

RESEARCH ARTICLE

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Key Points:

- NPP in a tropical dipterocarp forest was estimated over 3 years
- Soil factors did not explain spatial variation
- The forest is drought resilient with regard to NPP

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Partial net primary production of a mixed dipterocarp forest: Spatial patterns and temporal dynamics

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Abstract We examined how and why partial net primary production (NPP_{part}) varies across time and space in a Chinese dipterocarp forest. We hypothesize that (1) soil geochemistry explains the spatial pattern of NPP_{part} within the plot and (2) NPP_{part} can be used to measure the degree of drought resilience of a natural forest. Spatially, NPP_{part} was autocorrelated in the range of 75.3 m and homogenous. This spatial pattern could not be well explained by any of the soil properties individually or in combination. If drought sensitivity is defined by marked reduction in NPP_{part}, the studied forest is drought resilient even when a longer and drier than usual drought hit. Although annual NPP_{part} was unchanged (vary within 18.24 and 18.52 t ha⁻¹ yr⁻¹) after the drought, the allocation of NPP_{part} to short-lived litterfall increased, which has further effects on the ecosystem net carbon balance.

1. Introduction

Forests are important and persistent carbon sinks which can mitigate climatic warming [Pan *et al.*, 2011]. To quantify carbon sink capacity, we measure the difference between net primary production (NPP) and heterotrophic respiration [Schulze *et al.*, 2000]. A well-quantified NPP can help determine the global location and magnitude of carbon sinks. Furthermore, NPP feeds most heterotrophic organisms on earth, including human beings. Therefore, NPP has remained an important area of research since its initial description around one century ago [Boysen-Jensen, 1932].

Tropical forests occupy only 22% of the world's potential vegetation area [Melillo *et al.*, 1993], but they have been estimated to account for 43% of the world's potential terrestrial NPP [Field *et al.*, 1998]. Thus, a tropical forest has a disproportionately large impact on the global carbon cycle and climate mitigation. However, the mechanistic underpinnings of tropical forest NPP remains little known, especially in Africa and Asia [Malhi *et al.*, 2011; Kho *et al.*, 2013].

NPP provides a comprehensive index which incorporates several key ecosystem processes, including photosynthetic production, respiration loss, and carbon allocation. Variation in regional NPP can indicate changes in ecosystem stability and health [Tilman *et al.*, 2006]. NPP is the new organic matter carbon produced during a certain period (usually a year) [Fahey and Knapp, 2007]. In theory NPP can be estimated as the difference between gross primary production (GPP) and autotrophic respiration (R_A) [Gower *et al.*, 2001]:

$$\text{NPP} = \text{GPP} - R_A \quad (1)$$

However, NPP is not estimated using this “top-down” approach because GPP cannot be measured directly and autotrophic respiration is difficult to measure [Gower *et al.*, 2001]. It is especially impractical to assess NPP with “top-down” methods in multispecies forests, which are predominantly composed of large and tall trees. A common way in estimating forest NPP is a “bottom-up” approach which adds each NPP component sequentially [Clark *et al.*, 2001a]:

$$\text{NPP} = \text{NPP}_{\text{woody}} + \text{NPP}_{\text{canopy}} + \text{NPP}_{\text{fineroot}} + \text{NPP}_h + \varepsilon \quad (2)$$

where NPP_{woody}, NPP_{canopy}, NPP_{fineroot}, NPP_h and ε are woody, canopy, fine-root, and herbivore-consumed NPPs and residual term, respectively.

In practice, few NPP components are measured empirically in field studies, especially in native forest ecosystems [Clark *et al.*, 2001a]. Instead of providing a fully accounted NPP, most studies only quantify the

easily measured components, i.e., aboveground litterfall, and coarse woody biomass increment and therefore derive a partially biometric NPP (NPP_{part}) [Clark *et al.*, 2001a; Malhi *et al.*, 2011]. The result of lacking empirical data on other NPP components prevents accurate calculation of the true carbon budget for natural forest systems [Luyssaert *et al.*, 2007; Kho *et al.*, 2013].

Field-derived measurements of NPP have frequently been reported as the annual budget of various ecosystems [Clark *et al.*, 2001b]. How and why NPP varies over space and time are largely unknown and rely on indirect inferences from satellite-based vegetation indices [Goetz *et al.*, 2000; Hicke *et al.*, 2002]. Knowledge of field-derived temporal dynamics of NPP is critical to validate, calibrate, and provide mechanistic explanations of remotely sensed analyses of NPP. One example of the importance of the use of ground-based calibration of remotely sensed NPP data is the Amazon rainforest. Based on satellite data Amazon forests were found “green-up” during severe drought [Saleska *et al.*, 2007]; however, ground-based inventory data showed that drought caused additional carbon losses in tropical forests [Phillips *et al.*, 2009]. In recent years spatial and temporal issues with sensor calibration of satellites have led to conclusions on changes in NPP for various regions, which were later found to be due to sensor inaccuracies [Samanta *et al.*, 2010]; therefore, ground-based calibration is critical in order to obtain robust and reliable data.

Spatially, studies frequently regard NPP as relatively homogenous at the plot level; however, this hinders a mechanistic understanding of the drivers of NPP at a realistic ecological scale [Raich *et al.*, 1997; Sierra *et al.*, 2007]. There is very little empirical knowledge of how NPP varies within a plot, whether it shows autocorrelation, and, if so, what are the drivers of such spatial patterns. This information is, however, necessary in both to provide a solid and reliable measure of NPP and in order to use NPP as a surrogate measure of other ecological processes and patterns, such as biodiversity.

Former studies attribute variation in NPP at a landscape level to a number of environmental processes, including various climatic processes, in addition to topographic and soil factors. Soil fertility and biomass were regarded as two major factors which control the spatial variation of NPP at a regional scale [Malhi *et al.*, 2006; Vicca *et al.*, 2012]. Such factors influence the volume of moisture and the availability of nutrients to growing plants, and thus, on the local scale, soil and biomass are likely to be major drivers of NPP variability. Therefore, we examined whether soil fertility and biomass could explain the within-plot variation of NPP in this study.

In Southeast Asia dipterocarp family trees dominate primary tropical rainforests [Yoda, 1974; Whitmore, 1984]. However, most studies on dipterocarp forest have been carried out in equatorial areas with plentiful rainfall all year and little or no water stress (except for decadal El Niño-associated droughts) [Kho *et al.*, 2013]. Little is known about dipterocarp forest at the northern edge of its natural distribution, at around 23.4° latitude and on the very edge of the Southeast Asian tropics. These northern dipterocarp forests must withstand strongly seasonal climates, including periodic droughts and monsoons, as it is at the very edge of its natural range this forest is expected to be especially resilient to climatic perturbations and changes.

To explore temporal variation in NPP within testing natural conditions, we calculated the NPP of a natural forest dominated by Chinese dipterocarp (*Parashorea chinensis*) (located in Xishuangbanna prefecture of Yunnan province) over three years (2010–2012). We attempt to fully quantify all aspects of NPP (except the residual term), for the forests of the region. Our major aim is to know how and why NPP varies across time and space in order to understand the spatiotemporal factors responsible for variation in NPP. Specifically, we tested two hypotheses: (1) soil geochemistry does explain the spatial pattern of NPP within the plot and (2) NPP can be used to measure the degree of drought resilience of a natural forest.

2. Methods

2.1. Study Site

Our study took place in a dipterocarp forest on the northern edge of tropical Southeast Asia, in Mengla County, Xishuangbanna prefecture, Yunnan Province, China, at 21°37'N, 101°35'E. The mean annual rainfall is approximately 1500 mm in the region (Figure 1), but the rainfall is unevenly distributed seasonally. More than 87% of the total annual rainfall occurs from May to October. The remaining 13% (195 mm) occurs in the dry half of the year, when the monthly total rainfall is usually less than 50 mm.

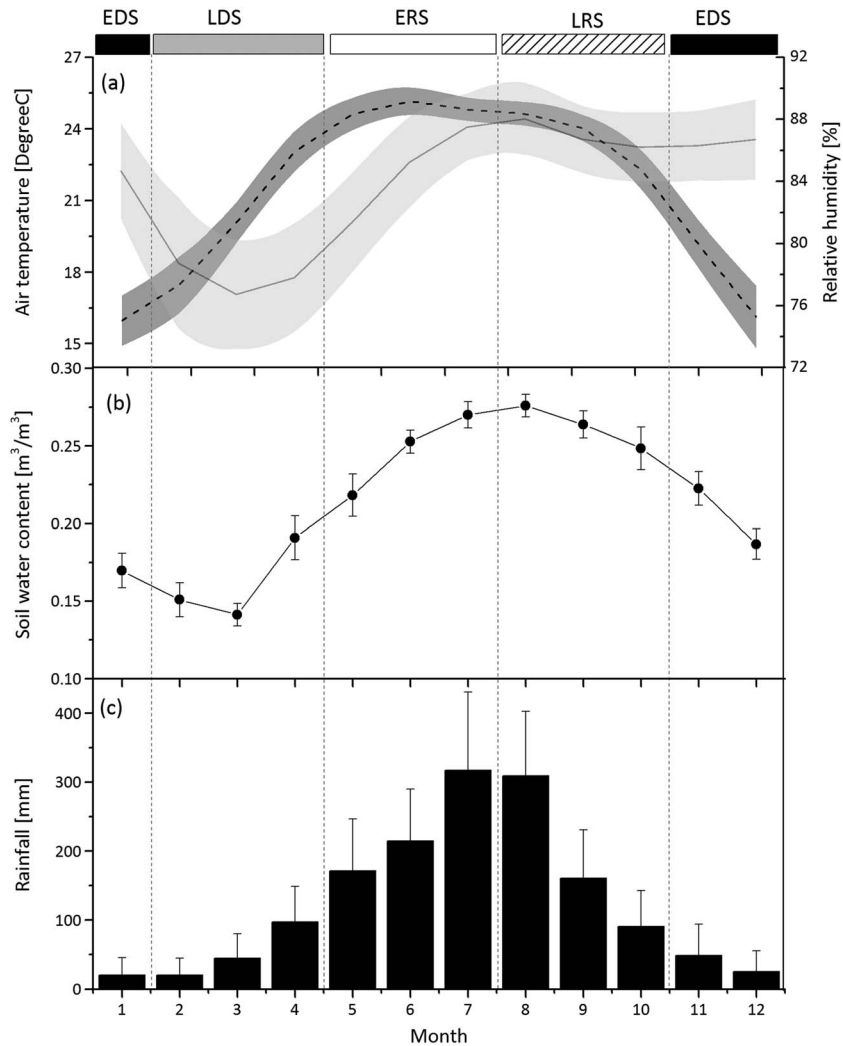


Figure 1. Regional climatic pattern. (a) Temperature (dashed line) and relative humidity (solid line). (b) Soil water content. (c) Monthly rainfall. EDS, early dry season; LDS, late dry season; ERS, early wet season; LRS, late wet season. Data presented here are collected from a climatic station 70 km away.

The mean annual air temperature is 21.8°C, and the annual range of air temperature is up to 10°C. The coldest monthly average temperature is below 15°C; however, cold fronts can cause short temperature drops to 2–4°C. The forest canopy has multiple layers and is structurally complex, aiding the ability to buffer changes in temperature and humidity. A closed canopy exists at 25–35 m, while emergent trees (mostly *Shorea wantianshuae*) reach 50–60 m [Lan et al., 2008]. The mean basal area for trees with diameter at breast height (DBH) of above 1.0 cm is 42.34 ha⁻¹.

2.2. The 20 ha Plot

A 20 ha permanent plot was established for studying the structure and dynamics of the dipterocarp rainforest in 2007. The plot is 400 × 500 m² and covers an elevation gradient from 709 to 869 m above sea level, with the highest elevation located in the northwest (Figure 2). Three perennial streams join at the southwest of the plot.

All trees with DBH larger than 1 cm were tagged with sequentially numbered aluminum tags. DBH was measured at a height of 1.3 m above ground, except for buttress trees. In the case of buttress trees, we measured the nearest point where the stem was cylindrical. Trees with multiple stems were counted as a single individual, but each stem was tagged and measured [Condit, 1998]. The plot was divided into 500

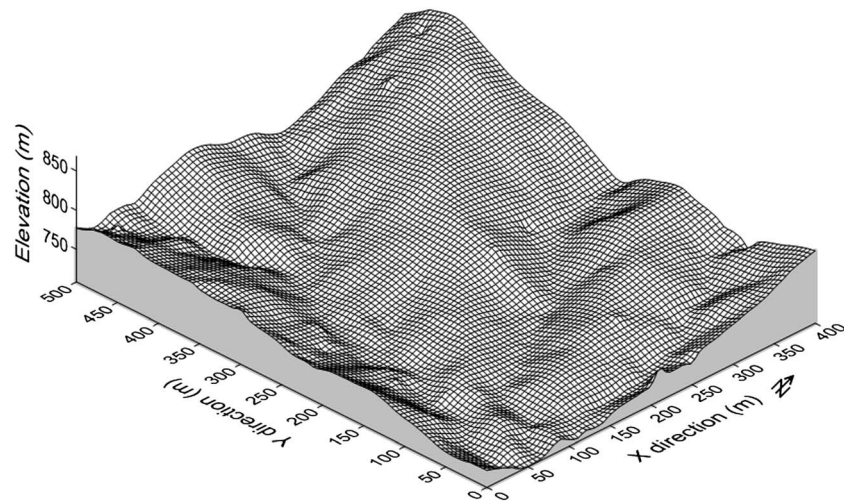


Figure 2. The terrain of the 20 ha big plot in Bubeng, Xishuangbanna, China.

subplots, $20 \times 20 \text{ m}^2$ each. All trees were identified to the species level based on the English version of “Flora of China.” A total of 70 plant families, 213 genera, 468 species, and 95,834 individuals were recorded in the 20 ha plot. The 10 most dominant plant species were *Pittosporopsis kerrii*, *Shorea wantianshuae*, *Garcinia cowa*, *Castanopsis echinocarpa*, *Mezzettiopsis creaghii*, *Sloanea tomentosa*, *Baccaurea ramiflora*, *Knerna furfuracea*, *Pometia tomentosa*, and *Phoebe lanceolata*. Specimens were collected for each species, and vouchers were stored at the herbarium of the Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences [Lan et al., 2008].

2.3. Dendrometers and Litterfall Traps

Dendrometers were installed on 2763 individual trees, including 2000 that were selected at random and 763 selected according to species (to obtain maximum diversity encountered within the plot). The dendrometers consist of stainless-steel spring strips in which a window has been left. The initial width of this window was recorded, and as tree diameter increased the window widens and is measured with a vernier caliper every 3 months (at the beginning of February, May, August, and November). Taking both the local climate (Figure 1) and our investigation time into consideration, we defined November, December, and January as early dry season; February, March, and April as late dry season; May, June, and July as early wet season; and August, September, and October as late wet season.

Litterfall (L) was sampled with square litter traps ($0.75 \times 0.75 \text{ m}^2$) located in the center of 151 of the 500 subplots; these subplots were selected randomly. The litter traps consisted of nylon netting (mesh size, 1 mm) supported by four PVC poles; the effective area of each trap, discounting the frame edges, was 0.5 m^2 . Litterfall was collected every 2 weeks to avoid significant losses to decomposition. All litter was transferred to the laboratory, where it was separated by type into leaf, twig, reproductive parts, and miscellaneous, after which it was dried and weighed.

2.4. Soil Sampling and Laboratory Analysis

Soil was systematically sampled, by dividing the whole 20 ha plot into a grid of $30 \times 30 \text{ m}^2$, which generated 252 base points. At each base point one sample was recorded in addition to two extra sampling points, which were selected randomly from the combinations of 2 m and 5 m, 2 m and 15 m, and 5 m and 15 m along a random compass bearing from the associated base point. At each point, we sampled 500 g topsoil (0–10 cm), which gave a total of 756 samples.

Soil physical and chemical analysis is conducted according to a Chinese textbook [Bao, 2008]. Soil water content (SWC) and soil temperature (Ts) were measured using a drying method and a portable sensor. The pH levels were measured using fresh soil samples. A small sample of soil was collected, and an indicator solution was added to form a paste. The paste was then coated with barium sulfate powder, which changes color depending on the pH of the soil. Finally, pH was determined by comparing the color with a color chart.

Soil bulk density (BD) was determined with the corer method. The $\text{H}_2\text{SO}_4\text{-K}_2\text{CrO}_7$ oxidation method was used to measure soil carbon content (TC). Total (TN) and available nitrogen (AvN) were measured using the micro-Kjeldahl method and the microdiffusion method, respectively. Total phosphorus (TP) and potassium (TK) were measured using an inductively coupled plasma atomic-emission spectrometer (Thermo Jarrell Ash Co., Franklin, USA) and $\text{HNO}_3\text{-HClO}_4$ soil solution. Available phosphorus (AvP) was estimated colorimetrically based on a $0.03 \text{ mol L}^{-1} \text{ NH}_4\text{F}$ and $0.025 \text{ mol L}^{-1} \text{ HCl}$ soil solution. Available potassium (AvK) was extracted from a neutral $1 \text{ mol L}^{-1} \text{ CH}_3\text{COONH}_4$ solution analysis by using the same method as used for total potassium.

2.5. NPP Calculations

2.5.1. NPP and NPP_{part}

NPP was estimated according to equation (2). We defined a partial NPP (NPP_{part}) as

$$\text{NPP}_{\text{part}} = \text{NPP}_{\text{woody}} + \text{NPP}_{\text{canopy}} \quad (3)$$

NPP_{part} is close to but not equal to aboveground NPP since coarse-root production has been included.

2.5.2. $\text{NPP}_{\text{woody}}$

Woody NPP was also denoted as biomass increment (ΔB) [Clark *et al.*, 2001a; Gower *et al.*, 2001]. It was calculated as

$$\text{NPP}_{\text{woody}} = \Delta B = M_{i+1} - M_i \quad (4)$$

where M_i and M_{i+1} are biomasses at i and $i + 1$ inventories. Biomass (M) was estimated with tree size data (based on diameter at breast height, DBH) and site-specific allometric equations as

$$M = 0.1102 (\text{DBH})^{2.5246} \quad (5)$$

Biomass volume is the sum of biomass in branches, stems, and coarse root in kilograms, and DBH is diameter at breast height in centimeters. This allometric equation was derived from 46 *Parashorea chinensis* tree samples [Tang *et al.*, 2008] and 123 other sample trees [Lv *et al.*, 2007]. Site-specific allometric equations that include tree height are also available [Feng *et al.*, 1998]. However, reliable tree height measurements were not available to us, especially for the tall canopy of up to 60 m, so we chose to use the single DBH-dependent allometric equation.

Since not all the trees (over 90,000 individuals with DBH more than 1 cm in the 20 ha plot) had mounted dendrometers, we estimated total ΔB in the plot from the 2763 dendrometers with the following equation:

$$\Delta B = \frac{\sum (M_{i+1} - M_i) M_d}{t \cdot 20} \frac{M_d}{M_{20}} \quad (6)$$

where M_i or M_{i+1} is biomass at time t or time $t + 1$ in months, \sum indicates the sum of biomass increments for all trees with dendrometers, t is time (months), 20 is a coefficient to scale the equation to a 1 ha area, M_d is the total biomass of trees with dendrometers, and M_{20} is the total biomass of the entire 20 ha plot.

We made some corrections to the dendrometer data before calculating the biomass increment. We first calculated the relative growth rate (RGR) as

$$\text{RGR} = [(\text{WSZ}_{i+1} - \text{WSZ}_i) / (3\pi)] / \text{WSZ}_i \cdot 100 \quad (7)$$

where WSZ is the width of window left in dendrometer. Then, we removed values larger than the 95th percentile and smaller than the 5th percentile of the relative growth rate in the period. This step removed noisy data that might have been caused by recording or data entry errors.

2.5.3. $\text{NPP}_{\text{canopy}}$

$\text{NPP}_{\text{canopy}}$ was usually regarded as aboveground litterfall production (L) and is calculated as the sum of litter collected in the trap. Short-lived plant material such as leaf litter will be shed and produced within a year [Clark *et al.*, 2001a]. Thus, litterfall cannot capture the seasonal dynamics of leaf production because it reflects the timing of dry-matter loss rather than production [Kho *et al.*, 2013]. In order to obtain seasonal dynamics of NPP_{part} , we calibrated litterfall with a leaf area index (LAI) following the method of Doughty and Goulden [2008]. In the calibration, leaf produced in a specific interval is the sum of changes in LAI and litterfall captured by trap,

$$L^* = \frac{d\text{LAI}}{\text{SLA}} + L \quad (8)$$

where L^* is calibrated litterfall production for estimating seasonal dynamics of NPP_{part} ; LAI is a leaf area index, which was measured with a canopy analyzer (LAI-2000, Li-Cor., USA) in another forest in the same

region [Lin et al., 2011]; d is the differences between months; and SLA stands for specific leaf area, for which we used the mean value of 426 samples collected in the same 20 ha plot [Yang et al., 2014].

2.5.4. NPP_{fineroot} and NPP_h

We did not quantify fine-root NPP (NPP_{fineroot}) or herbivore-consumed NPP (NPP_h) experimentally in this study but adopted experimental results from another primary rainforest under the same climate, 70 km away in the same region. Thirty soil cores were sampled from three plots four times annually to estimate NPP_{fineroot}. It was estimated according to the method of McClaugherty et al. [1982] and reported to be 3.77 t ha⁻¹ yr⁻¹ [Fang and Sha, 2005]. NPP_h was estimated with the method according to Proctor et al. [1983]. A 0.2 m² circle was used to sampling leaf litter on the forest floor. The proportion of loss from each leaf was graded by severity: 0%, 1–20%, 21–40%, 41–60%, 61–80%, and more than 80%. NPP_h estimated from a total of 816 leaves samples was 1.82 t ha⁻¹ yr⁻¹ [Zheng et al., 1990].

2.6. Geostatistics

Geostatistics were used to reduce the effects of autocorrelated data and to quantify the degree of heterogeneity prior to interpolation [Xu, 2002]. Variogram analysis was used to analyze spatial data to (1) determine whether data were spatially correlated and to what extent they are autocorrelated; (2) quantify the degree of heterogeneity; (3) interpolate all variables (ΔB , litterfall, and soil properties) to all 20 ha with 20 × 20 m² resolution.

Semivariance (γ), a key variable in variogram analysis, is calculated as

$$\gamma(h) = \frac{1}{2N} \sum_{i=1}^{N(h)} [y(i) - y(i+h)]^2 \quad (9)$$

where $y(i)$ is the value of the variable y at point i , $y(i+h)$ is its value at a point at a lag distance h , and $N(h)$ is the number of observation points separated by the distance h . An exponential model was fitted to the semivariance to estimate structure parameters such as range, nugget variance, and sill.

The isotropic fractal number (D) was calculated to quantify the degree of heterogeneity. The isotropic fractal number is a measure of the relative balance between long- and short-range sources of variation and usually estimated from the slope of a double logarithmic plot of the semivariance [Burrough, 1983]. Specifically, the isotropic fractal number was calculated based on the following relationship:

$$2\gamma(h) = h^{4-2D}. \quad (10)$$

After variogram analysis, all variables were extrapolated to 20 ha using Kriging method. Kriging interpolation is given as

$$Z_X^* = \sum_{i=1}^n \lambda_i Z(X_i). \quad (11)$$

where Z_X^* is the predicted value and λ_i is the weight of observation $Z(X_i)$. λ_i is calculated with minimum variance.

2.7. Multivariate Statistics

All statistical analyses used MATLAB software version 7.1. We used principal component analysis (PCA) to explore variation in soil geochemical properties and NPP_{part} after normalizing all variables using princomp.m in MATLAB. PCA is a well-known method in data reduction [Xu, 2002]. It extracts a smaller set of underlying new variables that are uncorrelated, orthogonal, and represented by linear combinations of original variables. These new variables, usually denoted as principal components (PCs), are calculated to explain the majority variance of an original data set.

Stepwise regression was used to identify appropriate explanatory equations using stepwise.m in MATLAB. STR is widely used for model selection [Xu, 2002]. In a large set of candidate predictor variables, stepwise regression could be helpful in finding a simple but good predictive model.

3. Results

3.1. Spatial Pattern of NPP_{part} and Its Relations to Soil Properties

The spatial pattern of NPP_{part} was generally not consistent with that of terrain as expected (Figures 2 and 3). The direct spatial correlation between NPP_{part} and elevation was -0.279 ($P < 0.0001$). This suggested that NPP_{part} was significantly higher at lower elevations within the plot (i.e., streams) than in higher ones

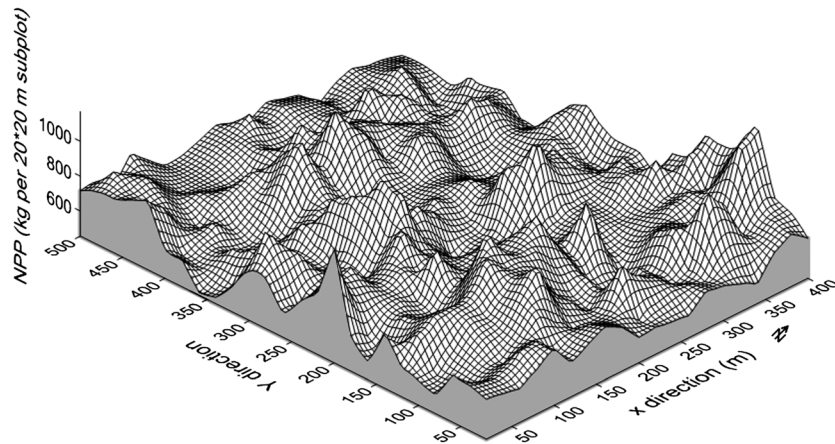


Figure 3. The spatial pattern of partial net primary production (NPP_{part}) interpolated by Kriging method.

(i.e., ridges). However, terrain could only explain a small part of the spatial pattern, as indicated by the low correlation. Spatially, NPP_{part} was normally distributed (fitted by a three-parameter Gaussian equation with $P < 0.0001$). The mean NPP_{part} for each $20 \times 20 m^2$ subplot was 704 ± 115 kg (coefficient of variance at space, CV: 16.33%). Though NPP_{part} varied from 468 to 1190 kg among these subplots, 95% of NPP_{part} fell between 525 and 925 kg.

NPP_{part} was autocorrelated in the range of 75.3 m, as shown by variogram analysis (Figure 4 and Table 1). The autocorrelation range (scale) was similar to that of pH (90.6 m) and larger than that of soil nutrients (i.e., soil carbon, 19.8 m; nitrogen content, 26.4 m; available nitrogen, 20.5 m; phosphorus, 31.8 m; and potassium, 37.5 m). The degree of spatial heterogeneity is reflected by the isotropic fractal number, and the sill proportion [Burrough, 1983] for NPP_{part} is at median status compared with other soil properties (Table 1).

NPP_{part} was poorly correlated with each soil property individually (Pearson's $|r| < 0.3$; Table 2). From PCA we selected three principal components based on the contribution ratio (Table 3). None of these three components were highly correlated with normalized NPP_{part} (Figure 5). Stepwise regression produced the following explanatory equation:

$$NPP_{part} = -0.197AvP + 0.255pH + 0.117SWC + 0.220M \quad (r = 0.335, P < 0.01) \quad (12)$$

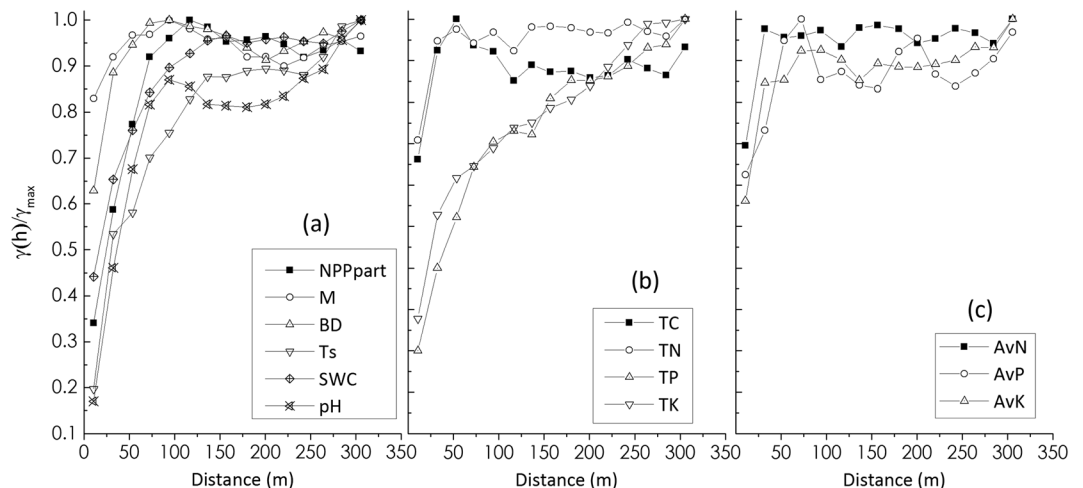


Figure 4. Normalized semivariance of partial net primary production (NPP_{part}) and related soil physical and chemical variables.

Table 1. Structure Parameters (Range (Γ), Sill Proportion (η), and Isotropic Fractal Number (D)) of Partial Net Primary Production (NPP_{part}) and Related Soil Properties After a Variogram Analysis

Dependent	NPP_{part}	$\Gamma(m)$ 75.3	η 0.701	D 1.877
Soil chemical and physical properties	pH	90.6	0.980	1.790
	BD	34.5	0.904	1.955
	Ts	171.6	0.906	1.794
	SWC	129.0	0.706	1.890
	TC	19.8	0.973	1.979
	TN	26.4	0.905	1.965
	TP	275.4	0.866	1.780
Available soil nutrients	TK	411.6	0.709	1.827
	AvN	20.5	0.971	1.976
	AvP	31.8	0.940	1.957
	AvK	37.5	0.907	1.944

The low correlation reflected by the low r value supports that soil properties cannot well explain the spatial pattern of NPP_{part} directly.

We examined the main controller of NPP_{part} in the autocorrelated range by analysis of the semivariances (Figure 4). Stepwise regression produced the explanatory equation:

$$NPP_{part} = 0.461pH + 1.005SWC - 0.529TK$$

$$(r = 0.992, P < 0.01) \quad (13)$$

Soil water content and pH play roles in both direct spatial correlations and

correlations in the autocorrelated range. Since soil water content and pH were not correlated (Pearson's $r = 0.020$), the effects of soil water content and pH on the spatial pattern of NPP_{part} can be regarded as independent. The negative contribution of AvP to spatial NPP_{part} might result from correlation between AvP and pH ($r = 0.668$).

3.2. Temporal Dynamics of NPP_{part}

The climate is strongly seasonal in the study region (Figure 1a). Temperature is higher in the wet season than in the dry season. The warm climate in the wet season benefits tree growth and leads to a higher biomass increment (ΔB) in that period (Figure 6a). The lower ΔB in the dry season is caused by temperature or water limitation or both. In the late dry season, temperature rises and reaches a near-peak value at the end of the subseason. In this period, the water vapor pressure deficit peaked (Figure 1a, solid grey line), while soil water content (Figure 1b) was at its lowest level. Generally, ΔB is higher in the late dry season than in the early dry season (the later compared with early point in the dashed area in Figure 6a), except in the dry season of 2010. This suggests that the major limiting factor on ΔB in the dry season is temperature, rather than water. If water was the major limiting factor, lower ΔB would be expected in the late dry season, since the lowest soil water content and the highest vapor pressure deficit occurred in that period. ΔB was higher in the early dry season than in the late dry season in 2010 (Figure 6a), in contrast to the following two years. There was a prolonged regional drought during 2009–2010 (Figure 7) (see Qiu [2010] for a detailed report). In the prolonged drought, ΔB was further inhibited and showed its lowest value for the observation period. Temperature is generally the major controlling factor on ΔB . In the prolonged drought, water limitation becomes more important and can shift the usual ΔB temporal dynamics.

The canopy shed litter all year in the evergreen forest (Figure 6b), but litterfall was not distributed evenly through the year. There was obvious seasonal dynamics, with an intensive litter shed period in the late dry

Table 2. The Pearson Correlation Matrix for Partial Net Primary Production (NPP_{part}) and Related Soil Variables

	NPP_{part}	M	BD	Ts	SWC	pH	TC	TN	TP	TK	AvN	AvP	AvK
NPP_{part}	1.000												
M	0.224	1.000											
BD	0.114	0.071	1.000										
Ts	-0.056	-0.097	-0.076	1.000									
SWC	0.167	0.001	0.207	-0.122	1.000								
pH	0.166	0.182	0.355	-0.461	0.020	1.000							
TC	-0.091	0.004	-0.619	0.044	-0.287	0.173	1.000						
TN	-0.034	0.047	-0.426	-0.220	-0.355	0.396	0.803	1.000					
TP	0.104	0.137	0.162	-0.390	-0.077	0.810	0.360	0.642	1.000				
TK	0.054	-0.083	-0.070	-0.266	0.059	0.204	0.104	0.340	0.422	1.000			
AvN	-0.012	0.059	-0.431	-0.133	-0.251	0.338	0.813	0.897	0.607	0.242	1.000		
AvP	-0.005	0.220	0.106	-0.206	-0.227	0.668	0.393	0.486	0.729	0.007	0.478	1.000	
AvK	0.041	0.133	0.083	-0.312	-0.071	0.643	0.238	0.447	0.670	0.441	0.399	0.465	1.000

Table 3. Component Matrix for Principal Component Analysis^a

	PC ₁ (38.897%)	PC ₂ (19.989%)	PC ₃ (10.841%)
<i>M</i>	0.161	0.206	0.476
<i>BD</i>	-0.179	0.828	0.210
<i>Ts</i>	-0.380	-0.431	0.314
<i>SWC</i>	-0.259	0.403	-0.380
<i>pH</i>	0.714	0.571	0.128
<i>TC</i>	0.677	-0.632	0.054
<i>TN</i>	0.874	-0.375	-0.066
<i>TP</i>	0.880	-0.341	-0.005
<i>TK</i>	0.405	0.130	-0.731
<i>AvN</i>	0.830	-0.410	-0.015
<i>AvP</i>	0.734	0.208	0.453
<i>AvK</i>	0.708	0.336	-0.152

^aPC₁-PC₃: the first three components selected according to contributions (values in the parentheses).

season (Figure 6b). The lowest litterfall occurred in the early dry season (around 10 g per trap). Litterfall production (*L*) was around 10–20 g per trap in the wet season and increased to 40–50 g per trap in the late dry season. The intensive litter-shedding time advanced, and the litter amount increased during the prolonged drought in 2010 (Figure 6b and Table 4).

The 3 year mean NPP_{part} was 18.38 ($\pm 0.12/2.99$, interannual/spatial standard deviation (SD)) $t\ ha^{-1}\ yr^{-1}$ (Table 4). The interannual variation in NPP_{part} was slight, from 18.24 $t\ ha^{-1}\ yr^{-1}$ in 2011 to

18.52 $t\ ha^{-1}\ yr^{-1}$ in 2012. The prolonged drought in 2010 did not reduce annual NPP_{part} . The decrease in ΔB was offset by increased litterfall and resulted in a near-constant annual NPP_{part} during the 2010 drought. NPP_{part} was highest in the early wet season (Figure 6c). NPP_{part} in the wet season was higher than in the dry season for calibrated NPP_{part} (Table 4). In contrast, the uncalibrated NPP_{part} was slightly lower in the wet season than in the dry season for the 3 year period except during the 2010 drought.

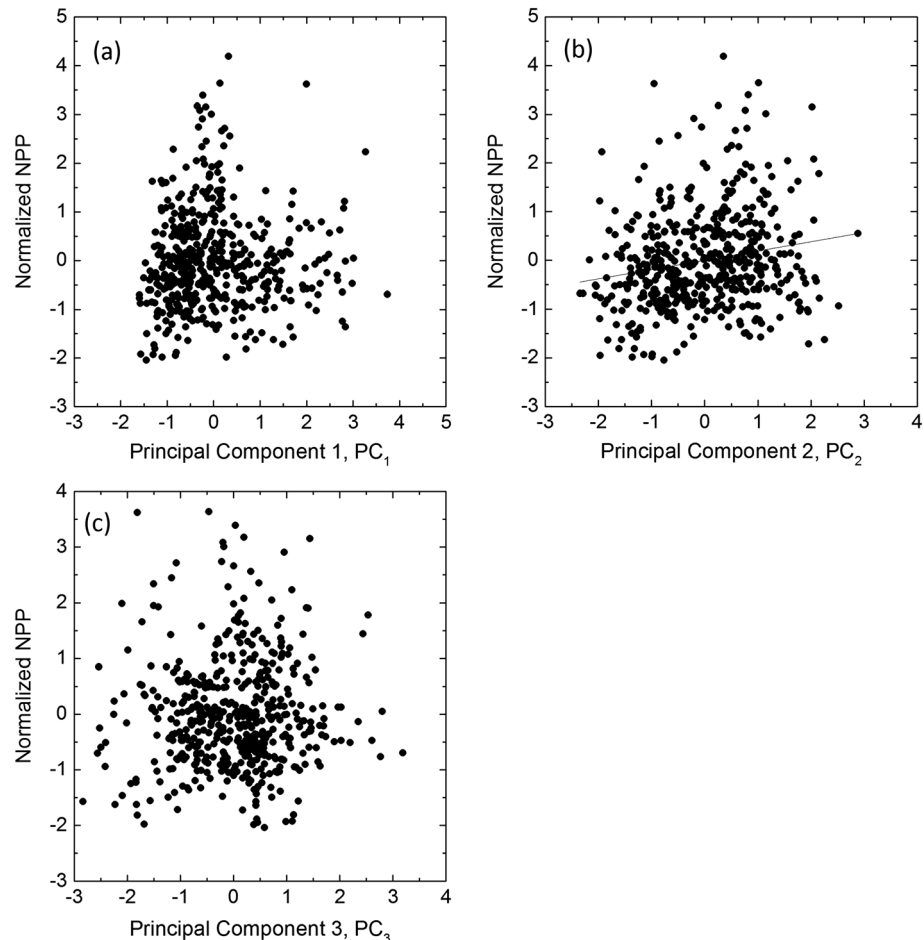


Figure 5. The relationship between normalized partial net primary production (NPP) and the first three principal components (PCs) after principal components analysis (PCA).

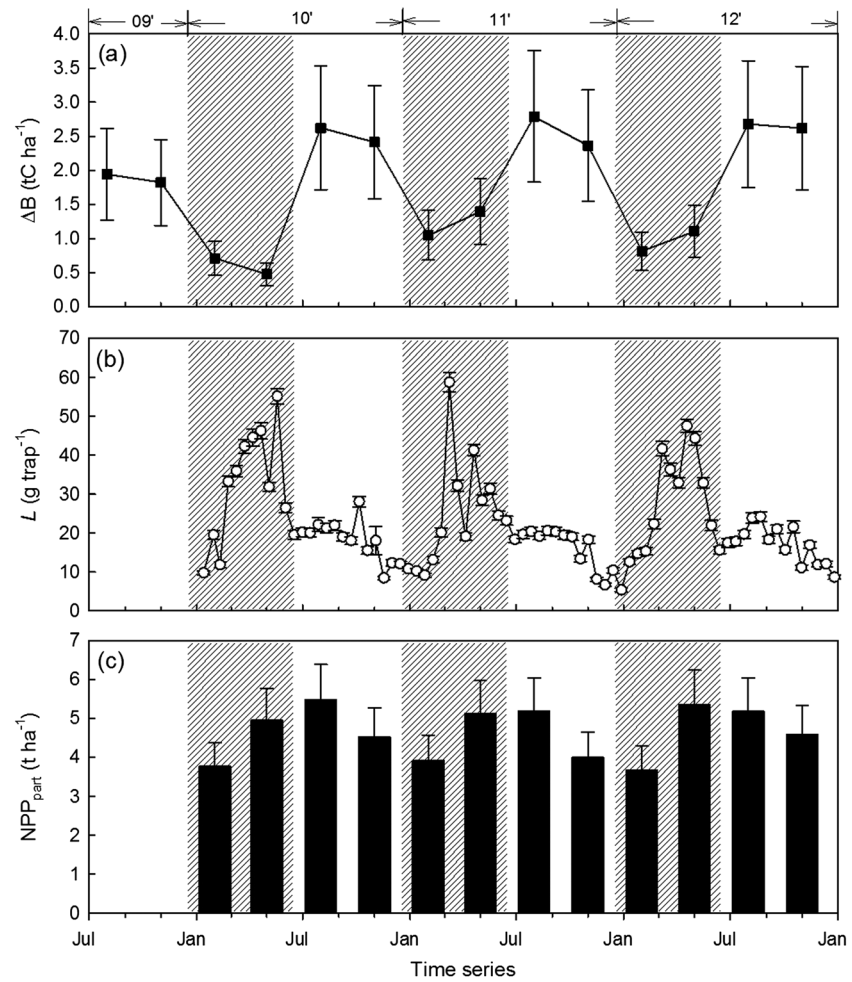


Figure 6. The temporal dynamics of partial net primary production (NPP_{part}) and its components: (a) biomass increment (ΔB), (b) litterfall production (L), and (c) net primary production (NPP_{part}). Dashed area represents climatic dry season.

4. Discussion

The factors which control the forest NPP vary in space and time. Interannual variations of tropical forest NPP is affected by long-term variations in factors such as water availability and light intensity and quality [Nemani et al., 2003]. Spatially, variation of NPP among sites is usually explained by available soil phosphorus and leaf

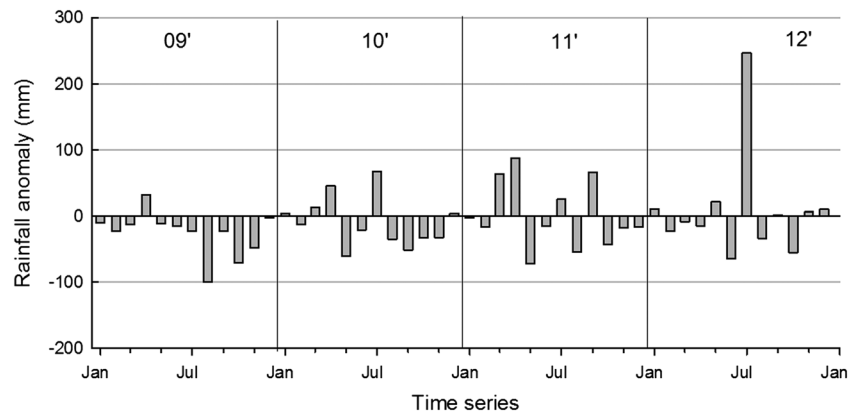


Figure 7. Monthly rainfall anomaly during January 2009 through December 2012 as compared with half a century mean values.

Table 4. Annual and Dry and Wet Season Values of Partial Net Primary Production (NPP_{part}) and Its Components^a

		ΔB	L	L^*	NPP_{part}	$^*\text{NPP}_{\text{part}}$
2010	Dry season	1.19	7.75	6.90	8.94	8.09
	Wet season	5.04	4.55	5.40	9.59	10.44
	Annual	6.22	12.3	12.3	18.52	18.52
2011	Dry season	2.44	7.02	6.17	9.46	8.61
	Wet season	5.15	3.77	4.62	8.92	9.77
	Annual	7.59	10.79	10.79	18.38	18.38
2012	Dry season	1.92	7.32	6.48	9.24	8.40
	Wet season	5.29	3.71	4.56	9.00	9.84
	Annual	7.21	11.03	11.03	18.24	18.24

^aAll values are expressed as tons of dry matter per hectare. ΔB is woody production, L is canopy production, and L^* and $^*\text{NPP}_{\text{part}}$ are leaf area index calibrated L and NPP_{part} , respectively.

nitrogen [Aragão *et al.*, 2009]. Here we analyzed the role of soil physical and chemical factors and functioning on the spatial pattern, in addition to variability in water availability on the interannual dynamics of NPP in a dipterocarp forest near tropical of cancer, and compared our results with previous studies.

4.1. Uncertainties and Reliability of Tropical Forest NPP Estimates

Generally, uncertainties in complete estimated NPP are predominantly associated with measurement methodology, spatial heterogeneity, and temporal heterogeneity [Hanson *et al.*, 2000]. Forest NPP is normally estimated annually [Roxburgh *et al.*, 2005], and the interannual variation of NPP_{part} in our study is slight (with $\text{CV} = 0.7\%$, and negligible uncertainty). Spatial heterogeneity, however, could result in substantial uncertainties in NPP_{part} as shown in the spatial CV (16.3%). Most of the spatial heterogeneity is contributed by $\text{NPP}_{\text{woody}}$ (Figure 6, error bars). We also noticed that the uncertainty of tropical forest NPP estimated from other studies is similar to our study (see Clark *et al.* [2001b] and Aragão *et al.* [2009] for details). This suggests that uncertainties in tropical forest NPP estimate caused by spatial and temporal heterogeneity is generally restrained less than 20%.

Uncertainties associated with methodology are hard to quantify, and we found the bottom-up method to be the only direct way to measure forest NPP (and with no current means to independently validate results). We applied large number of dendrometers (2763) to track tree growth. However, the change of dendrometers window size is not completely due to tree growth but also from changes in stem water storage [Sheil, 2003]. This stem water changes marked by the dendrometer band is an important component of seasonal stem growth, which is rarely accurately incorporated in monitoring [Chitra-Tarak *et al.*, 2015]. We used site-specific allometric equations to convert DBH into biomass. These allometric equations were generated with 169 sample trees, and all determinant coefficients in nonlinear regression are larger than 0.9. Thus, uncertainties caused by this issue are limited. Incorporation of wood density [Chave *et al.*, 2014] may increase the predictive accuracy of these allometric equations. Overall, the best way to quantify uncertainties of bottom-up NPP is to develop independent measures for NPP. Using equation (1) is impractical to calculate NPP [Clark *et al.*, 2001a; Gower *et al.*, 2001]. Advances in methodology, precision of equipment, and combination of GPP from eddy covariance system and autotrophic respiration derived by metabolism theory [Mori *et al.*, 2011] have the potential to provide us alternative solutions for accurate NPP estimation.

4.2. NPP of Dipterocarp Forests and Its Components

The dipterocarp family is most diverse in Southeast Asia, which is famous for its characteristically tall trees, which often dominate tropical forests throughout the Asian region. Initial studies on NPP of dipterocarp forest were conducted in half a century ago [Kira *et al.*, 1967; Kira, 1978]. Though lacking of further detail taking spatial and temporal variation of NPP and its causes, the annual NPP estimated from these studies is substantial and showed high reliability, which advanced little since. We reviewed NPP data in dipterocarp-dominated forests and list them in Table 5. The information in Table 5 illustrates that (i) NPP varied little between sites ($\text{CV} = 12.0\%$); (ii) no clear relationship with latitude can be seen (linear regression $p = 0.45$); and (iii) mean NPP is $2692 \pm 324 \text{ g m}^{-2} \text{ yr}^{-1}$, with more than half (56.8%) is contributed by litterfall production. The mean NPP here for dipterocarp forests is slightly higher than the mean value from 10 tropical forests in Amazon ($2566 \pm 519 \text{ g m}^{-2} \text{ yr}^{-1}$, calculated with 1 g dry matter, which equals 0.5 g carbon [Aragão *et al.*, 2009]).

Table 5. Net Primary Production and Its Components in Dipterocarp Forests of Southeast Asia^a

Site	Country	Latitude	Longitude	<i>M</i>	ΔB	<i>L</i>	MPP _h	NPP _{fineroot}	NPP _{all}	Reference
Xishuangbanna	China	21.60°N	101.56°E	421	700	1137	182	377	2396	This study
Khao Chong	Thailand	7.58°N	99.80°E	334	530	2330	—	—	2860	<i>Kira et al.</i> [1967]
Lambir clay	Malaysia	4.20°N	114.03°E	442	1048	1578	54	392	3178	<i>Kho et al.</i> [2013]
Lambir loam	Malaysia	4.20°N	114.03°E	521	642	1198	42	372	2458	<i>Kho et al.</i> [2013]
Pasoh	Malaysia	2.96°N	102.30°E	426	583	1412	32	400	2570	<i>Kira</i> [1978]
Mean				428	700	1531	77	385	2692	
Standard deviation				66	204	479	70	12	324	

^aBiomass (*M*) is in the unit of tons of dry matter per hectare; production and its components are in the unit of gram dry matter per square meter per year.

However, we still lack data on other ecosystem production terms (i.e., GPP) for SE Asia dipterocarp forests. A further comprehensive assessment on other ecosystem productions, along with NPP, will improve our understanding of ecosystem processes and functioning, and their responses to global climate change [*Malhi et al.*, 2009].

4.3. Plot-Scale Spatial Pattern of NPP_{part} and Its Controls

The spatial pattern of NPP_{part} within a plot is not homogenous [*Fahey and Knapp*, 2007], even though previous studies usually assume uniformity when sampling [*Goulden et al.*, 2011; *Girardin*, 2014]. NPP_{part} shows spatial autocorrelation (Figure 3) and heterogeneity across the region (Table 1). However, these spatial variations could not be well explained by any of the soil physical or chemical properties (Tables 2 and 3). Most interestingly, we failed to find a close positive relationship between available phosphorous and NPP_{part} ($r = -0.005$), even though it has been suggested that tropical rainforest is limited by available phosphorus [*Vitousek*, 1984; *Cleveland et al.*, 2011]; this shows that at least in this region phosphorus availability is not a limiting factor.

The failure to explain the NPP_{part} spatial pattern with soil geochemical properties might result from the following issues:

1. *Within-plot NPP_{part} variation is mainly controlled by factors other than soil properties*, for example, light condition and forest gaps. Forest gap plays an important role in the dynamics of tropical forests by directly changing the light quality and intensity [*Denslow*, 1987]. Species present may also cause significant variations in NPP, and in a forest which may have lost many of its former seed dispersers the resulting clumping of individuals of a single species may cause variability in NPP due to community structure [*Hu et al.*, 2012].
2. *NPP and soil properties have different structure scales*. The autocorrelation range of NPP_{part} was larger than that of the soil nutrients (Table 1). This prevents identifying a direct linear correlation between soil nutrients and NPP_{part} since they have different spatial scales [*Robertson et al.*, 1993].
3. *Failure of sampling design*. Forest soil properties usually are not normally distributed and are more variable than agricultural soils [*Boone et al.*, 1999]. It is difficult to create a sampling design that could adequately describe spatial patterns at different scales. A similar situation also exists for NPP_{part} estimation. The litter captured by each trap was assumed to represent litter in the whole subplot when estimating NPP_{part}; however, this assumption may not always hold true.

Although we were unable to explain the spatial pattern, this was the first attempt to investigate within-plot NPP spatial patterns. We emphasize the importance of this topic, not only because it will favor sampling design for more reliable NPP estimation but also because it is important for understanding ecological processes (e.g., forest dynamics and biodiversity).

4.4. Drought Resilience of the Forest Under the NPP_{part} Perspective

NPP is a frequently used index for ecosystem stability [*Tilman et al.*, 2006]. We addressed the ecosystem stability by examining temporal NPP_{part} across dry seasons and a year when a severe drought hit. If NPP_{part} is significantly reduced during a dry season or dry years, the ecosystem would be regarded as sensitive to drought; if not, it would be considered drought resilient. NPP_{part} was significantly lower during the dry season than during the wet season after litterfall was calibrated (paired *t* test, $P = 0.044$, $n = 3$), although the difference was small (1.65 t ha^{-1}). There was no difference between dry and wet seasons NPP_{part} before

litterfall was calibrated (paired t test, $P = 0.914$, $n = 3$). This shows the necessity of litterfall calibration when studying seasonality of NPP_{part} , on one hand, and indicates that the forest is sensitive to seasonal drought. The interannual variation in NPP_{part} was slight: 18.52, 18.38, 18.24 $\text{t ha}^{-1} \text{yr}^{-1}$ for 2010, 2011, and 2012, respectively. The highest, and not the lowest, NPP_{part} was observed in the driest year (2010), when a regional drought hit (Figure 7). A similar pattern was observed in Bolivian Amazon forests [Doughty et al., 2014], where this phenomenon was attributed to nonstructural carbohydrate use. Overall, from the NPP_{part} perspective, the studied forest is drought resilient to severe regional drought.

Although NPP_{part} was not different in the year when a severe drought occurred, the partitioning of NPP_{part} to ΔB and litterfall did change. In dry years tree growth slowed and dry matter accumulated in biomass reduced from 7.59 and 7.21 to 6.22 $\text{t ha}^{-1} \text{yr}^{-1}$, which was offset by increased litterfall in the corresponding period. A similar pattern was also observed in tropical forests of Costa Rica (Jennifer Powers, personal communication, 2014) and Bolivian Amazon [Doughty et al., 2014]. Thus, trees are able to respond adaptively to water shortages and continue to grow (though more slowly) even when water is limiting.

Although NPP_{part} shows little variation between years, the change in NPP_{part} partitioning has a significant effect on the net carbon balance. Carbon allocated to stem, branch, or coarse-root growth shows a long turnover time, of between several years and decades [Clark et al., 2001a]. Carbon allocated to fine litterfall, however, is short lived or has a short turnover, of between several months and one year. Increasing litterfall may directly increase ecosystem heterotrophic respiration, resulting in more carbon release into the atmosphere [Gatti et al., 2014].

Concerning the drought sensitivity or resilience of a forest ecosystem, it is worth noting which index is used. Consistent with reports from the Amazon rainforest [Phillips et al., 2009], the biomass increment reduced during droughts. If we take biomass increment as the index to indicate drought response, the studied forest would be viewed as drought sensitive. However, if NPP_{part} is the index, the forest is drought resilient; thus, the use of different metrics determines the outcomes of the study and thought using NPP as a metric showed no sensitivity to droughts. The changes in biomass denote an adaptive response to the changing availability of moisture. We prefer NPP as an index on drought sensitivity as we noted it is a comprehensive index including several key ecological processes. Since drought sensitivity of tropical forest is still an open question, a new experiment or a new analysis is suggested to throw some light on this cliffhanger.

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