



## Precipitation influences on the net primary productivity of a tropical seasonal rainforest in Southwest China: A 9-year case study

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### ABSTRACT

The net primary productivity (NPP) of tropical forests is a key part of the global carbon cycle. Numerous studies have estimated tropical forest NPP, yet most of them focus on how annual NPP dynamics vary over several years. Little is known about how NPP responds to long-term climatic variation at the monthly or seasonal scales. We estimated NPP at three-month intervals from 2009 to 2017 for a tropical seasonal rainforest in Xishuangbanna, Southwest China using data from > 2000 dendrometer bands and litter fall traps within a 20-ha permanent forest dynamics plot. We asked which climatic factor has the greatest effect on forest NPP at the sub annual scale, and how the relationships vary with seasonality. Calculations showed that NPP ranged from 12 to 20 t ha<sup>-1</sup> yr<sup>-1</sup>, and that forest productivity showed a slight, but insignificant increase from 2009 to 2017. NPP was significantly higher in the wet season than that in the dry season and was significantly related to precipitation only when all data were concerned. During the dry season, precipitation had a significant positive influence on NPP, but no effect during the wet season. We further identified that there was a threshold effect of precipitation on NPP. Specifically, productivity increased more rapidly when monthly precipitation below 229 mm. In summary, we conclude that periods of low rainfall strongly regulate the productivity in this tropical seasonal rainforest which could guide the management design of water use efficiency in tree based land-use system, like agroforestry ecosystems.

### 1. Introduction

Tropical forests store and cycle almost half of the world's terrestrial carbon (Bonan, 2008; Pan, 2011). Tropical rain forests also play important role in providing vital ecosystem services (Eitzel et al., 2013; Geta et al., 2014). Carbon sequestration, soil, biodiversity and water conservation are the main ecosystem service of tropical rain forest which are safeguarded via proper forest management activities (Miura et al., 2015; Tilman et al., 2012). Forest management is defined as "the proper stewardship of land or forest for more than one purpose, such as wood production, water quality, wildlife, recreation, aesthetics, and clean air" (FAO, 2013). Protecting conserved forest areas (e.g., those in established nature reserves) from anthropogenic disturbance is one of the best forest management practices (Boncina, 2011), which ensuring the provisioning of above mentioned ecosystem services from tropical forest.

One prominent service of protected nature reserved tropical forests is relative high level of net primary productivity (hereafter NPP) than

that of other terrestrial ecosystems (e.g. temperate forests or grasslands) (Skovsgaard, and Vanclay, 2013). NPP is the net amount of organic matter produced by live plants over a specific time interval, and is often based on tree biomass calculations in a given area of forest (Clark et al., 2001a,b). NPP in tropical rainforests alone account for about one-third of total terrestrial NPP (Grace, 2004). NPP often affects terrestrial ecosystem sustainability through its relationships with biodiversity (Liang et al., 2016) and food chain length for various organisms in forest ecosystem (Arim et al., 2007). NPP estimation is important for carbon budget (Kim et al., 2017) and for assessing the dynamics of carbon in forest ecosystems (Baishya and Barik, 2011). Quantifying NPP over time gives forest stakeholders (e.g., forest managers, policy makers and ecosystem service users) an idea of how the ecosystem service potential of a forest is changing. For example, a reduction in forest biomass or NPP over time due to disturbance or other type of ecosystem stressor is directly related to a reduction in forest ecosystem service provisioning, like soil carbon storage capacity (Fischer and Günter, 2019). For these purpose, the United Nations FAO assessed

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global forest biomass change every 5–10 years and discusses its ecological consequences (FAO, 2020). However, the FAO method lacks the spatial and temporal detail, which is key to understand fine scale processes affecting forest productivity.

Inter-annual variation in tropical forest NPP is mostly related to annual variation in climate and long-term climate change. Some satellite-based studies have shown that forest NPP increases with increasing in temperature and precipitation (Hicke et al., 2002; Wang et al., 2016); while others demonstrated that forest NPP has been declining in recent decades (Zhao and Running, 2010). At global scale, Michaletz et al. (2014) showed that NPP was not affected by variation in temperature and rainfall. However, Chu et al. (2015) provided some evidence that climate has a direct influence on NPP at global scale. The difference in these conclusions may be due to model uncertainty and the difficulty in accurately estimating forest productivity. Chu et al. (2015) recommended that onsite biometric measurements of tree biomass at the local scale could help more-accurately evaluate climate-forest productivity relationship. Cleveland et al. (2011) reported that the observed change in global NPP over time was closely coupled with climate change, and its dynamics lead to a change in terrestrial carbon sequestration (Girardin et al., 2018; Nayak et al., 2013; Phillips et al., 2009).

Long-term monitoring of forest dynamics plots, coupled with litter fall measurements have some of the best potential to help understand temporal dynamics of variation in NPP (Anderson-Teixeira et al., 2015). Even though monitoring forest NPP dynamics through biometric measurement of trees (i.e., measuring tree diameters) is crucial, many of the emerging researches are remote sensing-based at large spatial and time scales (Malhi et al., 2015; Tan et al., 2012; Zhao et al., 2018), which often produce highly uncertain estimation. Given the strengthening of current global climate change trends (IPCC, 2014), there is an urgent need to clarify the relationships between local climate and forest productivity using ground-based measurements. Moreover, previous studies are usually based on short term study intervals (i.e., those less than 5 years) (Chen et al., 2016; Kohl et al., 2015; Malhi et al., 2009; Olivier et al., 2008; Phillips et al., 2009), and usually focus on how temperature, rainfall, atmospheric carbon dioxide influence NPP (Bazzaz, 1998; Bonal et al., 2016; Bonan, 2008; Christiaan and Coops, 2016; Del Grosso et al., 2008; Kurt et al., 1995; Shan et al., 2011); few studies has explained the effects of solar radiation and humidity. As relative humidity influences tree water use efficiency (Sellin et al., 2015) and radiation potentially controls tree photosynthesis at the canopy-layer (Park et al., 2018); we explicitly evaluate their effects on forest productivity in this study. In summary, it remains a challenge to determine how a certain climate parameter drives tropical forest productivity. Therefore, to fully understand the relationship between forest performance (e.g., productivity and radial stem growth) and environment, fine temporal and spatial scale measurements are critical.

The influence of climate on forest NPP is scale-dependent. Previous studies at different spatial scales present contrasting evidence on relationships of climate and tropical forest productivity (Verduzco et al., 2018). Recently, there was an effort of measuring temporal variability of NPP in a tropical seasonal rainforest (Tan et al., 2015), but the total temporal extent of this study was insufficient to test the significance of the NPP-climate relationship. However, fine temporal scale or intra-annual assessment of NPP dynamics may reveal more detailed effects of climatic drivers, which were usually ignored by previous studies (Chi et al., 2017). Moreover, there is a symmetrical seasonality shift in Southeast Asia caused by monsoons from the Indian Ocean. This shift may cause a change in which climatic factors limit NPP at finer temporal (i.e. seasonal) scales. Yearly-based NPP studies in tropical forest suggest that NPP increases with increasing rainfall in areas with up to 3000 mm/year mean annual precipitation, beyond which NPP declines (Chuur, 2003; Cleveland et al., 2011; Hofhansl et al., 2014). To the best of our knowledge, no study has reported threshold effect of precipitation on NPP at a seasonal scale. Therefore, threshold analysis of NPP-

climate relationship using fine temporal scale with ground-based measurement may help uncover how local climate drives NPP in tropical seasonal rainforest.

Accurate NPP estimation requires the use of allometric equations for tree biomass calculations. Most of the biometric-based NPP studies in tropical forests are only based on a few generalized allometric equations, which are developed for tropical forest regions regardless of intrinsic interspecific variation between species (Brown et al., 1989; Chave et al., 2005; Clark et al., 2001a,b; Tan et al., 2015). Using the general allometric equations, which are not site specific and do not allow for tree organ-base inference (i.e., stem, root vs. leaf NPP fractions), is one potential shortcoming when it comes to the accuracy of NPP estimates. In all, there is hardly NPP study using site/organ-based allometric equations. There have been numerous efforts to study the above ground biomass of trees in the highly diverse tropical seasonal rainforests of Southeastern Asia (Hua, 2006; Kira, 1991; Zhang et al., 2014; Zheng et al., 2006), but information about NPP across seasons with long-term dataset is limited.

To address the fine scale temporal dynamics of forest productivity, we estimated the NPP over 9 year's duration (2009–2017) with three-month intervals observation, and analyzed the effects of climatic drivers in a 20 ha tropical seasonal rainforest plot, Xishuangbanna, Southwest China. Specifically, we tested two hypotheses: (1) Local climate drivers (precipitation, temperature, radiation and relative humidity) have a significant influence on forest NPP during the study periods. This is due to the fact that trees are physiologically active to respond and adjust their phenology and growth rhythms for the changing climate. (2) Clear variation of NPP across season is detected, i.e., NPP is higher in rainy season than that in dry season.

## 2. Materials and methods

### 2.1. Study site

The study was carried out in Xishuangbanna National Nature Reserve, Southwestern China. It is free from long-term human anthropogenic disturbance. Hence, the study area was characterized by high diversity of native trees species with long life spans. This region is dominated by a typical monsoon climate with distinct dry and rainy seasons. The mean annual temperature and precipitation are 21 °C and 1,532 mm respectively. More than 80% of precipitation occurs from May to October (rainy season), and the rest occurs in dry season from November to April (Lan et al., 2009). Specifically, this study was conducted in a 20-ha tropical forest plot (101°35'07"E and 21°37'08"N), established in 2007 where all trees with stem diameters  $\geq 1$  cm are measured, mapped, identified. The plot (Fig. 1) is rectangular (400 m  $\times$  500 m) in shape with elevation ranging from 709 to 869 m above sea level (Cao et al., 2008; Lan et al., 2012). A total of 95,834 individuals were recorded at the first census (2007), belonging to 468 species, 214 genera and 70 families (Cao et al., 2008; Lan et al., 2012). The vertical structure of this forest is complex and roughly categorized into 5 canopy strata (Cao et al., 2008). The emergent layer (> 45 m), upper layer (30–45 m), lower layer (20–30 m), understory layer (10–20 m) and tree lets (5–10 m), which are mainly dominated by *Parashorea chinensis* of Dipterocarpaceae; *Sloanea tomentosa*, *Pometia tomentosa* and *Barringtonia pendula*; *Garcinia cowa*, *Knema furfuracea* and *Nephelium chryseum*; *Baccaurea ramiflora* and *Dichapetalum gelonioides*; *Pittosporopsis Kerri*, *Mezzettiopsis creaghii* and *Saprosma ternate*; respectively.

### 2.2. Dendrometer and litter fall

Dendrometer tree-growth bands were installed on > 2000 individuals with stem diameters  $\geq 5$  cm in January of 2009 (Fig. 1). Each dendrometer consists of a custom-fashioned stainless-steel band secured with spring. A measurement window between the trailing end of the

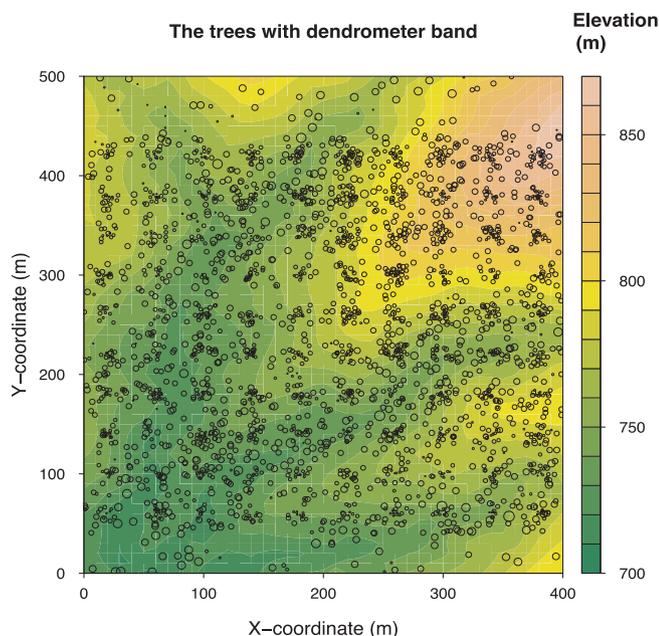


Fig. 1. The distribution of trees with Dendrometer band in the 20 ha Xishuangbanna forest dynamics plot. Colors show quadrat elevations in meters above sea level. Circle sizes denote tree stem diameters.

band and measurement notch allows for the precise measurement of tree bole diameters over time. The initial width of the window was recorded, and as tree diameter increases the window widens. Dendrometer windows have been measured with a Vernier caliper every 3 months (February, May, August, and November) since 2009. However, not all the individuals with dendrometer bands survived through the whole time period (2009–2017). Some individuals died due to various reasons (e.g., wind or pathogen). Our major purpose was to clarify the relationship between local climate and biomass increment of big trees, including their litter fall, the death trees were removed from the NPP calculation, and therefore we ignore their effect on NPP.

Litter fall (L) was sampled with square litter traps ( $0.75 \times 0.75$  m) located in the center of randomly-selected subplots within the larger forest dynamics plot (151 in total). Each litter traps consists of a 1 mm nylon netting supported by a PVC frame with four poles. The effective area of each trap, discounting the frame edges, is  $0.5 \text{ m}^2$ . Fallen litter is collected every 2 weeks to avoid significant losses to decomposition. All litter is transferred to the laboratory, where it was separated into leaf, twig, reproductive parts, and miscellaneous, dried, and weighed.

### 2.3. Climatic data

A weather recording instruments, which is 14 km away from the 20-ha plot, have long been installed for recording monthly temperature and precipitation in Mengla County. For monthly radiation and relative humidity, we take from weather recording station located in 500 m away from the 20-ha plot and but the data were available since October 2014 (Fig. 2).

### 2.4. Data analysis

#### 2.4.1. Prediction of radiation and relative humidity

To predict unknown values of monthly radiation and relative humidity from 2009 to 2014, we consider two things for modeling. First, we assumed that monthly temperature and precipitation could potentially predict both radiation and relative humidity. Accordingly, we fit linear modeling (lm), time series linear model (tslm) and dynamic linear model (dynlm) based on the actual observed climatic variables using data from 2014 to 2017 (Eq. (1)) and we confirmed that all of this

time series models performance is the same. Second we hypothesized that, instead of temperature and precipitation, the observed monthly radiation and relative humidity at time “t” depends on previous time (t - 1) value of its own, called autoregressive integrated moving average modeling (Eq. (2)) and we used “auto.arima” function. Finally we plot all predicated models (lm, tslm, dynlm and auto.arima) vs actual observations and auto.arima was selected as best fit (see supplementary information, Fig. S1). Therefore, monthly lag values of relative humidity and radiation were generated back to 2009–2013, using lag function.

$$RD_t = \alpha + \beta_0 T_t + \beta_1 RF_t + \varepsilon_t \quad \text{and} \quad RH_t = \alpha + \beta_0 T_t + \beta_1 RF_t + \varepsilon_t \quad (1)$$

$$RD_t = \alpha + \beta_0 RD_{t-1} + \varepsilon_t \quad \text{and} \quad RH_t = \alpha + \beta_0 RH_{t-1} + \varepsilon_t \quad (2)$$

where RD and RH are a monthly radiation and relative humidity respectively, T and RF direct record of monthly temperature and rainfall from a nearby climate (Mengla) station respectively. All analysis was performed in R statistical software (V.3.6.1; [www.r-project.org](http://www.r-project.org)) (R Core Team, 2019) using the lm, tslm, dynlm and auto.arima functions.

We used actual observed precipitation and temparture from Mengla station, as a proxy for our study plot. We described the detailed nine years monthly characteristics of local climate (Fig. 3).

#### 2.4.2. Estimation of NPP of the forest

Since NPP represents the major energy storage of forest ecosystems (Sala and Austin, 2000), accurate estimation is the main concern. The partitioning of NPP by tree organs (i.e., leaf production, stem, reproductive materials, and roots) is common (Clark et al., 2001a,b). Quantifying all of these NPP components separately is difficult and confounded by challenging methodologies (Clark et al., 2001a,b). Typically, precise temporal measurement of tree diameters is coupled with collections from litter fall traps. The diameter measurements can be converted to whole tree biomass using allometric equations, and the collected litter fall can be used to estimate leaf and reproductive material production. Total NPP is commonly calculated as the sum of each of the organ-based compartments, or tree biomass flux plus litter fall (leaf & productive), defined as  $NPP_{\text{partial}}$  (Clark et al., 2001a).

$$NPP_{\text{partial}} = \Delta B + L \quad (3)$$

where  $\Delta B$  is the biomass change between two successive tree diameter censuses, and L is the total ecosystem litter fall production during that time interval (Fang et al., 2007; Tan et al., 2010). To estimate the  $\Delta B$  more precisely, we separately estimated the biomass of different tree organs at different DBH sizes with the Xishuangbanna-specific allometric equation developed by Lv et al., 2007. Total tree biomass was the sum of biomass of all tree organs. They developed these equations using destructive sampling method and took samples from each organ. They measured the biomass of leaves, branches, stems and roots to come up with the following allometric equation (Table 1).

Since not all tree individuals within the 20-ha plot had installed dendrometers; we needed to scale our measurements of total tree individual biomass (B) from the sampled individuals which did have dendrometer band. We did so with the following equation:

$$B = \frac{BS}{N} * \frac{0.02}{n} \quad (4)$$

where B = biomass of all trees in a 20 ha, BS = biomass of sampled individuals, N is roughly estimated total number of individuals (estimated as 90,000) in a 20 ha plot, n is number of sampled individuals, 0.02 is fraction coefficient to scale the equation to tone/ha from a 20 ha plot. BS was determined according to size class allometric regression equation (Table 1). Before biomass calculation for each individual, we removed tree diameter values larger than the 95th percentile and smaller than the 5th percentile in each inventory period. This step removed noisy data that might have been caused by recording or data entry errors. The biomass increment of each year for forest ecosystem

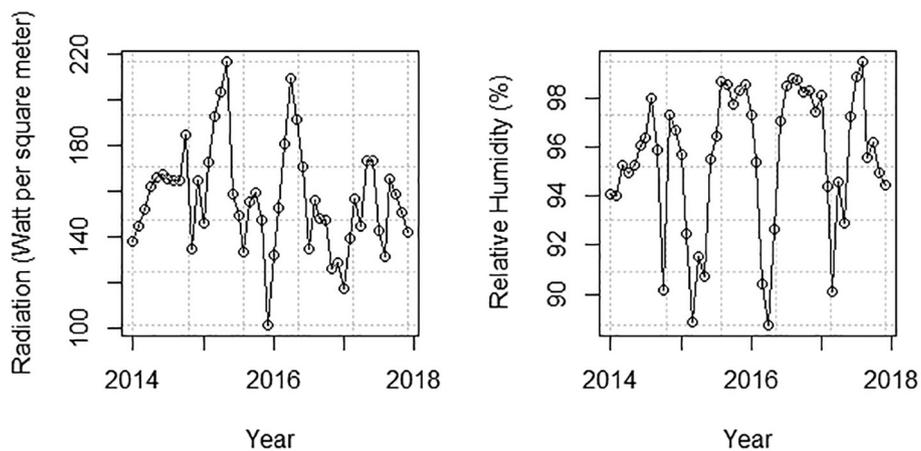


Fig. 2. Time series observed radiation and relative humidity since 2014 to Nov 2017.

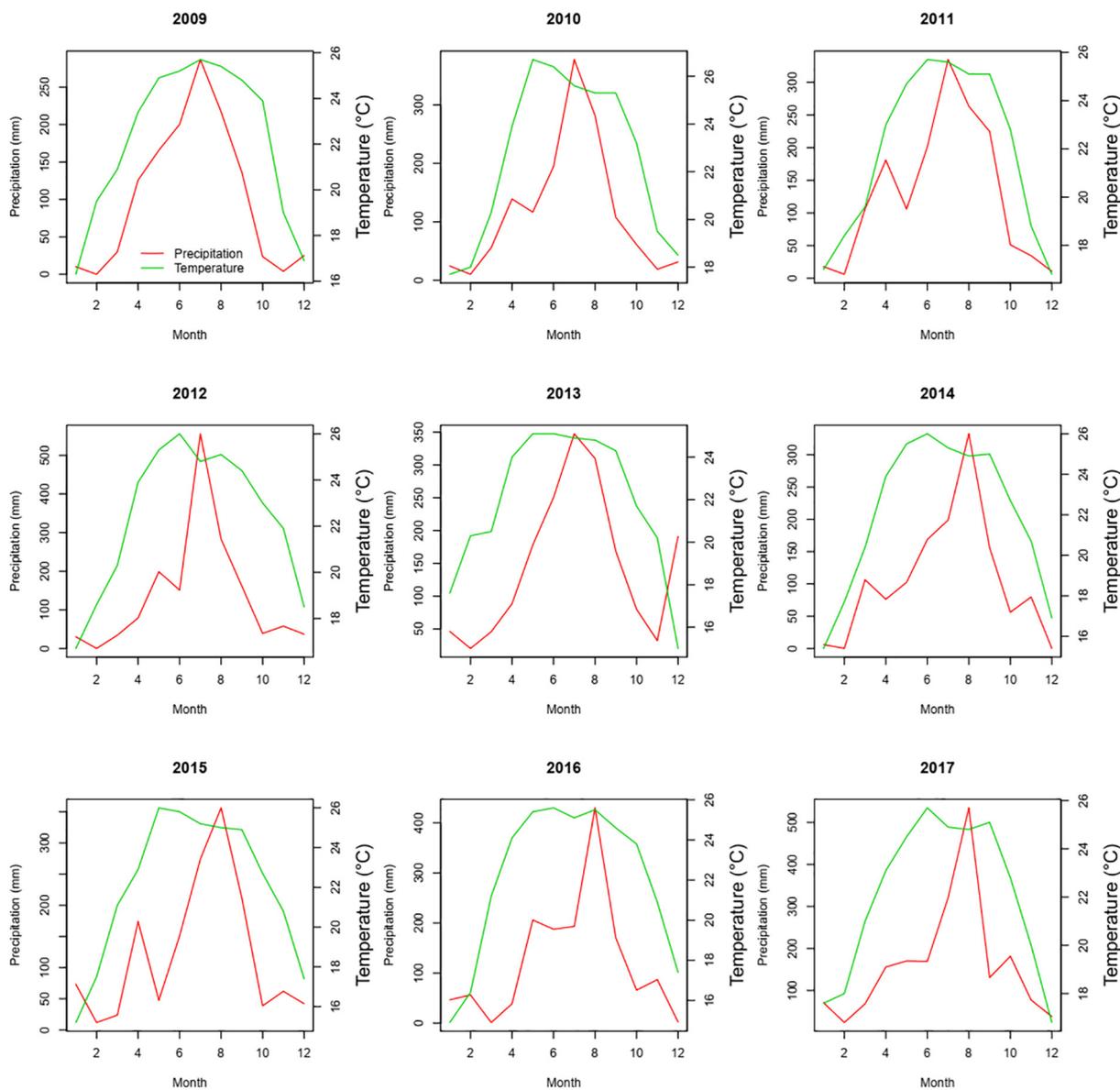


Fig. 3. Monthly precipitation and temperature between years 2009–2017.

**Table 1**  
Tree layer biomass allometric equations of the tropical seasonal rain forest in Xishuangbanna, Southwest China (Lv et al., 2007).

DBH classes	Organs	Regression biomass equation (D = diameter)	Correlation coefficient ( $p < 0.001$ )
2 cm ≤ DBH ≤ 5 cm	Stem	0.0733 (D) <sup>2.5884</sup>	0.803***
	Branch	0.0135 (D) <sup>2.5158</sup>	0.536***
	Leaf	0.0394 (D) <sup>1.456</sup>	0.456***
	Root	0.028 (D) <sup>2.399</sup>	0.683***
5 cm ≤ DBH ≤ 20 cm	Stem	0.1086 (D) <sup>2.3169</sup>	0.894***
	Branch	0.0186 (D) <sup>2.4685</sup>	0.743***
	Leaf	0.0455 (D) <sup>1.6636</sup>	0.589***
	Root	0.0242 (D) <sup>2.4205</sup>	0.876***
DBH > 20 cm	Stem	0.0401 (D) <sup>2.6752</sup>	0.934***
	Branch	0.0829 (D) <sup>2.0395</sup>	0.835***
	Leaf	0.0979 (D) <sup>1.3584</sup>	0.636***
	Root	0.0111 (D) <sup>2.6801</sup>	0.938***

was determined by adding biomass increment of all trees with in each inventory period with in the year. Litter fall is also the dry mass litter within this specified time.

### 3. Statistical analysis

#### 3.1. Auto-regressive model

We tested time series autocorrelation in NPP. Prior to modeling, all continuous predictor variables were standardized and normality of residual errors was also checked. An autoregressive modeling approach was recently used for timescales based tree growth and NPP analysis by Macias-fauria et al. (2016). Therefore, we carried out autocorrelation function (ACF) test to determine how many lag periods affect the measured NPP based on ACF-lag plot. We found a clear time autocorrelation at lag 2 and we incorporated in the regression model, meaning that NPP at the beginning of measurement year (Feb.2009) is influenced by the previous month's NPP ( $NPP_{t-2}$ ). Since the measurements take place at three-month intervals, we generated two lagged NPP time series (6 months back to Feb 2009) using lag function to consider in modeling.

The full time series model for the fitting NPP value looks like the following (Vlam et al., 2013).

$$NPP_t = \alpha + \beta_0 NPP_{t-1} + \beta_1 T_t + \beta_2 TRF_t + \beta_3 RD_t + \beta_4 RH_t + \varepsilon_t \quad (5)$$

where t refers to time in months where NPP is calculated (usually every three-month interval since Feb 2009),  $\alpha$  is the intercept,  $\beta_0$ – $\beta_4$  is the predictor coefficient for the climate and lag effect of NPP itself and  $\varepsilon$  is the error term. Finally from all possible candidate linear regression models, the best one was chosen based on AIC value using the “re-subsets” function (Bolker et al., 2009).

#### 3.2. Threshold analysis

As precipitation increases, its influence on NPP might weak beyond a certain threshold, which was the level of some quantity needed for a process to take place or a state to change. Here we examined the rainfall threshold level in order to understand at which rainfall level NPP shows more drastic responses based on three-month interval data. To identify whether there was a threshold effect of precipitation, we applied threshold regression with “chngt” package in R (Fong et al., 2017).

#### 3.3. Seasonal NPP variation analysis

We also partitioned NPP analysis in to two seasons (dry and rainy) and tested for significant differences between seasons using a *t*-test. Multiple regressions for each season was executed separately to

examine whether the key climatic factors underpin the NPP was different between the two seasons or not.

#### 3.4. Inter-annual local climate and NPP temporal trend analysis

We tested the temporal trend association between time in months and local climate variables using Pearson correlation (*r*) and similarly, between time and NPP. A negative and positive Pearson coefficient showed the decreasing and increasing trend respectively with in the study periods.

## 4. Results

#### 4.1. Temporal trends of local climate and NPP

According to the Pearson correlation test between time (in months) and local climate variables (temperature, precipitation, radiation and relative humidity), there was no significant relationship between time and any local climate variable. The general trend showed that temperature and radiation decreased over time, but this trend was not significant. The minimum monthly temperature was 16.23 °C and the maximum 26.23 °C since 2009–2017 (Fig. 3), while radiation ranged from 149 to 161 W/m<sup>2</sup>. Trends in precipitation and relative humidity showed a slight increase over time. The maximum annual rainfall event was recorded in 2017 (1941.9 mm) and 2013 (1758.7 mm), while the lowest events were recorded in 2009 (1224.5 mm) and 1282.9 mm in 2014 (Fig. 3).

There was an insignificant variation in annual NPP across years and the general trend showed an increasing pattern ( $P = 0.18$ ,  $t = 1.48$ ), with NPP increasing by 0.41 t ha<sup>-1</sup> year<sup>-1</sup>. The highest NPP was recorded in 2013 (20.61 t ha<sup>-1</sup>), whereas the lowest was 12.58 t ha<sup>-1</sup> in 2009 and details of three-month interval and yearly NPP value is indicated in the figure below (Fig. 4).

#### 4.2. Local climate effects on NPP

After applying model selection on the NPP with all the climatic variables and autocorrelation variable models, we found that only precipitation was chosen in the parsimonious model ( $NPP = 1.985 + 0.006 \cdot \text{precipitation}$ ,  $R^2 = 0.59$ ,  $p < 0.001$ ). To discern the seasonal effect, we conducted model selection for NPP in rainy and dry seasons, separately. Model selection in both seasons showed a consistent pattern that only precipitation was chosen in the parsimonious models. However, the precipitation showed significant and insignificant effects in dry ( $NPP = 0.271 + 0.021 \cdot \text{precipitation}$ ,  $R^2 = 0.600$ ,  $p < 0.001$ ) and rainy ( $NPP = 3.129 + 0.004 \cdot \text{precipitation}$ ,  $R^2 = 0.190$ ,  $p = 0.07$ ) season, respectively. This seasonal difference suggested that there may be an existence of a threshold response of forest productivity to increasing precipitation. To verify our assumption, we implemented a segmented continuous threshold regression on NPP using only precipitation as a predictor variable.

The model uncovered a significant threshold in NPP with precipitation (Fig. 5(a)). The change point of precipitation was 229.2 mm (95% confidence interval, 81.8–376.6 mm), and the threshold effect was significant with a *p*-value < 0.001 by bootstrap test (Fig. 5(b)). Our results suggested that precipitation could facilitate the NPP but weaken when reaching its maximum threshold.

The maximum NPP value in rainy season and dry season is 8.26 t/ha and 7.61 t/ha respectively. The minimum mean value is 2.95 t/ha and 0.1 t/ha in rainy and dry season respectively. The mean in rainy and dry season is 5.60 and 2.98 respectively, shows a higher significant seasonal variation based on two-sampled test ( $t = 4.98$ , 95% confidence interval = (1.55–3.69) and  $P < 0.001$ ). Violin plot below showed distribution of NPP in the two seasons (Fig. 6).

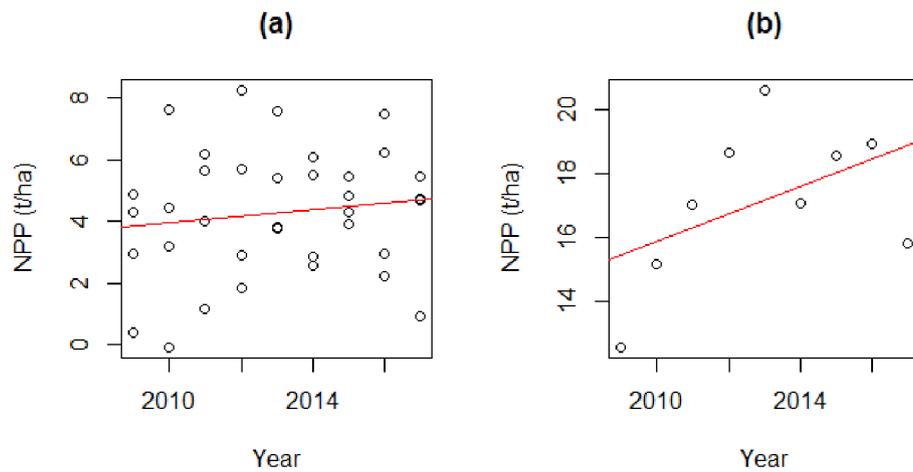


Fig. 4. (a) Three-month interval based NPP and its increasing trend since February 2009- December 2017, and (b) Annual NPP dynamics at Xishuangbanna dynamic plot, South-west China.

5. Discussion

5.1. Local climate and NPP temporal dynamics

In our study plot, all local climate variables and NPP didn't show statistically significant temporal variation from 2009 to 2017, but the NPP increased over time (Fig. 4). A three years interval study since 1969–2012 in Paosh forest, Malaysia shows a decrease in NPP, due to logging disturbance (Yoneda et al., 2016). Similarly, another study from Malaysian tropical rainforest with four years observation period (1994–1998) reported that, NPP decreased through time due to mortality (Hoshizaki et al., 2004). Whereas, our study rainforest has been free of any human disturbance for more than 50 years since it was designated as a nature reserve, which contributes for the increased productivity over years. Our study shows a slight variation from previously monitored NPP from the same forest (Tan et al., 2015). Differences in the our results and Tan et al (2015) are likely due to our use of specific allometric equations based on tree sizes and organs. Our mean value of NPP is within the range of values reported from different tropical forests (Table 2). Differences in NPP estimates are mainly attributed to the following reasons. Differences in species richness and stem densities (Flombaum and Sala, 2008; Gross et al., 2014; Morin et al., 2011), species difference response ability to climate change, temporal and spatial climate variability (Schelhaas et al., 2003; Terradynamic et al., 2006; Wang et al., 2003), variation in the method of NPP estimation (remote sensing based and direct biometric field measurement) (Luyssaert et al., 2009; Ohtsuka et al., 2009).

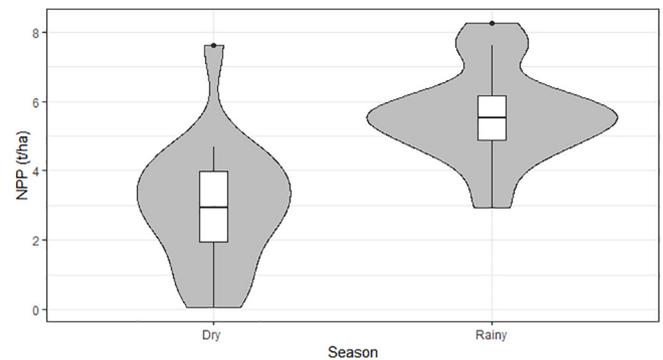


Fig. 6. NPP distribution across seasons.

5.2. The precipitation effect on NPP

Climate influence on forest productivity is scale dependent. Linear regression model results suggested that precipitation was the only and most important factor in driving the dynamics of NPP in Xishuangbanna tropical seasonal rainforest 20-ha plot. Similarly, at local scale, the studies in tropical forests (Cao et al., 2015; Del Grosso et al., 2008; Toledo et al., 2011; Wagner et al., 2014; Wang et al., 2016) showed that precipitation was more strongly linked to NPP than other climatic and edaphic factors. The increase in precipitation across years resulted in rising of soil moisture, increasing in photosynthesis and productivity of vegetation (Brazeiro et al., 2016; Gustafson et al., 2017; Nayak et al.,

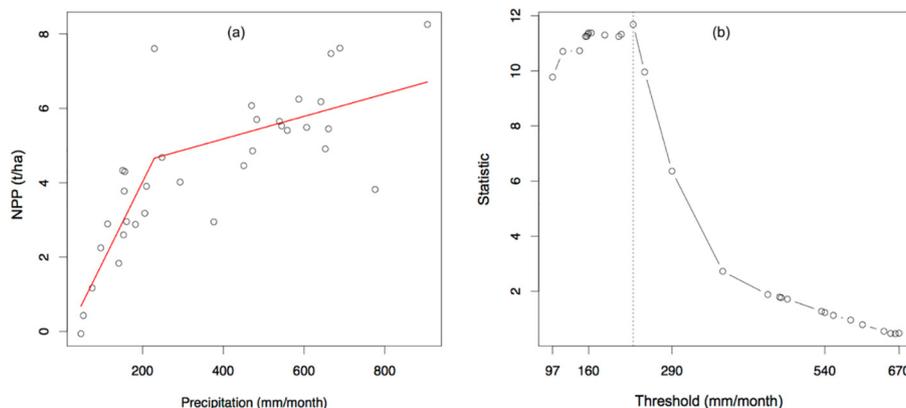


Fig. 5. (a) The scatterplot of NPP vs. precipitation. The red line is the fitted segmented model. (b) The scatterplot of statistic vs. threshold and the optimal value in dashed line. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 2**  
Comparison of our study site NPP with other tropical forest.

Site	NPP(t ha <sup>-1</sup> yr <sup>-1</sup> )	Duration	Reference	Mean annual Precipitation (mm)
Xishuangbanna	17.17	2009–2017	This study	1527.2
Xishuangbanna	18.38	2010–2013	(Tan et al., 2015)	1631.5
Costa Rica	15.18	2007–2010	(Cao et al., 2015)	1391
Amazon	17.74	2003–2007	(Girardin et al., 2010)	na
Borneo, Malaysia <sup>a</sup>	30	1992–2008	(Kho et al., 2013)	2540
Pasoh, Malaysia <sup>a</sup>	27	1971–1973	(Kira et al., 2013)	2054
Khao chong, Thailand <sup>a</sup>	28.6	1962–1965	(Kira et al., 2013)	2312
Chinese forest <sup>b</sup>	14.4	1989–1993	(Ni et al., 2003)	1250

Note: a = including loss to herbivore, b = country wise estimation, na = data not available.

2013) in some parts of tropical regions, and this offers a possible explanation for the strong relationship between precipitation and NPP (Table 2). On the contrary, temperature was a more important predictor for NPP than precipitation (Cleveland et al., 2011; Dura et al., 2018; James et al., 2006; Reich et al., 2014; Sun, 2018; Williams et al., 2013). Studies from Amazonian and tropical Asian rain forests showed that the increase in net primary production and tree growth are owing mainly to decreased cloud cover and the resulting increase in solar radiation (Dong et al., 2012; Nemani et al., 2014), but radiation didn't play a significant role globally (Churkina and Running, 1998). In summary, because of the complex nature of tropical forests, it is difficult to generalize that a certain climate factor drives tropical forests ubiquitously. Therefore, temporal and spatial fine scale measurement is important to fully understand the relationship between forest performances (e.g., productivity, tree mortality, and radial stem growth) and environment.

Tropical seasonal rainforest productivity response to precipitation is scenario dependent. Interestingly in our study, we further identified a significant threshold effect of precipitation on the NPP. NPP increase more quickly until reaching a threshold level, which is 229 mm (Fig. 5). There are no study reports with such fine temporal scale (three-month interval) threshold level elsewhere. Some studies only showed yearly threshold level. Example, in Hawaiian forest NPP decreased with increased mean annual precipitation from 2000 to 5000 mm (Schoor and Matson, 2001). Similarly, in tropical wet forest ecosystem, the relationship between NPP and precipitation was negative beyond 2445 mm/year as threshold (Chuur, 2003), and no relationship found in a Costa Rican tropical wet forest with mean annual rainfall 4000 mm (Clark and Clark, 1994). Our study forest is characterized by a mean annual precipitation less than 1600 mm, far below the standard of a typical rainforest, rainfall of which is usually more 3000 mm/year. Such optimum levels of rainfall in our study forest may promote soil aerobic condition (Schoor and Matson, 2001), accelerate soil nutrient uptake by plants and increase forest productivity (Cleveland et al., 2010; Cusack et al., 2009; Liptzin et al., 2015). Alternatively, forests with rainfall more than 3000 mm/year may experience lower solar radiation due to increased cloudiness, potentially limiting photosynthetic rates (Graham et al., 2003) and leads to reduce forest productivity.

Seasonality in NPP is one typical characteristic of this studied forest. We found that NPP is strongly seasonal and the same result was reported from lowland forest of Amazonia (Taylor et al., 2013). High degree of seasonal climatic variation, leads to seasonality of forest productivity in tropical forests (Girardin et al., 2018). Our result shows that, there is no single climatic variable influencing the NPP in rainy season. However, during dry season, precipitation is the most important factor that facilitates NPP. This is due to the strong water demands of trees during dry season and this suggests that the major limiting factor for NPP in this season is water. The overall annual NPP climatic driver is consistent with the dry season NPP, which showed that dry season was more responsible to drive ecosystem productivity than rainy season. Previous studies in this forest also reported that, NPP is higher in rainy season than dry season, but statistically insignificant (Tan

et al., 2015). Similarly, recent study in tropical forests found that seasonal precipitation positively correlated to forest productivity (Brazeiro et al., 2016; Wagner et al., 2016; Xu et al., 2018). Another study in tropical Asian forest showed that, forest productivity (growth) was significantly and negatively correlated with temperatures, and positively correlated with dry season precipitation levels (Vlam et al., 2013). Study in semiarid tropical Brazil forest showed that, rainfall explained much of the variation in plant productivity, and its influence is strong in extreme dry year (Salimon and Anderson, 2018), in line with our study during dry season. In Bolivian tropical lowland forests, the higher rainfall with a shorter and less intense dry period led to higher tree growth rates (Toledo et al., 2011). To summarize, this study demonstrates that forest productivity rates vary widely among seasons in the seasonal tropical rainforest.

## 6. Conclusion

This 9 year (2009–2017) case study revealed that NPP increased over time; hence it is a sink of carbon. Precipitation is the only local climate that drives NPP in this rainforest and it showed a significant threshold effect at the rainfall change point of 229 mm/three months. The observed clear variation of NPP between rainy and dry season demonstrates that, forests productivity is highly seasonal in tropical rainforest of Xishuangbanna, China. In all, our finding showed that climate is a key to NPP dynamics at the sub annual scale in the tropical seasonal tropical forests of southwestern China, which strengthens our understanding of the dynamics of NPP. As a result, this study is a potential reference resource for tropical forest managers and ecologists to compare NPP between well conserved forests and more-disturbed forests (e.g., fragmented forest). The threshold effect of precipitation on NPP that we present is a strong theoretical guidance for water use efficiency management to sustainably manage and design tree based land-use ecosystems. Future research is needed to determine if rainfall thresholds are present in wetter or drier tropical forest and how they change with local climate. Understanding the factors that control rainfall thresholds in tropical forest productivity can potentially help reduce uncertain in the forecasts of future tropical forest productivity in the climate change era.

## CRediT authorship contribution statement

**Ewuketu Linger:** Conceptualization, Data curation, Formal analysis, Software, Methodology, Writing - original draft, Writing - review & editing. **J. Aaron Hogan:** Writing - review & editing. **Min Cao:** Conceptualization, Data curation, Formal analysis, Software, Methodology, Writing - original draft, Writing - review & editing, Supervision, Project administration. **Wen-Fu Zhang:** Resource, Visualization, Investigation, Validation. **Xiao-Fei Yang:** Resource, Visualization, Investigation, Validation. **Yue-Hua Hu:** Conceptualization, Data curation, Formal analysis, Software, Methodology, Writing - original draft, Writing - review & editing.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2020.118153>.

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