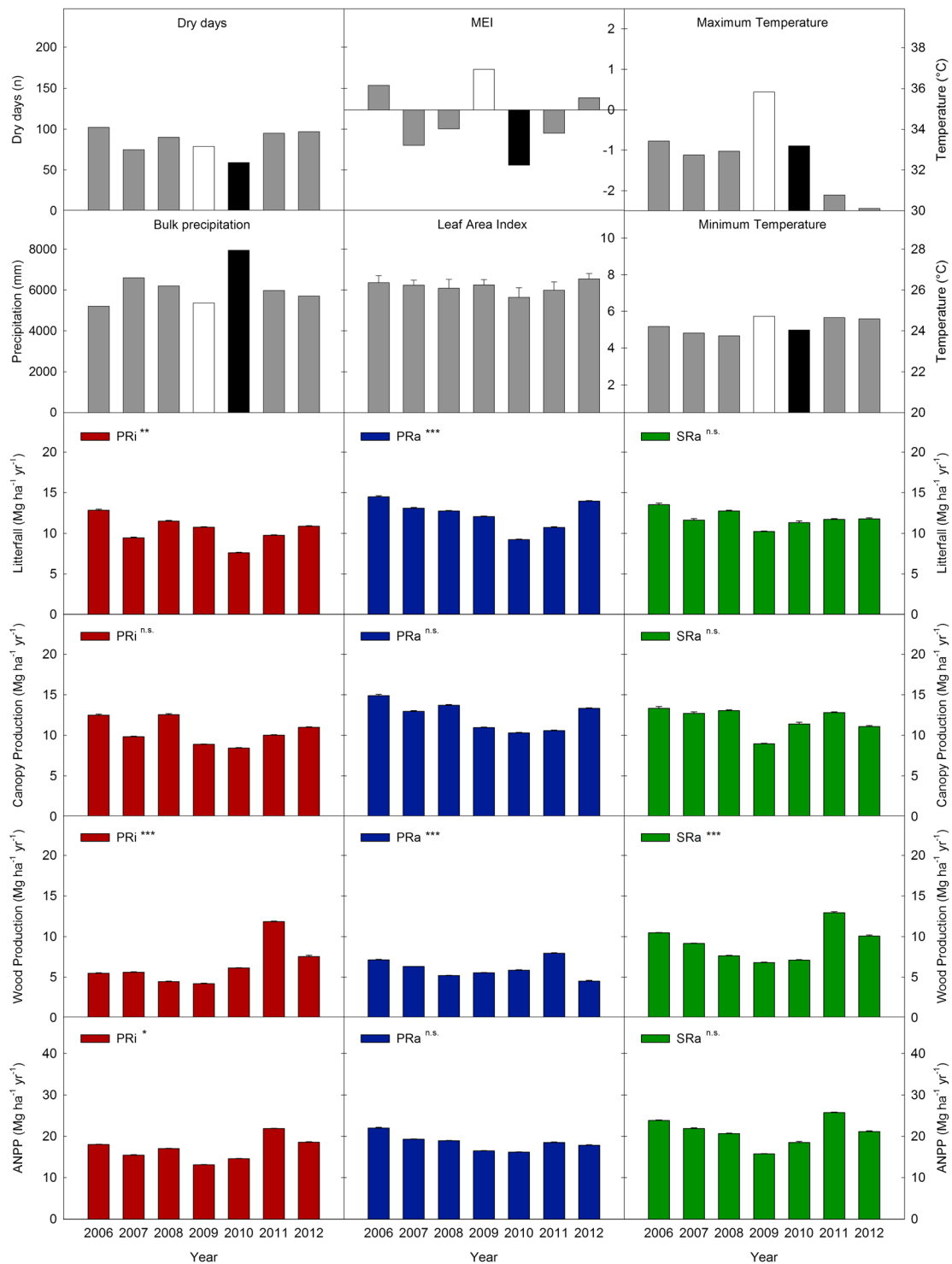


Figure 2. Interannual variation in the annual sums of climate and productivity variables: dry days (DD), multivariate ENSO index (MEI), mean monthly maximum temperature (T_{max}), mean annual bulk precipitation (MAP), mean annual leaf area index (LAI), mean monthly minimum temperature (T_{min}), as well as annual sums of litterfall (LF), canopy production (CP), wood production (WP), and aboveground net primary production (ANPP) recorded during the period 2006–2013 at primary ridge forest (PRI; red bars), primary ravine forest (PRa; blue bars), and secondary ravine forest (SRa; green bars) located in southwestern Costa Rica. The levels of significant interannual variation are indicated by asterisks (***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$; degree sign, $p < 0.1$; n.s., nonsignificant) and were calculated from seasonal detrended variables using one-way ANOVA (see Table S1 in the supporting information). Additionally, colored bars in climate variables (DD, MEI, T_{max} , BP, and T_{min}) represent respective climate anomalies during the El Niño dry period (white bars) as well as the subsequent La Niña wet period (black bars) compared to non-ENSO conditions (grey bars). The ENSO cycle year typically starts in May (year X) and ends in April (year X + 1); we therefore computed the annual sums of climate and productivity variables for the corresponding periods from May 2006 to April 2013.

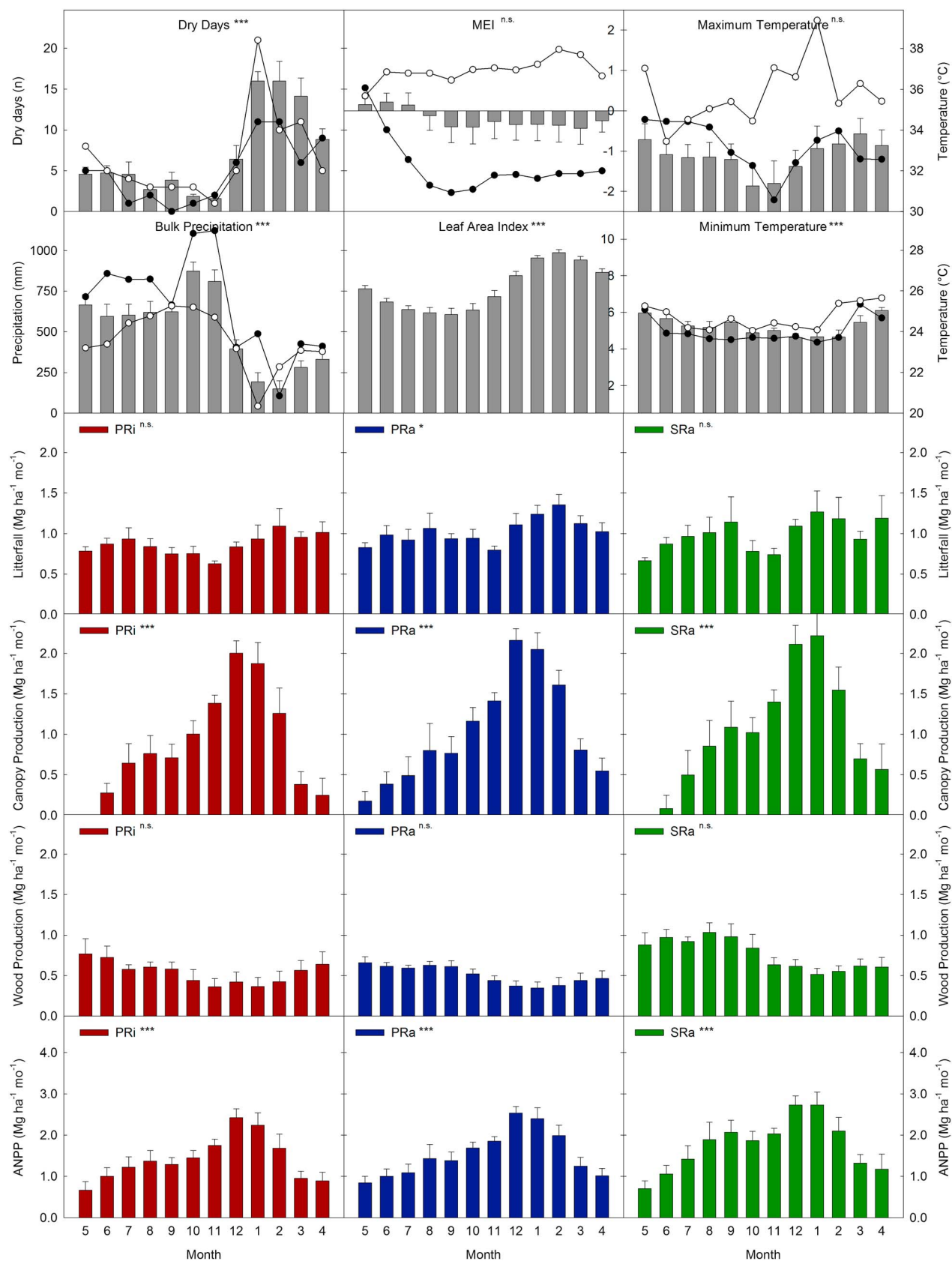


Figure 3

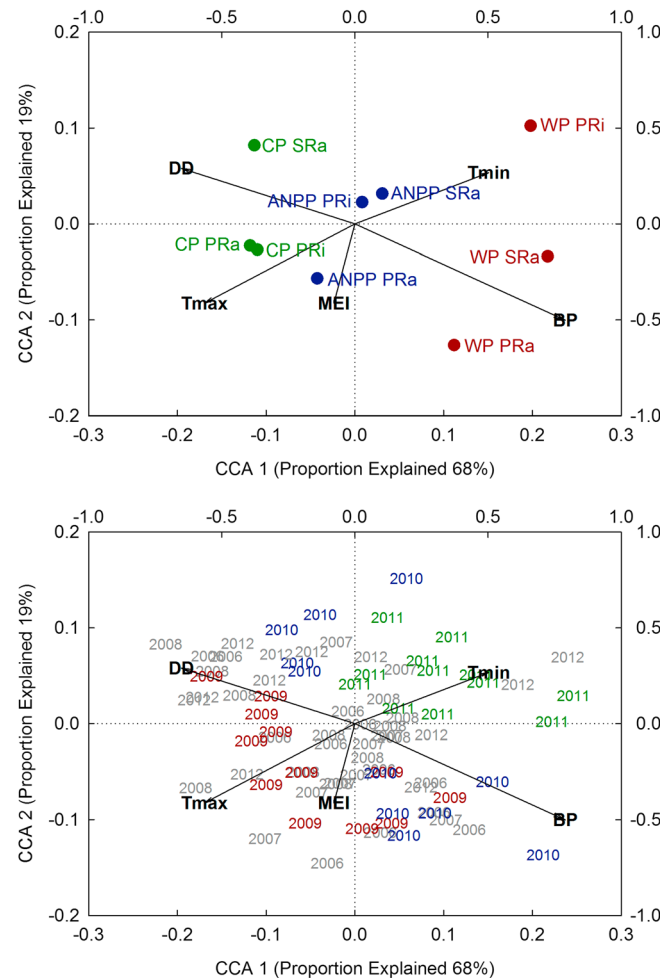


Figure 4. Canonical correspondence analysis indicating (a) the relation of the monthly means of climate variables: multivariate ENSO index (MEI), number of dry days (DD), precipitation magnitude (BP), maximum temperature (T_{\max}), minimum temperature (T_{\min}), and productivity variables: canopy production (CP; green symbols), wood production (WP; red symbols), and aboveground net primary production (ANPP; blue symbols) recorded during the period 2006–2013 at primary ridge forest (PRI), primary ravine forest (PRA), and secondary ravine forest (SRA) located in southwestern Costa Rica, as well as (b) the relation of climate variables (MEI, DD, BP, T_{\min} , and T_{\max}) to the 84 monthly records of productivity variables (CP, WP, and ANPP) with respect to the ENSO transition period (El Niño dry period 2009/2010 and La Niña wet period 2010/2011).

T_{\min} was negatively related to CP and ANPP, whereas T_{\max} negatively affected WP at the PRI and SRA but not the PRA forest site (Table 1).

We furthermore applied the decomposition of time series to dissect seasonal and interannual climate variations and investigate seasonally detrended interannual signals of climate and productivity variables (Figure 5). The analysis confirmed that interannual variations in the amplitude of climatic variables were associated with the ENSO signal. While MEI decreased during the period of 2006–2008 and peaked at the end of 2009, the detrended interannual signal of BP showed a negative peak in 2009 (inverse but lagged to the detrended interannual signal of DD) and thus indicated a prolonged period of drought during the El Niño period. Correspondingly, the interannual trend of T_{\max} revealed a dramatic temperature increase of around 3°C at the end of the dry period in 2009. However, interannual trends of the seasonally detrended time series were only significant for the climate variables DD ($\chi^2 = 69.33$, $p < 0.001$), T_{\max} ($\chi^2 = 5.91$, $p < 0.05$), and T_{\min} ($\chi^2 = 6.22$, $p < 0.05$; Table S3 in the supporting information). Concomitantly, seasonally detrended interannual time series of ANPP components showed fluctuations in response to the ENSO signal (Figure 5). Whereas CP showed no significant response to either the dry-warm El Niño period (2009/2010) or

Figure 3. Seasonal variation in the monthly means of climate and productivity variables: dry days (DD), multivariate ENSO index (MEI), mean monthly maximum temperature (T_{\max}), bulk precipitation (BP), mean annual leaf area index (LAI), mean monthly minimum temperature (T_{\min}), as well as monthly means of litterfall (LF), canopy production (CP), wood production (WP), and aboveground net primary production (ANPP) recorded during the period 2006–2013 at primary ridge forest (PRI; red bars), primary ravine forest (PRA; blue bars), and secondary ravine forest (SRA; green bars) located in southwestern Costa Rica. The bars represent the monthly means, and the whiskers represent the standard errors. The levels of significant seasonal variation are indicated by asterisks (***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$; degree sign, $p < 0.1$; n.s., nonsignificant) and were calculated from interannual detrended variables using one-way ANOVA (see Table S2 in the supporting information). Additional line plots in climate variables (DD, MEI, T_{\max} , BP, and T_{\min}) represent respective climate anomalies during the El Niño period (open symbols) as well as the subsequent La Niña period (closed symbols) compared to non-ENSO conditions (grey bars). The ENSO cycle year typically starts in May (year X) and ends in April (year X + 1); we therefore computed the monthly means of climate and productivity variables for the corresponding periods from May 2006 to April 2013.

Table 1. Effects of Climate on Tropical Aboveground Forest Productivity^a

Parameter	Estimates		P		Estimates		P		Estimates		P		Estimates		P		Estimates		P	
	Estimates	P	Estimates	P	Estimates	P	Estimates	P	Estimates	P	Estimates	P	Estimates	P	Estimates	P	Estimates	P	Estimates	P
Const	19,216.00	0.00	20,253.20	0.00	17,945.60	0.00	293.89	0.84	802.64	0.39	1,482.61	0.27	19,509.90	0.00	21,055.90	0.00	19,428.20	0.00		
MEI	182.22	0.04	157.85	0.05	-30.98	0.77	-9.86	0.82	25.79	0.35	65.48	0.10	172.36	0.04	183.64	0.02	34.50	0.75		
DD	-24.84	0.25	-21.56	0.27	-42.52	0.11	1.57	0.88	-1.01	0.88	-4.81	0.62	-23.27	0.25	-22.57	0.23	-47.33	0.08		
BP	-1.26	0.01	-1.39	0.00	-2.15	0.00	-0.05	0.84	0.17	0.26	0.14	0.53	-1.31	0.01	-1.21	0.01	-2.00	0.00		
T_{min}	-587.58	0.00	-630.36	0.00	-520.10	0.00	90.12	0.08	-11.17	0.74	56.57	0.24	-497.46	0.00	-641.53	0.00	-463.54	0.00		
T_{max}	-98.75	0.01	-92.73	0.01	-89.92	0.04	-58.97	0.00	-3.14	0.78	-64.72	0.00	-157.72	0.00	-95.87	0.00	-154.64	0.00		
R square	0.37		0.46		0.33		0.17		0.07		0.26		0.42		0.47		0.31			
P value	0.00		0.00		0.00		0.01		0.31		0.00		0.00		0.00		0.00			

^aResults of multiple regression models investigating the effects of the monthly means of climate variables: multivariate ENSO index (MEI), number of dry days (DD), bulk precipitation (BP), minimum temperature (T_{\min}), and maximum temperature (T_{\max}) on the monthly means of tropical aboveground productivity: canopy production (CP), wood production (WP), and aboveground net primary production (ANPP) recorded during the period 2006–2013 at primary ridge forest (PRi), primary ravine forest (PRa), and secondary ravine forest (SRa) located in southwestern Costa Rica.

the wet-cool La Niña period (2010/2011), WP in contrast slightly decreased during the dry-warm El Niño period, but subsequently strongly increased due to a lagged response to the wet La Niña period (Figure 5 and Table S3 in the supporting information). As a result, ANPP decreased in response to the drought period but subsequently showed a lagged recovery after the ENSO anomaly (Figure 5).

We eventually performed lagged cross-correlation analysis of seasonally detrended climate and productivity data (by subtracting the monthly means to derive the interannual anomaly) and found that the recent ENSO anomaly (2009–2011) exhibited significant and moreover lagged effects (ranging from 0 to 36 months) on tropical ANPP and its components, CP and WP (Table S4 in the supporting information). The analysis revealed few significant effects of interannual climate fluctuations on CP but strong, significant, and lagged effects on WP and thereby on ANPP (Figure 6). Although MEI significantly decreased WP and ANPP during the first 12 months, following the El Niño drought period, WP subsequently peaked 27 months after the drought anomaly due to a lagged response (12–15 months) to the La Niña wet period (Table S4 in the supporting information). Whereas DD showed only weak effects on CP, WP, and ANPP, BP primarily increased WP peaking 18 months after the drought and thus during the onset of the wet period. Interestingly, T_{\min} positively affected WP peaking after 9 and after 27 months, whereas T_{\max} negatively affected WP during the first 9 months following the drought but 27 months later showed strong positive effects on WP. We furthermore found that the climate sensitivity of WP differed between tropical lowland forest sites. Most strikingly, T_{\max} significantly decreased WP at the more exposed ridge (PRi) and secondary (SRa) forest sites but did not significantly affect WP at the downslope ravine (PRa) forest site (Figure 6). Therefore, this analysis highlights the differential climate sensitivity of nearby tropical lowland forest sites in terms of WP (and thus C sequestration) to ENSO anomalies.

4. Discussion

Current predictions of increasing climate variability and climate extremes [Lintner *et al.*, 2012] highlight the need of high-resolution and long-term investigations of tropical NPP [Clark *et al.*, 2013]. Only then the effects of interannual climate variations such as those associated with El Niño–Southern Oscillation (ENSO) can be distinguished from seasonal patterns in order to assess seasonally detrended interannual climate-productivity couplings and apply these as a proxy for global change effects on tropical ecosystems processes [Clark, 2007].

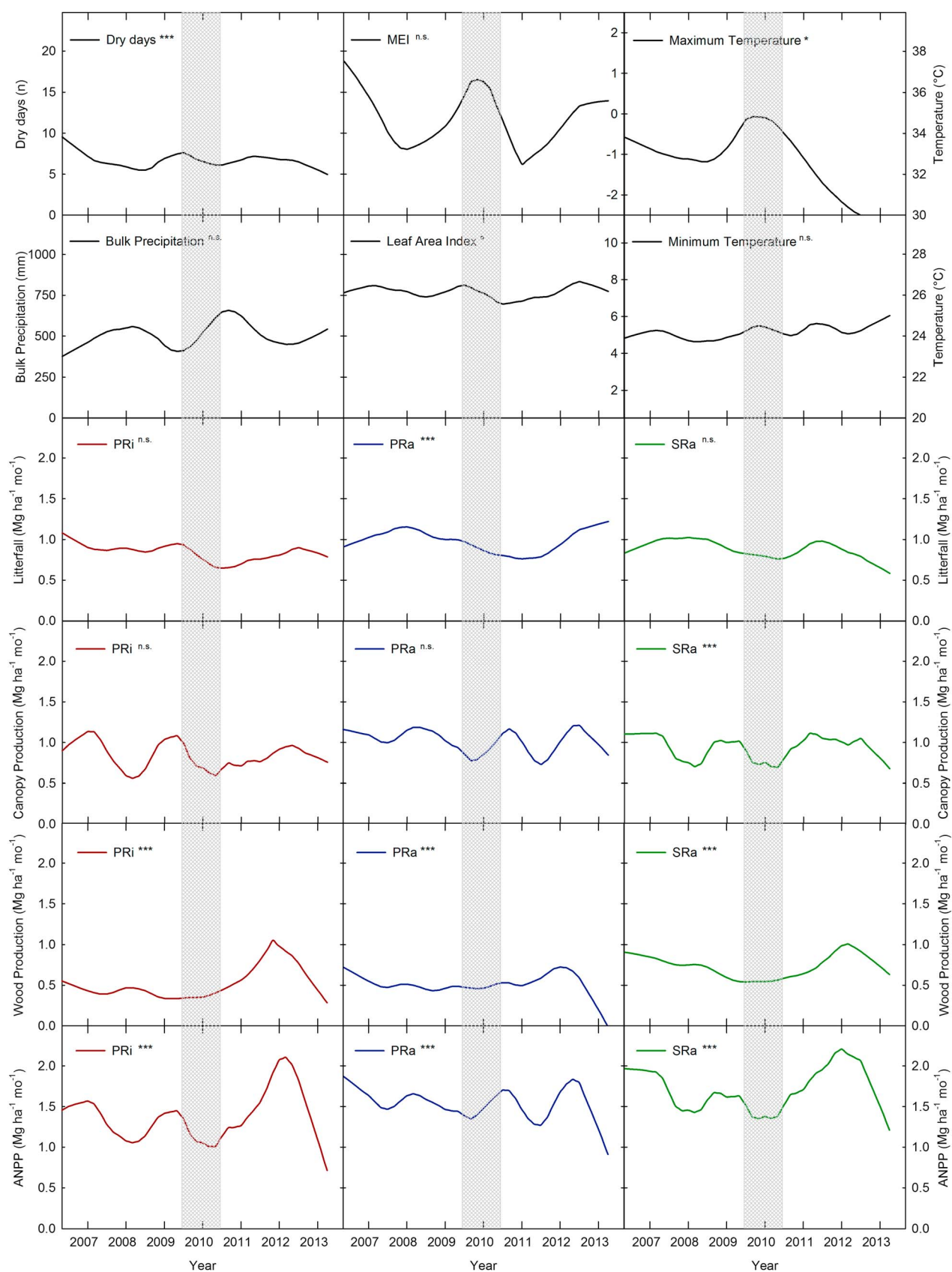


Figure 5

Hence, we here investigated the sensitivity of tropical lowland aboveground net primary production (ANPP) by evaluating a unique data set including 7 years of monthly recorded data on tropical canopy production (CP) and wood production (WP) from forest sites differing in topography and disturbance history located in southwestern Costa Rica.

4.1. Seasonal Variation and Climate-Productivity Coupling

What determines the seasonal and interannual variations of tropical ecosystem processes has become a recent subject of studies investigating the productivity of tropical forest ecosystems [Rowland *et al.*, 2013; Malhi *et al.*, 2014; Doughty *et al.*, 2014]. So far, it remains unknown whether direct effects of climate on tropical NPP or rather inherent phenological rhythms in growth allocation dominate the growth response of tropical forests ecosystems to seasonal climatic signals. Similar to our findings, it was reported that leaf and wood production showed asynchronous seasonal patterns, as leaf production peaked at the beginning of the dry season and wood production during the onset of the rainy season [Wagner *et al.* 2013]. Therefore, Malhi *et al.* [2014] suggested that phenological rhythms rather than direct climatic controls (such as water stress) seasonally drive tropical NPP allocation in Amazonian lowland forests. In accordance, the strong seasonality in NPP of Peruvian montane forests was reported to be driven by changes in photosynthesis and variation in solar radiation, such that trees invested more in biomass production in the cooler season with lower solar radiation and more in maintenance during the warmer high solar radiation period [Girardin *et al.*, 2013]. As a result, temporal or spatial variation in the allocation of NPP between wood, canopy, and fine roots could have the potential to be an important feature determining the C sink strength of tropical forest ecosystems [Doughty *et al.*, 2014].

4.2. Sensitivity of Lowland ANPP Components to Climate Anomalies

During seven consecutive years of monthly recorded data on tropical forest ANPP in this study, we found that a recent ENSO transition (2009–2011) reduced ANPP by 20% in response to increased drought (-780 mm MAP) and maximum temperatures ($+3^{\circ}\text{C}$ MAT_{max}) during the El Niño drought period. However, subsequently ANPP recovered by 24% due to a lagged growth response after the La Niña wet period, such that drought-induced reductions were overcompensated (Figure 6). Only recently, it was proposed that trees may require large C investments in storage pools to maintain hydraulic transport during episodes of severe stress, and therefore, plants experiencing soil water deficit tend to accumulate nonstructural carbohydrates and reduce growth [Sala *et al.*, 2012; Fatichi *et al.*, 2014]. Accordingly, we found that the lagged growth response was largely due to variations in woody biomass production rather than leaf production as CP and WP followed distinct temporal patterns during the 84 months of the study period (Figure 2 and Figure 3). Whereas CP showed strong seasonal variation (CV 81%; Table S2 in the supporting information) but did not differ significantly between years (CV 13%; Table S1 in the supporting information), WP showed less seasonal variation (CV 43%; Figure 3) but did respond more sensitively to interannual climate variation (CV 25%; Figure 2). This could indicate that WP rather than CP accounts for drought-induced reductions of tropical ANPP in response to interannual climate anomalies and thus would highlight the importance of WP in terms of the C sequestration potential of tropical forest ecosystems.

Indeed, we here show that CP and WP responded to different climatic controls, such that CP increased with the number of dry days and maximum temperatures, whereas WP was positively affected by bulk precipitation and negatively by maximum temperatures (Figure 4). Our findings emphasize recent studies investigating the climate sensitivity of tropical forests, reporting that ANPP in tropical forests was positively related to precipitation inputs and soil water content but negatively affected by maximum temperatures [Clark *et al.*, 2013; Rowland *et al.*, 2013; Gliniars *et al.*, 2013]. Most strikingly, this emerging pattern of climate-induced ANPP variation was found largely due to a response in wood production rather than litterfall

Figure 5. Seasonal detrended time series of climate and productivity variables: dry days (DD), multivariate ENSO index (MEI), mean monthly maximum temperature (T_{max}), bulk precipitation (BP), mean annual leaf area index (LAI), mean monthly minimum temperature (T_{min}), as well as monthly means of litterfall (LF), canopy production (CP), wood production (WP), and aboveground net primary production (ANPP) recorded during the period 2006–2013 at primary ridge forest (PRi; red bars), primary ravine forest (PRa; blue bars), and secondary ravine forest (SRa; green bars) located in southwestern Costa Rica. The levels of significant variation in time series are indicated by asterisks (***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$; degree sign, $p < 0.1$; n.s., nonsignificant) and were calculated from seasonal detrended variables using linear mixed effects models (see Table S3 in the supporting information). Additional grey areas indicate the impact of the 2009/2010 El Niño drought period on climate and productivity variables.

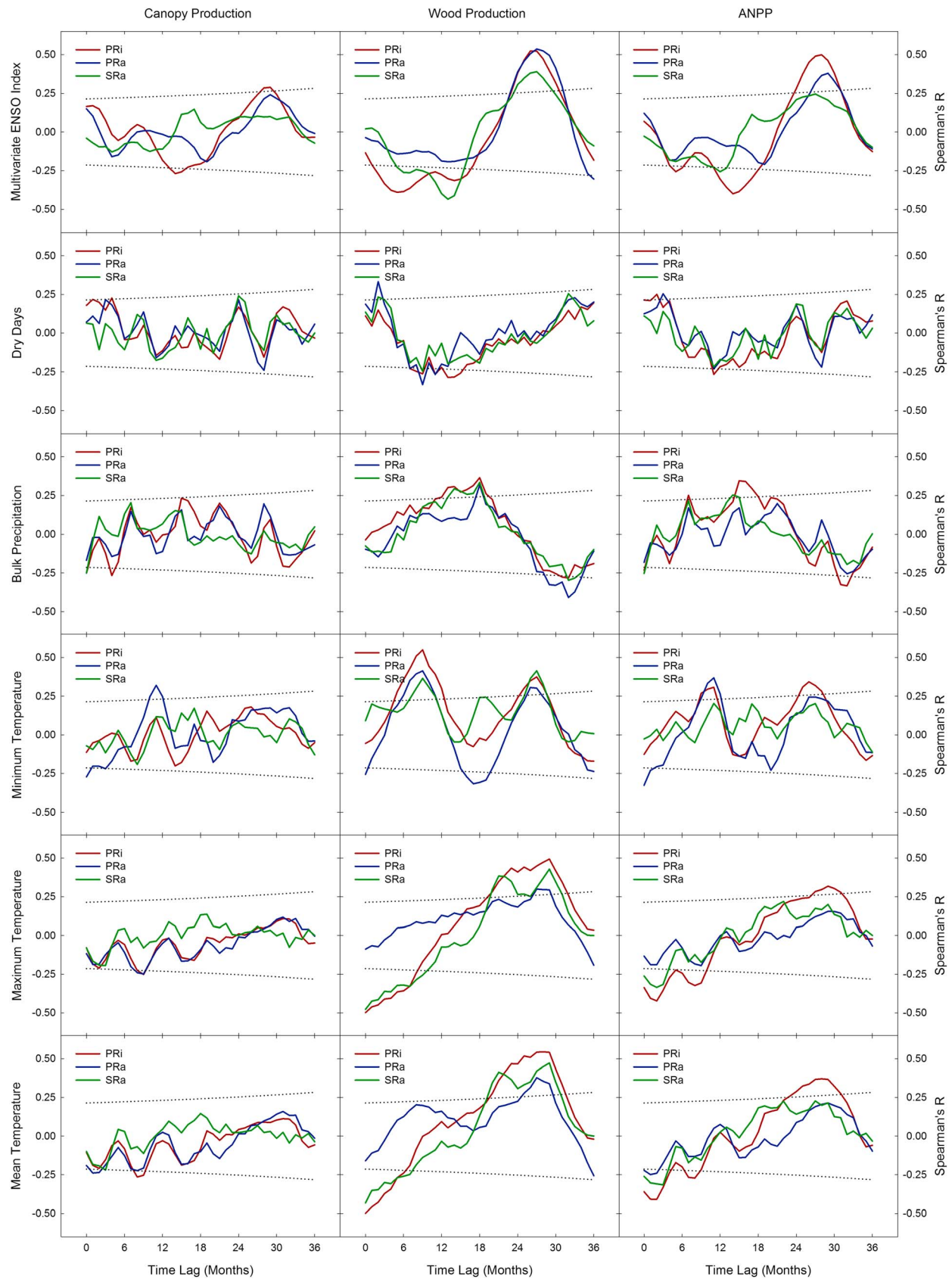


Figure 6

[Vasconcelos *et al.*, 2012]. Supporting this finding, it has been demonstrated that there exists a substantial decoupling between the irradiance driven leaf renewal and the water-driven wood production, triggering a temporal asynchronism in leaf and wood production in tropical forests [Wagner *et al.*, 2013]. Accordingly, in this study CP peaked during the dry season associated with high levels of irradiance, whereas WP was significantly reduced during the drought period but subsequently recovered in response to increased water availability (Figure 6).

Adding to this, recent studies suggest that C allocation strategies in tropical forests trigger a temporal decoupling between NPP components [Doughty *et al.*, 2014]. During their 4 year high temporal resolution study in two forest plots in the Bolivian Amazon, a strong 2010 drought strongly reduced photosynthesis, whereas NPP remained constant and even increased in the 6 month period following the drought. The authors concluded that allocation trade-offs might dominate the response of tropical forest growth to environmental changes due to C allocation priorities and nonstructural carbohydrate storage in tropical trees. In detail, they reported that allocation initially increased toward canopy production followed by increased allocation to fine root production in the following year, such that trees grew wood more slowly because they prioritized the buildup of new leaves or roots during the dry period [Doughty *et al.*, 2014]. We here similarly found a lagged response of tropical wood production, such that WP peaked 27 months after the drought period (Figure 6). This might indicate that during drought anomalies, initially increased CP is used to replenish C stores in tropical trees, followed by greater fine-root production to explore soil water resources, which finally result in increased wood production when water availability is restored after the drought period. The strong resilience of forest WP (52% increase after the drought period) could indicate that wet tropical forests have the potential to overcome short-term ANPP reductions when water availability is recovered after the drought period. Moreover, this further suggests that tropical lowland forests possess the potential to strongly recover C stocks (and thus C sequestration) after short-term climate anomalies.

4.3. Effects of Local Site Characteristics (Topography and Disturbance History)

We found that local site characteristics modified the responses of forest WP to large-scale climate anomalies (Figure 6). Reductions in WP were most prominent at the exposed ridge forest site (PRi; −35%) but less intense at the ravine forest site (PRa; −26%) and the downslope secondary regrowth forest site (SRa; −26%). This site-specific difference in climate sensitivity was attributed to topographic differences in soil type and soil depth and thus water availability as was indicated by differences in soil bulk density and soil moisture between the respective study sites [Wanek *et al.*, 2008]. It is therefore plausible that increased T_{\max} and decreased BP triggered drought stress of trees at the more exposed ridge forest and secondary regrowth forest site but did not significantly affect WP at the moist ravine forest site (Table 1).

In accordance, a recent analysis investigating the response of tropical forest growth to seasonal and interannual droughts in the Bolivian Amazon reported site-specific differences associated to topoedaphic characteristics of the respective forest site [Doughty *et al.*, 2014]. The authors found that although soil type and soil texture were relatively similar between the two Amazonian forest plots, the major difference was due to differences in soil depth and thus water availability between shallow and deep soil plots. These topoedaphic differences caused increased water stress at the shallow-soil plot compared to the deep-soil plot and thus led to differences in the composition of tree species. Whereas the deep-soil plot was inhabited by species typical of humid regions, the shallow-soil plot comprised species more typical of a dry deciduous forest with more seasonal leaf and wood production. As a result, the shallow-soil plot showed a more regular seasonal but also substantial interannual variation in NPP, suggesting a greater interannual drought sensitivity of dry deciduous tree species [Doughty *et al.*, 2014]. Therefore, local topoedaphic characteristics associated with water availability have the potential to determine the composition of tree species, which in turn could have important consequences for the tolerance of tropical lowland forests to climate anomalies.

Figure 6. Spearman's R values of lagged cross correlations between seasonally detrended climate variables: multivariate ENSO index (MEI), number of dry days (DD), precipitation magnitude (BP), minimum temperature (T_{\min}), maximum temperature (T_{\max}), mean temperature (T_{med}), and seasonally detrended productivity variables: canopy production (CP), wood production (WP), and aboveground net primary production (ANPP) recorded during the period 2006–2013 at primary ridge forest (PRi), primary ravine forest (PRa), and secondary ravine forest (SRa) located in southwestern Costa Rica. The dashed lines indicate the 95% confidence limits of significant lagged cross-correlation coefficients between seasonal detrended climate and productivity variables ($p < 0.05$; for detailed results of lagged correlation analysis see Table S4 in the supporting information).

It has been shown that the drought sensitivity of tropical tree growth differed among neotropical tree species, such that diverse growth responses among coexisting tree species were related to species-specific responses of wood formation to water availability [Mendivelso *et al.*, 2014]. More sensitive species require more water and more efficient water transport for growth than less sensitive species, and thus, drought sensitivity is related to the different life history strategies of drought-tolerant versus fast growing opportunistic species that determine water use and storage [Markestijn *et al.*, 2011]. Consistently, the sensitivity of wood production to climate variations was found to be associated to functional trade-offs between early and late successional species in Amazonian lowland rainforests [Rowland *et al.*, 2013]. In general, early successional tree species with low wood density invest in rapid growth to prevent shading, whereas late successional climax species tend to be shade tolerant but slow growing to reduce mortality risks [Rowland *et al.*, 2013]. As a result, short-term drought anomalies could have the potential to kill trees selectively since fast-growing, light-wooded trees might be especially vulnerable to drought by cavitation or C starvation [Condit *et al.*, 1996; McDowell *et al.*, 2008]. In accordance, Phillips *et al.* [2009] found that Amazonian tree species dying during the drought period had lower wood densities than those dying before. Therefore, species with denser wood were less vulnerable to drought and thus may become dominant after longer periods of water deficit [Phillips *et al.*, 2010]. Indeed, we here found evidence for this relationship, as low wood density trees showed a trend of increased tree mortality during the 2009/2010 El Niño period ($F = 2.33$, $p = 0.06$, data not shown).

Moreover, it was reported that long-term drought-induced shifts in the functional composition of tropical forest trees in favor of drought-tolerant species were associated with an increase in aboveground biomass [Fauset *et al.*, 2012]. Similar findings of increasing biomass over recent decades in other African [Lewis *et al.*, 2009] and Amazonian forests [Phillips *et al.*, 2009] suggest that despite such long-term droughts, these forests are capable to maintain their C stocks due to compositional shifts of tree species in response to low-intensity disturbances [Fauset *et al.*, 2012]. However, during more extreme and short-term droughts, increased tree mortality dominates the proposed long-term natural selection effects and thus causes substantial decreases in aboveground biomass [Fauset *et al.*, 2012].

Therefore, our findings of differential responses of tropical ANPP between lowland forest sites could be based on differences in the composition and thus functional trade-offs among life history strategies of tropical tree species. Indeed, earlier studies conducted at the same set of sites have found pronounced differences (92–99%) in the composition of tree species [Hofhansl *et al.*, 2011] and reported differences in site-averaged wood density for primary ridge (PRI; 0.57 g/cm^3), secondary ravine (SRA; 0.54 g/cm^3), and primary ravine (PRA; 0.52 g/cm^3) forest sites [Hofhansl, 2014]. Although the primary ridge forest with the highest mean wood density faced the strongest reductions in WP (PRI; -35%) compared to the lower wood density secondary (SRA; -26%) and ravine forest site (PRA; -26%), it also most strongly recovered by more than twofold (PRI; $+83\%$) compared to the secondary (SRA; $+41\%$) and ravine forest site (PRA; $+31\%$) after the drought anomaly. Our findings therefore likely relate to the inverse effects of topography on edaphic parameters (water availability) as well as on life history strategies (drought tolerance) among tropical tree species that eventually determine the site-specific sensitivity of tropical lowland ANPP to climate anomalies. It is therefore plausible that the greater climate sensitivity of low-density trees at the moist ravine forest site (PRA) was buffered via high soil water availability and less temperature fluctuations, whereas high wood density trees at the more exposed ridge forest site (PRI), though being better adapted to droughts, were more prone to anomalous climate extremes. This further indicates that on the one hand, local topography and water availability override functional adaptations of tropical tree species in terms of drought tolerance but on the other hand highlights that drought-adapted communities show a higher degree of resilience and recovery after such climate excursions.

Overall, these results suggest that (1) the proximate short-term tolerance to the strong El Niño drought period is predetermined by topoedaphic factors such as soil water availability and that (2) the functional adaptation of the respective tree community could potentially compensate short-term disturbances via drought-induced shifts in tree species composition that further regulate the long-term sensitivity of tropical lowland rainforests to climate anomalies.

5. Conclusions

Predicted changes in tropical climate are stated to result in intermittent precipitation events and increasing temperatures, causing prolonged periods of drought and thus water deficit [Prentice *et al.*, 2007]. Such

climate excursions and long-term climate change might shift the C balance of tropical rainforest ecosystems toward decreased wood production and thus decrease the C stocks of high productive lowland forests.

While short-term climate extremes generally trigger increased tree mortality, long-term responses to periodic climate anomalies are related to species turnover and thus compositional shifts of the remaining tree species community. This indicates that tropical lowland forests are on the one hand prone to climatic changes, but on the other hand exhibit the potential to maintain their C stocks by shifting tree species composition in favor of drought-tolerant species.

Our findings of site-specific differences in drought sensitivity suggest that changes in future climate could differentially affect the C sequestration potential of tropical lowland rainforests, i.e., primary versus secondary forests as well as uphill versus downslope forests due to differences in local resource availability and tree species composition.

Therefore, the spatial diversity of tropical lowland rainforests—associated with differences in soil moisture and forest disturbance—will likely prevent uniform responses of tropical lowland net primary production to projected global changes and highlights the need of further high-resolution and long-term studies in tropical forest ecosystems.

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