



# Investigating the contribution of climate variables to estimates of net primary productivity in a tropical deciduous forest in India

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**Abstract** Investigating the impact of climate variables on net primary productivity is crucial to evaluate the ecosystem health and the status of forest type response to climate change. The objective of this paper is (1) to estimate spatio-temporal patterns of net primary productivity (NPP) during 2001 to 2010 in a tropical deciduous forest

based on the input variable dataset (i.e. meteorological and biophysical) derived from the remote sensing and other sources and (2) to investigate the effects of climate variables on NPP during 2001 to 2010. The study was carried out in Katemiaghat Wildlife Sanctuary that forms a part of a tropical forest and is situated in Uttar Pradesh, India, along the Indo-Nepal border. Mean annual NPP was observed to be highest during 2007 with a value of  $878 \text{ g C m}^{-2} \text{ year}^{-1}$  and  $781.25 \text{ g C m}^{-2} \text{ year}^{-1}$  for sal and teak respectively. A decline in mean NPP during 2002–2003, 2005 and 2008–2010 could be attributed to drought, increased temperature and vapour pressure deficit (VPD). The time lag correlation analysis revealed precipitation as the major variables affecting NPP, whereas combination of temperature and VPD showed dominant effect on NPP as revealed by generalized linear modelling. The carbon gain in NPP in sal forest was observed to be marginal higher than that of teak plantation throughout the study period. The decrease in NPP was observed during 2010, pertaining to increased VPD. Contribution of different climatic variables through some link process was revealed in statistical analysis and clearly indicated the co-dominance of all the variables in explaining NPP.

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## Introduction

Net primary productivity (NPP) establishes an important link between atmosphere and biosphere, influencing

nutrient and hydrological cycle. NPP is defined as the difference between autotrophic photosynthesis and its respiration and the amount of the photosynthetically fixed carbon available to the first heterotrophic level in an ecosystem (Field et al. 1998). NPP plays a significant role in climate dynamics by influencing atmospheric CO<sub>2</sub> concentration and consequently the carbon cycle. A vital role of vegetation to sequester carbon has been inspiring the scientific community to model NPP for effective forest carbon management as well as for policymakers to deal with greenhouse gas mitigation (Zhao and Running 2010). Forest areas that consistently add carbon to the ecosystem by photosynthetic production are of potential importance as present and future sink of carbon. The association of interannual NPP to climate variability encourages researchers to model the spatio-temporal pattern to understand the variation in atmospheric carbon, monitor the metabolism of an ecosystem (Crabtree et al. 2009) and for the improved estimates of the carbon cycle (Cao et al. 2004). The inter-annual pattern of NPP is governed by various climate variables, i.e. temperature, precipitation and solar radiation (Zhang et al. 2004). The interaction of climatic variables to NPP is determined by various mediated eco-physiological (i.e. stomatal conductance, respiration) and soil-plant characteristic (i.e. permanent wilting point, field capacity, root distribution) processes, and their seasonal interaction determines the intensity of temperature and moisture stress (Zomer et al. 2008). For example, temperature can affect photosynthesis directly through the metabolic rates of the enzymatic reactions in the Calvin cycle and indirectly through the increased leaf to air vapour pressure deficit (VPD; Lloyd and Farquhar 2008). Various patterns of NPP at global scales show higher sensitivity of tropical forests primarily towards climate along with the secondary factors, i.e. ecological, geochemical and anthropogenic (Zhao et al., 2005; Nemani et al. 2003).

Studies from micro- to macroscale have shown reduced carbon gain with a marginal increase in temperature (Kindermann et al. 1996; Loescher et al. 2003). However, few studies have shown a positive trend of NPP in relation to increased mean temperature (Raich et al. 2006; Chitale et al. 2012). In addition, precipitation trends in tropics also play an important role in deriving NPP as it positively correlates with the annual sum of precipitation (Tian et al. 1998), and tree growth is highly influenced by seasonal rainfall (Wagner et al. 2014; Gliniers

et al. 2013). Zhao et al. (2010) showed the decreased global NPP from 2000 through 2009 especially manifested by hydrologic cycle. Studies have indicated the control of climate on NPP including extreme events, e.g. El Nino-driven rainfall minima and high temperatures have led to decline in NPP (Cramer et al. 2001; Liu et al. 2012) and positive anomaly of NPP during La Nina (Cao et al. 2004; Nayak et al., 2013).

The influence of climate on NPP is not instantaneous and sometimes expresses delayed effects (Steele et al. 2005; Peng et al. 2008). Rainfall may impose delayed effects on plant growth by influencing the variation of water content in the soil. For example, leaf area index (LAI) and normalized difference vegetation index (NDVI) normally follow the phenological stages of vegetation and thus are related to precipitation movements (Bobee et al. 2012). The width of tree ring in 1 year may depend on the climate of several preceding years because of changes in crown density and photosynthates. Immediate physiological alterations and delayed biogeochemical adjustments can be revealed in time-lagged serial correlation analysis (Steele et al. 2005). Such evidence strongly support the notion of changes in the structure and functioning of tropical forests as a response to climate change. The physiological responses of vegetation to climate stress based on plant communities help better understand their roles in terms of matter and energy processes in an ecosystem (Diaz and Cabido 1997). Leaf phenological variability has been considered as an important variable in describing major plant communities (Condit et al. 1996). Tropical forests are among the first to be severely impacted by climate change since these are among the warmest ecosystems, with narrow optimum temperature range (Cunningham and Reed 2002) and with low shifting capacity due to low seasonal variation in temperature (Gundersson et al. 2010). However, comprehensive studies on the carbon cycle of tropical forests are limited to a few sites (Malhi et al. 2009; Girardin et al. 2010).

*Shorea robusta* (sal) and *Tectona grandis* (teak) are among the most dominantly occurring timber tree species with high economic value (Suoheimo 1999) and qualify for different plant communities based on their distinct functional behaviour such as growth, phenology and dispersal. Sal, the most important climax species, is a spring-flushing (vegetative bud breaks around the spring equinox, March–

April), shade-loving semi-evergreen tree with a prominent tap-root system; requires comparatively more soil moisture; and is very sensitive to temperature variations. In contrast, teak is a strong light demanding, surface rooter and deciduous tree, remaining leafless for about 5 months (Shadangi and Nath 2008). Ram et al. (2008) observed a significant positive relationship of moisture index and rainfall with a variation of tree ring width, an indicator of tree growth and climate influence, in central India for teak. Tyagi et al. (2011) attributed micro-environmental factors, viz., soil moisture and light intensity as important factors that affect the natural regeneration of sal under different canopies. Chitale and Behera (2012) have predicted the distribution of sal to shift towards moisture regimes in India.

In the present study, authors explored the impact of climatic variables, i.e. temperature (Tavg), precipitation, solar radiation (SR), vapour pressure deficit (VPD) and relative humidity (RH) on NPP of two plant communities, i.e. sal forest and teak plantation for the decadal years 2001 to 2010. The decade has been the years of climate extremes with the warmest decade on record (WMO 2013) along with the severe drought in India (Kumar et al. 2013; Rajeevan and Sridhar 2008). Katerniaghat wildlife sanctuary (KWLS) was selected as the study area. Past studies in KWLS included analyses of microclimate in response to different plant communities, assessment of phenological events, biomass and productivity estimation and analysis of the community structure (Chauhan et al. 2008; Tripathi et al. 2009; Behera et al. 2012). Remote sensing-based light use efficiency (LUE) approach was implemented to estimate NPP for sal and teak. The main objectives are (1) to investigate spatio-temporal patterns of NPP for the years 2001 to 2010 over the KWLS based on the input variable (i.e. meteorological and biophysical) datasets derived from the remote sensing and other sources and (2) to study continuous and the delayed effects of climate variables on NPP.

## Materials and methods

### Study area

Katerniaghat Wildlife Sanctuary forms a part of a tropical forest and is situated in Uttar Pradesh, India, along the Indo-Nepal border. The sanctuary was established in 1976 and is spread over an area of 400 km<sup>2</sup>, representing

a typical Terai ecosystem characterized by moist forests, wetlands, woodlands and hygrophilous grasslands spread across alluvial plains.

The area is located between 28° 6' and 28° 24' N latitudes and 81° 19' and 81° 24' E longitudes with an elevational range of minimum 123 m to maximum 181 m asl (Figure S1). The main plant communities of the sanctuary are as follows: sal (*Shorea robusta* C.F.Gaertn.) forest, teak (*Tectona grandis* L. f.) plantation, mixed deciduous forest, lowland swamp forest and grasslands. *S. robusta* represents the climax species along with other associates such as *Mallotus philippensis* (Lam.) Müll.Arg. and *Terminalia alata* B.Heyne ex Roth (Chitale et al. 2012). The Terai landscape comprises one of the most important ecoregions of the world, well known for its unique biodiversity and high productivity (Johnsingh et al. 2004). The sanctuary area is made up of rich alluvial soil. The four distinct seasonal periods are summer monsoon (June–August), winter monsoon (December to February), spring or pre monsoon (March–May) and autumn or post monsoon (September to November). The annual rainfall is nearly 1000 mm in the region. The mean maximum and minimum temperature vary from 22 °C and 8 °C in January to 40 °C and 27 °C in May and June respectively. The interannual temporal variation of climatic variables is displayed in Figure S2.

### NPP estimation

The LUE approach (Monteith 1972) is widely accepted method to estimate NPP (Potter et al. 1993; Nayak et al. 2013; Tripathi et al., 2018) and is defined as the product of light use efficiency and absorbed photosynthetic active radiation (PAR) as follows:

$$\text{NPP} = \varepsilon \times \text{APAR} \quad (1)$$

where APAR is absorbed photosynthetically active radiation and is derived as the product of PAR and fraction of absorbed PAR (*f*PAR).

Here, PAR was assumed to be 50% of solar radiation (Spitters et al. 1986). We used MODIS-derived *f*PAR data downloaded from USGS EROS Data Centre.  $\varepsilon$  is light use efficiency (LUE) and defines the efficiency of the radiation conversion to the plant biomass and may be reduced below its theoretical potential value by

environmental stresses such as low temperatures or water stresses (Landsberg 1986).

#### Satellite data

The satellite data of 8-day composite MODIS Surface Reflectance Product (MOD09A1) data for Land Surface Wetness Index (LSWI) sensitive to water stress (WS) and MODIS LAI/fPAR (MOD 15A1; 500 m resolution) were used to derive fPAR respectively on monthly basis and were downloaded from the USGS EROS Data Centre website (<https://modis.gsfc.nasa.gov/data/dataproduct/>).

#### Downregulation of LUE

Spatio-temporal variation of LUE is governed by vegetation types and temperature and moisture conditions. Therefore, in the present study, we down-regulated the maximum LUE during times of moisture and temperature stress, which is expressed as follows:

$$LUE = \varepsilon^* \times T_s \times W_s \quad (2)$$

where  $\varepsilon^*$  is maximum light use efficiency when environmental conditions are optimal and  $T_s$  and  $W_s$  are temperature and water stress scalars respectively.  $T_s$  (i.e.  $T_1$  and  $T_2$ ) was derived following Field et al. (1995) as follows:

$$T_1 = 0.8 + 0.02 \times T_{opt}(x) - 0.0005 \times (T_{opt}(x))^2 \quad (3)$$

$$T_2 = 1.1814 \quad (4)$$

$$/ \left\{ 1 + e^{[0.2(T_{opt}(x) - 10 - T(x,t))]} \right\} / \left\{ 1 + e^{[0.3(-T_{opt}(x,t) - 10 + T)]} \right\}$$

where  $T_{opt}(x)$  is defined as the average temperature in the month when the NDVI reaches its maximum for the year. The  $T_1$  and  $T_2$  represent monthly deviations from site-specific optimal temperature and from 20 °C respectively, where  $T_1$  involves the nearness of topt to a global optimum for all sites and  $T_2$  takes into account the difference between the optimum temperature (topt) and actual temperature (tempc) for a site (Todorovski et al., 2003).

Ws was quantified using LSWI which is sensitive to the canopy water stress (Xiao et al. 2005). LSWI uses near-infrared (NIR) and short-wave infrared (SWIR) regions of electromagnetic spectrum for stress

assessment. Ws was derived using Xiao et al. (2005) as follows:

$$(1 + LSWI)/(1 + LSWI_{max}) \quad (5)$$

where  $LSWI_{max}$  is maximum LSWI value of particular pixel.

Light use efficiency value, i.e.  $0.305 \pm 0.056 \text{ CMJ}^{-1}$  for sal and  $0.357 \pm 0.023 \text{ CMJ}^{-1}$  for teak, was estimated using the equation described by Kale and Roy (2012) as follows:

$$LUE = \frac{(\text{Net CO}_2 \text{ exchange from the leaves } (\mu\text{mol/mol}))}{(\text{Total PAR incident on the leaf surface } (\mu\text{mol/mm}^2/\text{s}))} \quad (6)$$

For the purpose, measurements were taken during the last week of August on clear, sunny days with no over-cast conditions since the maximum photosynthesis rates are obtained during this period due to the post-monsoon growing season with abundant moisture and optimum temperature. Total 12 g of carbon (molar mass of carbon) sequestered per mole of  $\text{CO}_2$  exchanged was considered for estimation of LUE. Three different sites were considered for sal forests, i.e. dense sal, moderately dense sal and mixed sal. Measurements were taken with the help of Licor portable photosynthesis system (Li-6400 XT) on 3 days in each location from 6.00 am to 6.00 pm and readings were logged as per minute values. Nearly 720 individual readings per day were generated to calculate average LUE values. A total of  $720 \times 9 = 6480$  readings were obtained in all the three sal forest types. PAR photosynthetically active radiation was measured with the help of quantum sensor Li-190, Li-191 and logged as per minute values.

#### Meteorological datasets

Meteorological data (maximum and minimum temperature) was downloaded from the site (<https://www.indiawaterportal.org/>) for the study area and the neighbouring districts (Kheri, Gonda, Sitapur and Bahraich) to derive spatial stress coefficient of temperature ( $T_1$  and  $T_2$ , mentioned in Eqs. 2 and 3). In addition, we collected the daily meteorological data (minimum temperature ( $T_{min}$ ), maximum temperature ( $T_{max}$ ), daily rainfall (precipitation), RH and sunshine hours for 10 years (2001 to 2010) from Indian Institute of Sugarcane Research (IISR), Lucknow, as the nearest meteorological station from the study area. Vapour pressure deficit (VPD) was derived as the difference between the saturated vapour pressure and the actual

vapour pressure using Penman-Monteith equation (Allen et al. 1998; see equation S1). This data was used to establish the statistical relationship with the mean NPP of sal and teak.

Statistical analyses

GLM

We performed Generalized linear modellings (GLMs) to analyse potential single and multiple response of climate predictors on NPP for each year. GLM models are an extension of linear models but support non-linear fittings between response and predictor variables. In GLMs, the distribution of the response variable can be non-normal and does not have to be continuous, and the dependent variable values are predicted from a combination of predictor variables, which are linked to the response variable via a link function (Nogués-Bravo 2009). Here, the NPP as the response was assumed to be a Poisson-distributed random variable. The Poisson-based prediction method of GLMs is different from ordinary least square regression, for example, GLM does not assume a linear relation between dependent and independent variables and uses maximum likelihood estimation (Dobson 2001). Prior to GLM, a correlation analysis was performed to investigate collinearity among explanatory variables in order to better formulate subsequent models. RH and solar radiation (SR) exhibited extremely high correlations (> 0.7) with VPD and Tavg respectively, and, therefore, were dropped from further analyses to avoid multicollinearity issues (Table S1).

To analyse the combined effect of climatic variables, we added the predictors sequentially into the model and built all the possible combinations starting from single, double to all the three climatic variables. Addition or elimination of predictor variables was based on the residual statistics obtained in the deviance table. At each step of the forward stepwise selection, the variable that caused the largest change in deviance was included in the model. The best single predictor or combination of predictors from each category was included into a combined multi predictor model. Statistical analyses were performed using the library glm2 in software R 3.0.2 for Windows (R Development Core Team 2018).

Time lag serial correlation analysis

Since the response of NPP to climate is not instantaneous and sometimes exerts delayed effects, time-lagged serial correlation analysis was performed, which is defined as follows:

$$R_k(x, y) = S_K(x, y) / S_x S_{y+k} \tag{7}$$

where  $S_K(x, y)$  is the sample covariance and  $S_x$  and  $S_{y+k}$  represent the standard deviations that are calculated by following Wang et al. (2013) as follows:

$$S_k(x, y) = \frac{1}{n-k} \sum_{i=1}^{n-k} (x_i - \bar{x}_i) (y_{i+k} - \bar{y}_{i+k}) \tag{8}$$

$$S_x = \left[ \frac{1}{n-k} \sum_{i=1}^{n-k} (x_i - \bar{x}_i)^2 \right]^{1/2} \tag{9}$$

$$S_{y+k} = \left[ \frac{1}{n-k} \sum_{i=1}^{n-k} (y_{i+k} - \bar{y}_{i+k})^2 \right]^{1/2} \tag{10}$$

The means are defined as follows:

$$\bar{x}_i = \frac{1}{n-k} \sum_{i=1}^{n-k} x_i \tag{11}$$

$$\bar{y}_i = \frac{1}{n-k} \sum_{i=1}^{n-k} y_{i+k} \tag{12}$$

where  $n$  is the sample number of  $x_i$  and  $y_i$  and  $k$  is the number of time lag. In this study,  $n$  is 12, and  $k = 0, 30$  and 60 days. When  $k$  is 0, it means there is no time lag, which reflects NPP immediate response to climate variation.

A long-term continuous biomass and productivity estimation has not been done in the region; however, NPP for the year 2010 was available from the same region from another study (Behera 2016), where primary productivity for each individual for each species was determined by assessing the net biomass increment over two successive years. To determine the net biomass increment, the aboveground biomass (AGB) of each individual tree for each species for previous year was subtracted from the next successive year AGB. Net biomass increment for all individuals was added, and the total species NPP was

calculated for next year. Finally, the net biomass increment of all species was added and annual NPP ( $\text{t ha}^{-1} \text{ year}^{-1}$ ) of each forest type was calculated for the respective years. Annual NPP for each forest type was calculated for 2010, 2011 and 2012. Few literature-based NPP for the two species from different regions of India and for different years (Table 1) was also used to compare the simulated NPP.

## Results

### Sensitivity analysis

We carried out a sensitivity analysis of the model to assess the role of LUE and stress scalars in the NPP estimation (Fig. 1a). We computed the LUE values as  $0.305 \pm 0.056 \text{ CMJ}^{-1}$  for sal and  $0.357 \pm 0.023 \text{ CMJ}^{-1}$  for teak using field measured data mentioned in the section downregulation of LUE.

The NPP for the year 2010 was estimated with the following inputs as:

- (1) Firstly, in the main run, simulation of NPP was carried out with variable LUE (from present study)

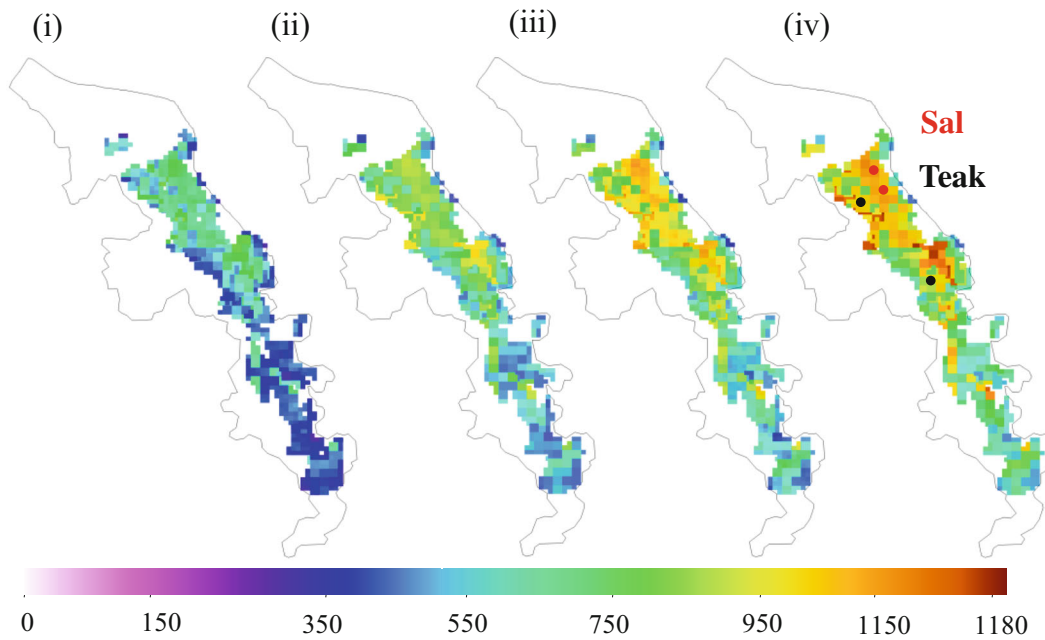
and with stress regulators, i.e. temperature and water stress. An overall spatial NPP clearly indicates a range between 50 and  $900 \text{ g C m}^{-2} \text{ year}^{-1}$  (Fig. 1a (i)).

- (2) Simulation of NPP is carried out similar to (1), where dropping of the downregulators was carried out but with a stepwise reduction. Dropping only water stress increases the annual mean of NPP by  $150 \text{ g C m}^{-2} \text{ year}^{-1}$  with an enhancement in the maximum range reaching up to  $1100 \text{ g C m}^{-2} \text{ year}^{-1}$  (Fig. 1a (ii)). Dropping only temperature stress leads to an enhancement of nearly  $250 \text{ g C m}^{-2} \text{ year}^{-1}$  for mean NPP (Fig. 1a (iii)). Temperature stress was observed to be more influential for NPP showing a clear enhancement of NPP when dropped.
- (3) Simulation of NPP is carried out similar to (1), but with no stress regulators leads to a maximum increase in NPP (Fig. 1a (iv)). Especially, the southern region clearly indicates a gain of mean NPP by more than  $300 \text{ g C m}^{-2} \text{ year}^{-1}$ .

To assess the change in NPP, we further extracted NPP pixel values representing four homogenous plots of sal and teak at different locations (Fig. 1b; location of homogenous plots is represented in Fig. 1a (iv)).

**Table 1** NPP ( $\text{g C m}^{-2} \text{ year}^{-1}$ ) of sal and teak forests in different regions of India in the past decade

Locality	Year	Forest	Age (years)	NPP ( $\text{g C m}^{-2} \text{ year}^{-1}$ )	Reference	Forest	NPP ( $\text{g C m}^{-2} \text{ year}^{-1}$ ) (present study)
Uttar Pradesh, North India	2003	<i>T. grandis</i>	1	209	Jha K.K. (2003)		
			5	1339			
			11	1052		<i>T. grandis</i>	636
			18	1041		<i>S. robusta</i>	710
			24	654			
	30	1035					
Chhindwara distt., M.P., India	2005	<i>T. grandis</i>	–	918	Pande P.K.(2005)		
				888		<i>T. grandis</i>	667
				740		<i>S. robusta</i>	745
				720			
Chhindwara distt., M.P., India	2010	<i>S. robusta</i> (open forest)	–	509	Pande and Patra (2010)		
			<i>S. robusta</i> (closed forest)	779			
Dehradun, Uttarakhand, India	2011	<i>S. robusta</i>	47 to101	209 to 922	Gautam et al. (2011)		
Katerniaghat, U.P., India	2010	<i>S. robusta</i>	–	893	Behera (2016)	<i>S. robusta</i>	633
	2010	<i>T. grandis</i>		1457		<i>T. grandis</i>	557



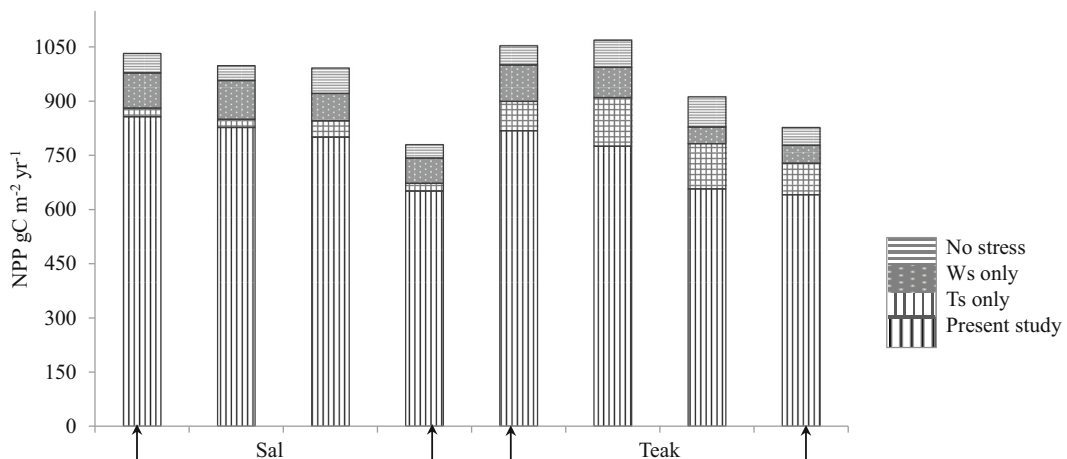
**Fig. 1 a** Sensitivity analysis of NPP ( $\text{g C m}^{-2} \text{ year}^{-1}$ ) (i) with variable LUE\* (main run; present study) (ii) same as (i) but without water stress (iii) same as (ii) but without temperature stress (iv) same as (ii) but with no stress scalars. Sensitivity analysis was performed for the year 2010; LUE\* represents maximum light use

efficiency maximum NPP was observed when all the stress regulators were dropped (Fig. 2). **b** Sensitivity analysis of NPP for the representative pixels of sal and teak. *Ws* refers to water stress and *Ts* for temperature stress; LUE\* for present study were measured as  $0.305 \pm 0.056 \text{ CMJ}^{-1}$  for sal and  $0.357 \pm 0.023 \text{ CMJ}^{-1}$  for teak

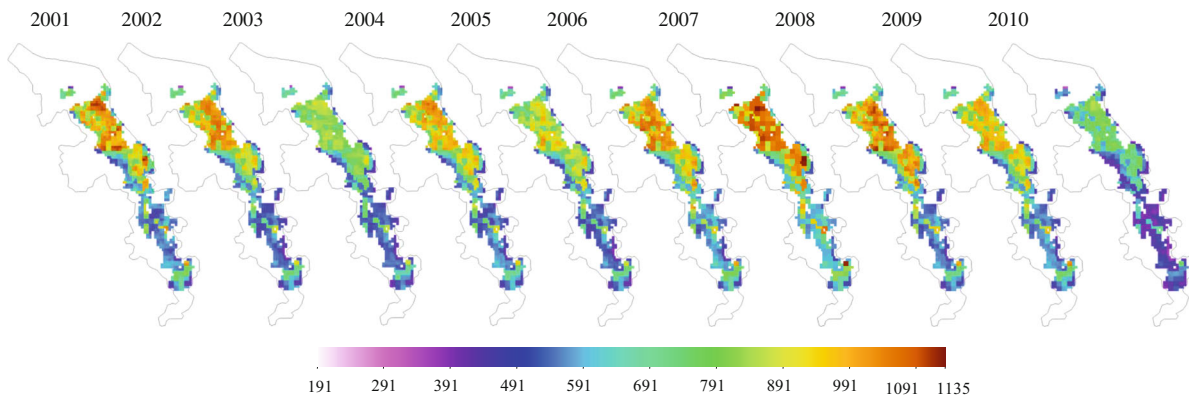
We observed that NPP was highest for all the pixels when no downregulators were incorporated (Fig. 1b (iv)). In the model with the influence of temperature stress (Fig. 1b (iii)), NPP was reduced by 46 to  $107 \text{ g C m}^{-2} \text{ year}^{-1}$  compared to no downregulators in the model (Fig. 1b (iv)). The gain of NPP was higher in teak compared to sal pixels, with no water stress showing a gain of nearly 80 to  $135 \text{ g C m}^{-2} \text{ year}^{-1}$ .

Comparison with ground-based and other literature-based NPP estimates

We compared our model estimated NPP with ground-based measurements for the year 2010 where the NPP was available for two plots within the study area (Behera 2016). The mean NPP was measured to be  $893 \text{ g C m}^{-2} \text{ year}^{-1}$  for sal and  $1457 \text{ g C m}^{-2} \text{ year}^{-1}$



**Fig. 1** (continued)



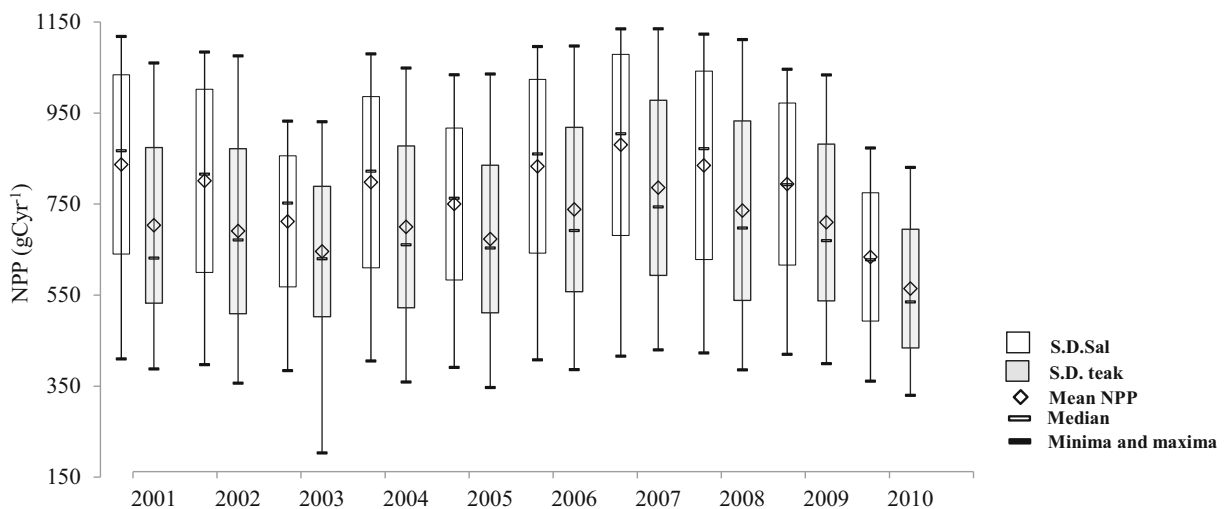
**Fig. 2** Spatio-temporal pattern of annual net primary productivity ( $\text{g C m}^{-2} \text{ year}^{-1}$ ) from 2001 to 2010

for teak in the year 2010 respectively. In contrast, model-estimated mean NPP values were observed to be  $633 \text{ g C m}^{-2} \text{ year}^{-1}$  and  $557 \text{ g C m}^{-2} \text{ year}^{-1}$  for sal and teak respectively. Field-based measurements showed a higher estimation compared to model estimation for teak. The NPP, when compared with the other cited literature, showed comparable results with our model estimates for different years (Table 1). Jha (2003) measured the mean NPP of differently aged teak for the year 2003, ranged from a minimum of 209 to a maximum of  $1339 \text{ g C m}^{-2} \text{ year}^{-1}$ . Pande (2005) showed NPP of nearly 720 to  $918 \text{ g C m}^{-2} \text{ year}^{-1}$  for teak in Madhya Pradesh. Pande and Patra (2010) estimated a mean NPP of sal for open and closed canopy forest showing a gain of nearly 509 and  $779 \text{ g C m}^{-2} \text{ year}^{-1}$ . Gautam et al. (2011) observed an

NPP of 209 to  $922 \text{ g C m}^{-2} \text{ year}^{-1}$  NPP for sal in Doon valley.

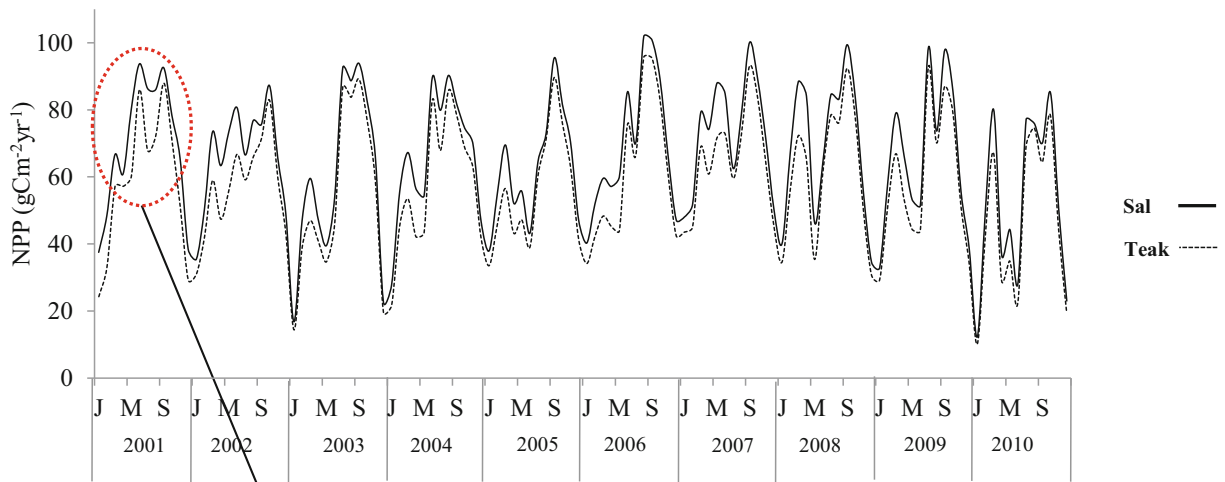
#### Spatio-temporal pattern of NPP

The spatio-temporal pattern of NPP for sal and teak is displayed in Fig. 2. The spatial pattern of NPP was almost similar for 10 years where the higher NPP gain of sal is clearly illustrated occupying most canopy at top of the upper middle part of the sanctuary. Most of the southern part incorporating teak showed less gain of NPP. No linear trend was observed for temporal variations (Fig. 2). A significant gain in mean annual NPP was prominent during 2001, 2004, 2006 and 2007, whereas a decline was observed during 2002, 2003, 2005 and 2008 to 2010 (Fig. 3). Both the communities showed a similar

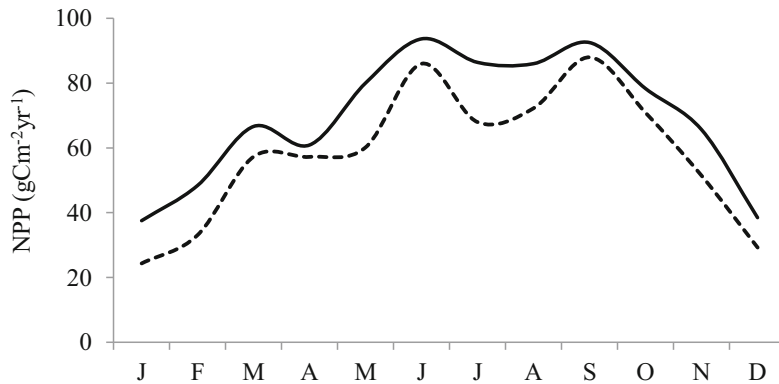


**Fig. 3** Minima, median, maxima and mean net primary productivity ( $\text{g C m}^{-2} \text{ year}^{-1}$ ). S.D. represents standard deviation from mean (Please note that figure represents values for spatial variation of the particular plant community)





(a) Seasonal variation in mean NPP for sal and teak (2001–2010)



(b) Zoomed version showing three crests of mean NPP for sal and teak in 2001

**Fig. 4** (a) Seasonal variation in mean NPP for sal and teak (2001–2010). (b) Zoomed version showing three crests of mean NPP for sal and teak in 2001

pattern of NPP among all the years in terms of increasing or decreasing behaviour. However, sal showed continuous marginal higher NPP than teak. The NPP was highest during 2007 with a mean NPP value of  $878 \text{ g C m}^{-2} \text{ year}^{-1}$  and  $781.25 \text{ g C m}^{-2} \text{ year}^{-1}$  and a maximum NPP value of 1135 and  $1134 \text{ g C m}^{-2} \text{ year}^{-1}$  for sal and teak respectively. Conversely, lowest mean NPP was observed during 2010 with a mean NPP value of 633 and  $557 \text{ g C m}^{-2} \text{ year}^{-1}$  for sal and teak respectively.

The seasonal pattern of NPP shows about 3 annual peaks for sal and teak in the study area, one occurring in March to April, one in June to July and another after monsoon season during September and October

(Fig. 4). Results revealed that NPP increased mainly in March and April during spring and from July to October with the highest peak of mean NPP followed by a decline from October to December. The mean monthly NPP was maximum in September with a maximum gain of  $100 \text{ g C m}^{-2} \text{ year}^{-1}$  in the year 2007 and  $96 \text{ g C m}^{-2} \text{ year}^{-1}$  in the year 2006 for sal and teak respectively. The lowest NPP was observed in January with a gain of 12.33 and  $10.19 \text{ g C m}^{-2} \text{ year}^{-1}$  in the year 2010 for sal and teak respectively. A decline in NPP ( $21.8 \text{ g C m}^{-2} \text{ year}^{-1}$ ) for the year 2003 w.r.t.2002 was observed during the spring season (Fig. 4). A decrease in NPP from 2008 to 2010 was attributed to the less gain of NPP during

**Table 2** Multivariate analysis using GLM to explain the variance explained by different climate variables with NPP during 2001 to 2010 for sal and teak plant communities

Variables	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010
<b>Sal</b>										
PPTN	39.85	7.76	35.9	28.2	5.56	8.49	2.69	23.4	41.1	21.3
Tavg	83.07	53.7	31.8	44.8	8.38	48.8	53.1	29.6	26.8	16.1
VPD	0.906	14.1	3.86	0*	11.1*	2.25	16.5	0.39*	0.88*	3.14
PPTN + Tavg	85.51	53.7*-	49.8	53.6	9.01**	49.6*-	55.7*-	34.3	47.1	28.3
PPTN + VPD	56.41	31.6	36.6*	32.3*	15.1*-	9.06*	29.2	32.4	44*	21.4*-
Tavg + VPD	88.85	56.6*-	67.6	68.7	46.3	66.5	53.1**	32.7*	48.6	45.4
Tavg + PPTN + VPD	89.38**	68.2	71	71.6*-	72.3	82.1	71	34.4***	49**	46.5*-
<b>Teak</b>										
PPTN	31.36	14	41.1	34.1	6.02	9.8	6.74	34.94	48.34	23.95
Tavg	78.36	36	31.9	35.5	10	36.53	45.4	28.11	23.02	14
VPD	2.34	2	5.35	1.66*	15*	8.23	5.08	1.56*	4.206	6.444
PPTN + Tavg	79.25	38*-	53.7	50.1	13.4**	36.53*-	45.52*-	40.56	51.29*-	28.98
PPTN + VPD	51.05	22	41.6*	34.9*	23.6*-	14.23	19.68	37.08*-	48.88*	24.88*
Tavg + VPD	80.95	49	72	69.3	58.5	63.98	49.41**	41.34	55.6	51.51
Tavg + PPTN + VPD	81.41**	61	74.7	71.7*-	78.5	77.18	73.81	41.83***	55.69**	53.26*-

All variables showed significance  $p < 0.01$ . ‘\*’ denotes insignificance of a particular variable and ‘-’ represents significance for variables in combination (e.g. Tavg + VPD\*- means that Tavg is insignificant in the combination)

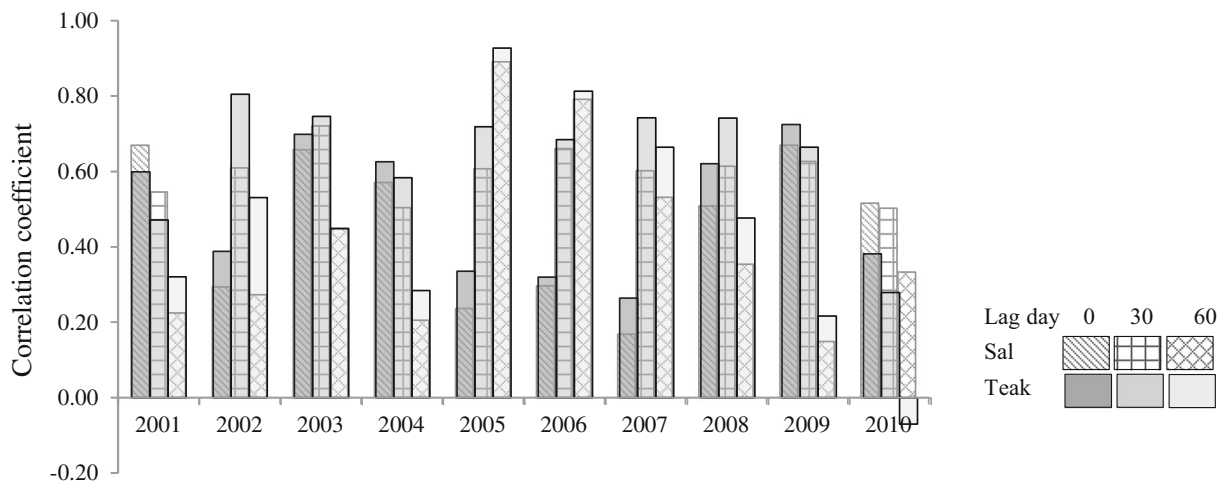
PPTN annual sum of rainfall, Tavg average temperature, VPD vapour pressure deficit

summer, autumn and winter season where almost 52 and 61 g C m<sup>-2</sup> year<sup>-1</sup> was declined in 2008 with reference to 2007 in sal and teak respectively (Fig. 4). The maximum decrease of NPP was observed within 2010 for both communities where a decline was observed in all seasons contributing to an overall decline in annual NPP.

NPP and climate relationship

GLM

To support the results mentioned in the previous section (spatio-temporal patterns of net primary productivity), we established GLM model and observed significant results



**Fig. 5** Time lag correlation between NPP and precipitation for sal and teak (2001–2010)

( $p < 0.01$ ). All the results from 7 possible combinations are presented in Table 2. GLM showed strong effects of climatic variables on NPP, where all variables alone (excluding VPD) exhibited a significant impact on NPP explaining more than 20% of the total variance in different years. Temperature alone explained  $> 75\%$  of the variance in 2001; in contrast, VPD had relatively weak effects on NPP explaining the maximum variance of 16.5% for sal and 15% for teak in the year 2007 and 2005 respectively. We observed each variable demonstrated its role significantly and no single variable had a dominant effect in deriving NPP from 2001 to 2010. In combination, maximum variance explained was 88% and 80% in the year 2001 for sal and teak respectively where Tavg and VPD contributed significantly at  $p$  value of  $< 0.001$ . Overall, a combination of temperature and VPD explained maximum significant variance followed by combination of all three variables, i.e. precipitation, Tavg and VPD (Table 1). In 2001, which had relatively high annual NPP, temperature explained 83% and 78% of spatial NPP variance for sal and teak respectively. In 2004, despite being the drought year as described by various studies (Francis and Gadgil 2010; Krishnamurti et al. 2010), an enhancement in NPP compared to 2003 was observed especially in spring which contributed to annual NPP increment. In 2006 and 2007, the contribution of all three variables was revealed by GLM explaining 82%, 71% of the variance for sal and 77%, 73% for teak respectively. Major enhancement of NPP in 2007 was observed due to the gain during autumn and spring.

The decline in NPP during 2003, 2009 and 2010 was mainly due to drought effect which had its impact on the proceeding years also, i.e. in 2010. In addition, increased VPD and Tavg also played their significant role in explaining maximum variance. In 2005, the declined NPP was a result of a sharp dip in NPP during summer, alone contributed from less gain in June due to high temperature, high VPD and low precipitation as significantly revealed by GLM analysis too. Despite maximum rainfall (Figure S1), there was a drop in mean NPP in 2008. This could be attributed to the total rainfall of 1438 mm in the year, where nearly 1363 mm was observed during June to September, resulting less availability of solar radiation (least among all years with a value of  $131 \text{ W m}^{-2}$ ).

#### *Time-lagged correlation analysis*

Time-lagged serial correlation analysis was adopted to study the delayed and continuous effects of climatic

parameters on seasonal fluctuations of NPP for sal and teak. Except precipitation, other variables could not show any significant relationship at 30- and 60-day time lag and are not displayed in the figure (Fig. 5). NPP exhibited significant positive correlation at 30-day and 60-day lag with precipitation. A strong correlation was observed for the year 2005 and 2006 with 60-day time lag (0.93 and 0.81 respectively) explaining strong correlation coefficient of 0.89 and 0.79 for sal and 0.93 and 0.81 for teak respectively. For the remaining years, precipitation had no influence on NPP of following seasons at 60-day lag.

#### **Discussion**

The impact of climatic variables on NPP was expressed using generalized linear modelling and time lag correlation analysis. Climatic conditions, especially precipitation during summers along with the optimum temperature during winter season, lead to higher NPP in 2001, 2004, 2006 and 2007. However, the decline in NPP during 2002, 2003, 2005 and 2008 to 2010 was mostly accompanied by the deficiency of precipitation along with the increased temperature and VPD.

In summary, our analyses revealed that among all the years, no single parameter emerged dominantly but the interaction of each parameter within season played a dominant role in GLM. Temperature along with VPD was more dominant in combination than precipitation in GLM. Impact of precipitation was prominently significant in time lag correlation. The decline in NPP during summers (2002, 2003, 2005 and 2010) was accompanied by a decrease in precipitation and an increase in Tavg and VPD. Temperature effects on NPP can be highlighted in two ways (1) positively, as temperature increases the length of growing season of vegetation thus enhancing productivity by improving photosynthetic efficiency (Zhao et al. 2012), and (2) negatively, an increase in temperature leads to water deficit by increasing evaporative demand (Liang et al. 1995). If the water loss through potential evapotranspiration (PET) in the higher temperature is not offset by increase in precipitation, a severe water deficit may reduce the NPP in the growing season. A reduced NPP during drought years (2002, 2009) and next to drought years was mostly accompanied by decreased precipitation and humidity. Pai et al. (2011)

discussed 2002 and 2009 as severe drought years in which most parts of north India experienced drought conditions due to a lack in rainfall during major part of the southwest monsoon season. Meteorological data of the study region also showed a decline in annual rainfall with the least precipitation in 2002 followed by 2010. A decreasing NPP might be attributed to an increase in soil moisture stress that led to a decrease in photosynthetic rate during summers along with increased VPD. Lower humidity causes reduced water use efficiency because of a higher VPD between the leaf and atmosphere and may lead to decreased NPP. Eamus et al. (2013) showed that drought plus increased VPD had a much larger impact on transpiration and NPP than drought plus increased temperature. In addition, NPP might be reduced due to excess rainfall as a result of more cloud cover and less solar radiation, i.e. in 2008, in the present study. Zhang et al. (2012) have also discussed that the enhancement effects of NPP due to higher rainfall might be suppressed by decreasing solar radiation or vice versa. GLM showed the contribution of all three variables, i.e. temperature, precipitation and VPD, but in a different manner.

The revelation of time lag analysis clearly illustrated the leading role of precipitation for NPP by explaining the significant positive correlation at 30-day lag duration. This could be due to infiltrated precipitation through the soil which later on gets absorbed by roots of plants and subsequently stored by the canopy and stems resulting in delayed growth of vegetation. The duration of response for different precipitation events sizes might vary from less than 20 days to a maximum of 32 days (Li et al. 2013). Chang et al. (2013) have discussed delayed impacts of moisture stress related to the preceding ENSO events that have induced drought-impaired vegetation growth in the subsequent growing season. Wang et al. (2013) have also observed a positive 32-day lagged correlation between seasonal variation of NPP and rainfall. Since the response of sal and teak to solar radiation is instantaneous and could not persist longer, we observed a positive correlation at 0 lag between NPP and solar radiation.

The temporal pattern of carbon accumulation was the same for both the communities. Sal showed marginal higher gains in all years than teak. Both communities are highly economical and their

physiology completely balanced by different physiological adjustments. Teak has a higher growth rate as per field data while showing less carbon accumulation in the simulation. This can be understood as follows: (i) sal being a semi-evergreen tree remaining leafless only for 15 days to 1 month which might be an indicator of its high functioning and thereby photosynthetic apparatus is regularly adding to annual carbon gain and (ii) deep root system of sal enables to maintain adequate water supply and supports it to tolerate seasonal droughts. Additionally, the moisture supply is regulated by the presence of fully and partially decomposed litter which covers the soil and reduces evaporation; (iii) teak is introduced in the sanctuary before 50 years in the gap filling areas (Behera et al. 2012), and therefore, it covers less sanctuary area. Most of the southern part of the sanctuary teak is open and mixed with another deciduous species leading to lower carbon gain and adding less carbon to the mean sanctuary NPP. The higher NPP of teak from field measurements could be due to the fact that measurements are taken in homogenous permanent plots covering the mid-northern sanctuary area, where tree density becomes higher with sufficient moisture.

## Conclusions

We observed the sensitivity of NPP towards climatic variables for both sal and teak. The pattern of carbon accumulation was the same for both the communities. The simulated NPP for sal showed an agreement with the field observations and other literature values clearly indicating the efficacy of the model in deriving NPP. Influence of climatic variables on NPP is notable with the implementation of the statistical analysis, i.e. GLM and time lag correlation, where the contribution of different climatic variables through some link process is revealed. No single variable could explain its dominant role in spatio-temporal pattern, clearly indicating the intercorrelated impact on NPP. Various studies (Jha and Pandey 1980; Rao et al. 2008; Bora and Joshi, 2014) have shown potentially strong physiological adaptation of these communities against climate stress. Such likely effects of climate on both the communities and their extreme economic and ecological values put them as future substitutes in forest management and in green environment development.

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