Environmental Management (2011) 48:1173–1181
DOI 10.1007/s00267-011-9710-8

The Potential Influence of Seasonal Climate Variables on the Net Primary Production of Forests in Eastern China

Zong Shan Li · Guo Hua Liu · Bo Jie Fu · Jin Long Zhang

Received: 13 May 2010 / Accepted: 8 June 2011 / Published online: 28 June 2011

Abstract Knowledge of the effects of climate factors on net primary production (NPP) is pivotal to understanding ecosystem processes in the terrestrial carbon cycle. Our goal was to evaluate four different categories of effects (physical, climatic, NDVI, and all effects[global]) as predictors of forest NPP in eastern China. We developed regression models with data from 221 NPP in eastern China and identified the best model with each of the four categories of effects. Models explained a large part of the variability in NPP, ranging from 46.8% in global model to 36.5% in NDVI model. In the most supported global model, winter temperature and sunshine duration negatively affected NPP, while winter precipitation positively affected NPP. Thus, winter climate conditions play an important role in modulating forest NPP of eastern China. Spring temperature had a positive affect on NPP, which was likely because a favorable warm climate in the early growing season promotes forest growth. Forest NPP was also negatively affected by summer and autumn temperatures, possibly because these are related to temperature induced drought stress. In the NDVI model, forest NPP was affected by NDVI in spring (positive), summer (negative) and winter (negative) seasons. Our study provides insight into seasonal effects of climate and NPP of forest in China, as well as useful knowledge for the development of climate-vegetation models.

Keywords Forest ecosystems · Net primary production (NPP) · Climatic variables · Eastern China

Z. S. Li · G. H. Liu (✉) · B. J. Fu
State Key Laboratory of Urban and Regional Ecology, Research Center for Eco-Environmental Science, Chinese Academy of Sciences, Beijing 100085, People's Republic of China
e-mail: ghliu@rcees.ac.cn

J. L. Zhang
State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, People's Republic of China

Introduction

Terrestrial net primary production (NPP) is among the most important ecosystem variables and one of the main sources for human food resources, wood products, and fuel (Knapp and Smith 2001; Myneni and others 2001). Recently, interest in regional patterns in NPP and their determinants has intensified because the earth experienced dramatic environmental changes in recent decades (Walther and others 2002). Besides dynamic ecosystem models that are capable of quantitatively simulating the NPP-climate relationships (Fang and others 2001; Schuur 2003; Del Grosso and others 2008), many recent studies have emphasized that multiple mechanisms (e.g., nitrogen deposition, CO_2 fertilization, forest regrowth, and climatic changes) have eased several critical climatic constraints to plant growth (Lucht and others 2002; Nemani and others 2003), such that NPP will increase globally in the future. The observed alterations in NPP can influence virtually all ecosystem processes (Sherry and others 2007; Rosenzweig and others 2008), so it is critically important to detect directional factors limiting NPP in the context of natural background in climate variability.

Chinese forests contain perhaps the widest range of vegetation types in the world (Editorial Committee for Vegetation of China 1980) and have a significant influence on regional and global carbon budgets (Fang and others 1998; Liu and others 2000). In China, there is an emerging

body of literature that demonstrates the coupled relationships between NPP and the climate system (Gao and others 2000; Fang and others 2001, 2002, 2005; Ni and others 2001; Ni 2004; Piao and others 2003, 2008, 2009; Hu and others 2007; Li and others 2007). Based on the NPP data for 690 forest stands from 17 forest types of China, Ni and others (2001) showed that the NPP of Chinese forests is highly correlated with annual mean temperature and rainfall, and annual potential evapotranspiration. Fang and others (2001) used an annual mean NDVI to quantify temporal NPP variability relative to precipitation variation for five biome groups (forest, grassland, desert, alpine vegetation, and cropland) across China. Recently, Piao and others (2009) used biomass and soil carbon inventories extrapolated by satellite greenness measurements, ecosystem models and atmospheric inversions, to analyze the current terrestrial carbon balance of China and its driving mechanisms during the 1980s and 1990s. Climate change has been proven to have significant effects on NPP of temperate grassland in the Inner Mongolian Plateau through changes in precipitation pattern, vegetation growth potential, and species diversity (Hu and others 2007). A large part of scientific interests on NPP-Climate relationships in China has focused on describing the influences of yearly climate variables, whilst potential impact of seasonal climate on NPP variability of terrestrial ecosystems are still rare and poorly studied (Piao and others 2003, 2008).

The Ecosystem Model-Data Intercomparison (EMDI) project was established to develop a consistent global NPP data set with which to compare and improve models and data collection methods, and improve our understanding of environmental controls of carbon allocation (Olson and others 2001). The EMDI project compiled NPP data for over 130 intensive sites, for 2000–2500 extensive sites, and 2000–3000 cells, representing the largest global NPP data set collected to date. The data assembled for EMDI likely have various ecological applications and are attracting the interests of global change modelers, ecologists, and remote sensing scientists worldwide (Cramer and others 1999; Ni and others 2001; Schuur 2003; Del Grosso and others 2008). Here we use NPP data for 221 forest sites and their related environmental variables for eastern China from the EMDI project, to quantify the response patterns of forest NPP in eastern China to seasonal climate variables.

Materials and Methods

Study Region

We defined eastern China as the humid to semi-humid zone of China east of a line from Daxing'anling Mountains to Taihang Mountain to Wushan Mountain to Xuefeng Mountain, characterized by the broad plains and hills (Fig. 1). This region belongs to the third and lowest terrace in China, with average elevation less than 1000 m, which is in contrast to the increasing topographies of high plateaus to the west (Zhou and Zheng 2008). The climate in the southern domain of eastern China was warm humid, the northern domain was cold sub-humid, and the intermediate domain was warm sub-humid. Overall, the climate was

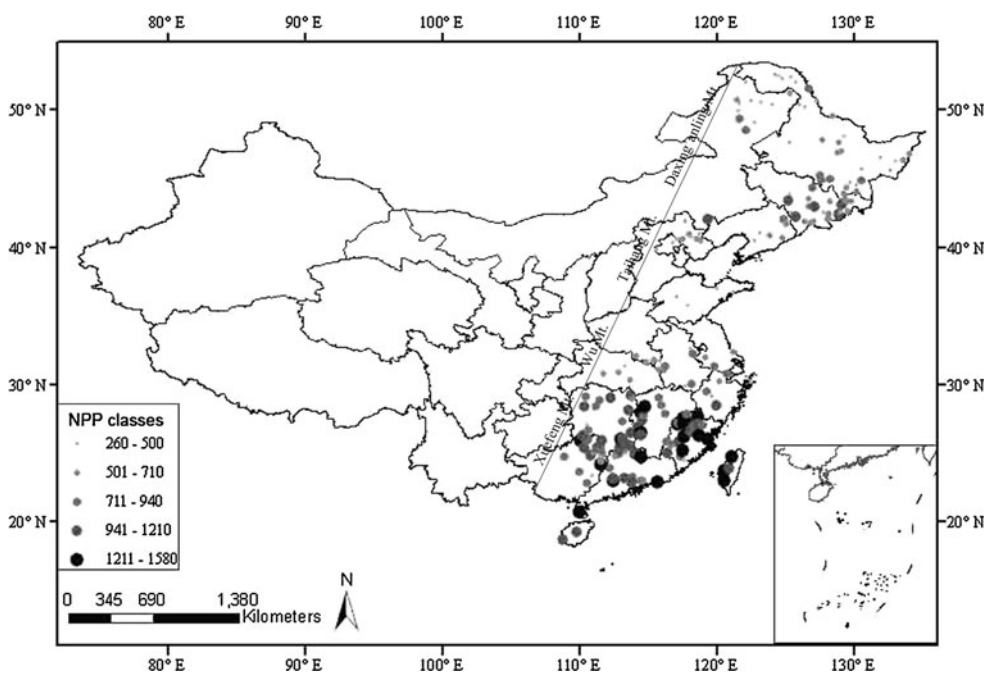

Fig. 1 Location and forest net primary productivity (NPP) class of 221 forest NPP sites in the EMDI project for eastern China

dominated by the East Asian Monsoon with greater influence from mid-latitude weather systems to the north, with a predominant northwest to southeast gradient in mean temperature and total annual precipitation and a distinct May-September rainy season (Tao and Chen 1987; Cheng 1993). A vegetation sequence is distributed along the North-South transect of apparent latitudinal gradients of climate in eastern China, including the cold temperature coniferous forest, temperate mixed forest, warm temperate deciduous broadleaf forest, subtropical evergreen coniferous forest, evergreen broadleaf forest and tropical rainforest from the north to south.

NPP Data

We primarily used the compilation of NPP estimates for 221 forest sites of eastern China from the EMDI project. Data points that were unrepresentative their general location or otherwise difficult to represent by a generalized NPP model were excluded from the EMDI review and outlier analysis (Olson and others 2001). EMDI includes both aboveground (ANPP) and total (TNPP) NPP data. We performed analyses only on TNPP; although ANPP was more reliably estimated, some data sets only report TNPP and previous models (e.g., Lieth 1975; Schuur 2003) only estimated TNPP. The dataset included the site name, latitude, longitude, elevation, estimated TNPP and the environmental driving variables for each record. Data on biomass and estimated NPP of major forest types of eastern China were compiled based on the inventories of the Forestry Ministry of China between 1989 and 1993. Additional data were obtained from published forest reports, as well as from more than 60 Chinese journals and some unpublished literature up to 1994 (Luo 1996; Ni and others 2001). The data covered six major forest biomes, and 17 forest types in China, ranging across a substantial geographical area, from sub-boreal *Larix* forests in northeast China (Heilongjiang Province: approx. 53°N, 122°E) to tropical rain forests of Hainan Island (approx. 18°N, 108°E) in southern China.

The climate data for the NPP forest sites in eastern China were extracted by Wolfgang Cramer and Stephen Sitch at the Potsdam Institute for Climate Impact Research (PIK), which used a combination of the long-term averages (1961–1990) from the PIK database (Leemans and Cramer 1991) based on the University of East Anglia climate database (New and others 1999, 2000). The Climate variables included mean temperature (TEM), total precipitation (PRE), and sunshine duration time (SUN) of four different seasons: spring (SPR: March to May), summer (SUM: June to August), autumn (AUT: September to November) and winter (WIN: December to February), averaged from monthly climate data.

Normalized difference vegetation index (NDVI), derived from red and infrared relative radiance data, is a useful tool for assessing extent and condition of vegetation (Kumar and Monteith 1982, Sellers and others 1996). It is calculated as (NIR − R)/ (NIR + R), where NIR is relative radiance in near infrared wavelengths and R is relative radiance in red wavelengths. Satellite-sensor-borne instruments, such as the Advanced Very High Resolution Radiometer (AVHRR), yield global-scale NDVI time series for estimating interannual changes in vegetation activity (Justice and others 1985, Malingreau 1986, Goward and others 1994, Myneni and others 1997). NDVI has been proven to have strong correlation with terrestrial NPP and is frequently used to predict NPP (Diallo and others 1991; Fang and others 2001). Therefore, we included seasonal measure of NDVI (spring, summer, autumn and winter) for the NPP sites based on available data for 1986, 1987, and 1990, compiled by the University of New Hampshire (James and Kalluri 1994).

Statistical Analyses

We performed ordinary least squares (OLS) multiple regression to fit four categories of NPP models (hereafter referred as OLS models), i.e. a physical model (NPP explained by latitude, longitude and elevation), a climate model (NPP explained by seasonal TEM, PRE and SUN) and a NDVI model (NPP explained by seasonal NDVI), and a global model (NPP explained by all factors). For each of the model categories, we used the backward selection of variables combined with the Akaike Information Criterion (AIC). In this approach, the model began with all the variables. Remove one variable based on some information criterion (typically the smallest AIC value). Continue this process until all remaining variables are above some pre-established AIC threshold (Burnham and Anderson 2002). We then compared the stepwise-selected models from each category and considered the model which minimizes AIC to be the most appropriate model (Akaike 1973). Although multiple regressions are commonly used for testing effects of many explanatory variables on a targeted response, the multicollinearity of confounded explanatory variables might threaten their statistical and inferential interpretation (Graham 2003). We assessed the effect of multicollinearity on parameter estimation by the mean of variance inflation factor (VIF) criterion (Graham 2003; Etien and others 2009), which was independently of the number of explanatory variables.

Spatial autocorrelation (SAC) in data, i.e. the higher similarity of closer samples, is a common phenomenon in ecology (Lennon 2000). Many studies have incorporated SAC into statistical models (termed spatial models) (Dormann 2007; Hawkins and others 2007; Kissling and Carl

2008; Bini and others 2009). Here, we compared the effects of the OLS models and simultaneous autoregressive (SAR) multiple regression NPP models (taking SAC into account, hereafter referred as SAR models) on the estimation of standardized coefficients, and the automated analysis procedure is performed by the statistical library developed for SAM (Rangel and others 2010). To quantify the effect of correcting for SAC on model coefficients, I used the following formula to transform spatial and non-spatial model coefficients (β_s and β_{ns}, respectively) into a relative SAC effect (rSACe) (Dormann 2007; Bini and others 2009): $\text{rSACe} = |\beta_{ns} - \beta_n|/\text{Maximum}(\beta_{ns} - \beta_n)$. This formula allows for a direct comparison of coefficients from OLS and SAR models: the larger rSACe is, the greater is the difference between coefficient estimates from OLS and SAR models.

Results

Forest NPP in Eastern China

The elevation of the forest study sites ranges from 30 m of temperate EBL(EBL: evergreen broad-leaf) forest in Jiangsu province, to 1966 m of temperate EBL in Hubei province, and the mean elevation of forest NPP sites is 472 m (Table 1). The lowest and highest NPP occur in the boreal ENL (ENL: evergreen needle-leaf) forest (260 c/m^2/y, 410 m) of the northernmost sites in Heilongjiang province and temperate EBL forest (1580 c/m^2/y, 600 m) in Jiangxi province of southern China, respectively. In order of biome, NPP of tropical EBL (916 c/m^2/y) and temperate EBL (930 c/m^2/y) forests are significant greater than temperate DBL (DBL: deciduous broad-leaf) forests (622 c/m^2/y), and the lowest value of NPP was found in needle-leaf forests, such as temperate ENL forests(422 c/m^2/y), boreal DNL(DNL: deciduous needle-leaf) forests (419 c/m^2/y) and boreal ENL forests (373 c/m^2/y). From the spatial patterns of NPP class in eastern China (Fig. 1), one noticeable feature is that NPP in the south domain is significantly greater than the north domain, and the highest NPP sites are all geographically distributed in the southern domain of eastern China, especially for the temperate EBL forest in Fujian province where taking possession of more than half of the top ten NPP sites (1390–1580 c/m^2/y) in eastern China.

Non-Spatial OLS Models

We compared four categories of statistical models to select the most appropriate fit to the data (Table 2). In the physical model, the lowest AIC value was obtained while combining latitude (negative, hereafter referred to as −) and longitude (positive, hereafter referred to as +), and elevation was not selected by the AIC test. The climatic model indicated that NPP was represented most appropriately by winter precipitation (+), as well as the temperatures in spring (+), summer (−) and winter (−) seasons. The climatic model ($R^2 = 0.438$, AIC = 2430.6) was slightly stronger compared with the physical model ($R^2 = 0.407$, AIC = 2438.4). Although NDVI model highlighted the effects of NDVI in spring (+), autumn (−) and winter (−) on NPP, statistically significant association was only found between winter NDVI and NPP. Furthermore, NDVI model was also the weakest model with the lowest explainable variability of NPP ($R^2 = 0.365$, AIC = 2455.7). The Global model, taking into account of all factors, indicated the most influential explanatory variables for NPP were latitude (−), longitude (+), sunshine duration time in winter (−), and temperatures in spring (+) and autumn (−). The Global model had more support than the best model from any single category ($R^2 = 0.468$, AIC = 2420.4).

Table 1 Descriptive statistics (mean, standard deviation and range) of total net primary productivity (TNPP) physical and environmental driving variables for the 221 forest sites in eastern China

	Mean	SD	Range	Time span
TNPP	770	320	260 to 1580	1989–1994
Latitude	34.19	9.54	18.7 to 52.63	–
Longitude	119.17	6.41	108.78 to 134	–
Elevation	472	315	30 to 1966	–
NDVI_SPR	0.35	0.08	0.16 to 0.54	1986, 1987, 1990
NDVI_SUM	0.60	0.08	0.38 to 0.75	1986, 1987, 1990
NDVI_AUT	0.48	0.08	0.27 to 0.62	1986, 1987, 1990
NDVI_WIN	0.28	0.15	0.04 to 0.54	1986, 1987, 1990
PRE_SPR	385	262	35 to 819	1960–1990
PRE_SUM	527	163	259 to 1465	1960–1990
PRE_AUT	193	89	60 to 751	1960–1990
PRE_WIN	114	83	4 to 264	1960–1990
SUN_SPR	112	54	44 to 203	1960–1990
SUN_SUM	120	21	71 to 175	1960–1990
SUN_AUT	144	32	85 to 212	1960–1990
SUN_WIN	135	54	55 to 220	1960–1990
TEM_SPR	10.10	7.04	−4.1 to 23.47	1960–1990
TEM_SUM	21.76	3.80	13.57 to 28.07	1960–1990
TEM_AUT	10.92	7.99	−5.5 to 24.03	1960–1990
TEM_WIN	−3.48	12.61	−29.77 to 17.83	1960–1990

The Detection of Multicollinearity for OLS Models

The mean variance inflation factor (VIF) of various predictors in physical, climatic, NDVI and global models was 2.86, 8.75, 3.4 and 7.48 respectively, which was far below

Table 2 Most supported ordinary least-squares regression models for four categories of effects hypothesized to affect forest net primary productivity (NPP) based on 221 forests sites (1989–1994) in eastern China

Model	R^2	Adjusted R^{2a}	P value	AIC[b]
Physical model				
$Y = -29.24 \times \mathrm{Lat}^* + 15.79 \times \mathrm{Long}^* - 111.21$	0.407	0.402	<0.001	2438.4
Climatic model				
$Y = 2.29 \times \mathrm{PRE}^*_{\mathrm{WIN}} + 103.29 \times \mathrm{TEM}^*_{\mathrm{SPR}} - 72.82 \times \mathrm{TEM}^*_{\mathrm{SUM}} - 35.21 \times \mathrm{TEM}^*_{\mathrm{WIN}} + 928.48$	0.438	0.428	<0.001	2430.6
NDVI model				
$Y = 718.2 \times \mathrm{NDVI}_{\mathrm{SPR}} - 417.4 \times \mathrm{NDVI}_{\mathrm{SUM}} - 854.6 \times \mathrm{NDVI}^*_{\mathrm{WIN}} + 533.6$	0.365	0.356	<0.001	2455.7
Global model				
$Y = -37.1 \times \mathrm{Lat}^* + 26.09 \times \mathrm{Long}^* - 2.58 \times \mathrm{SUN}^*_{\mathrm{WIN}} + 89.13 \times \mathrm{TEM}^*_{\mathrm{SPR}} - 97.36 \times \mathrm{TEM}^*_{\mathrm{AUT}} - 557.65$	0.468	0.456	<0.001	2420.4

Note In multiple linear regression, data are fit to a linear model that predicts values of a response (Y) as the weighted sum of explanatory variables (X_i) and random error (ε): $Y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \cdots + \beta_i X_i + \varepsilon$, where β_i is regression coefficient

* Significant level of <0.01 in Student's t test between NPP and its driving variables

[a] Adjusted R^2: adjusted to account for the number of terms in the model

[b] AIC: Akaike information criterion for model comparison

the pathological value of 10 (Neter and others 1996; Chatterjee and others 2000). This indicated that the overall severity of multicollinearity in our dataset was minimal, and the individual effects of explanatory variables on NPP in those models were true synergistic relationships rather than spurious correlations.

Spatial SAR Models

Irrespective of the moderate difference of coefficients for various predictors, SAR models generated results generally concordant with OLS models (Tables 2, 3). Furthermore, the value of rSACe calculated from OLS and SAR models was extremely small, ranging from 0.01 in global models to 0.03 in NDVI models. Therefore, spatial autocorrelation (SAC) was not a serious issue in this dataset and should not threaten analyses and subsequent inferential interpretation. Consequently, the explanatory variables predicted by OLS models should have the perceived importance. We also observed that AIC (from 3047.5 to 3039.9) of SAR models actually was higher than those (from 2420.4 to 2438.4) of OLS models (Tables 2, 3). This was not surprising, because SAR models incorporated the spatial autocorrelation in the residual covariance in comparison to OLS models.

Discussions

The physical and global models indicated that forest NPP in eastern China had significant negative correlation with latitude, and positive relationship with longitude. We found empirical support for the common hypothesis that forest NPP in China decreases from south to north in relation to the decreasing temperature and precipitation, and increases from west to east in relation to the moisture gradient. Some previous studies assumed that elevation might lead to uncertainties in the relationship between climate and NPP (Ni and others 2001). However, based on our physical and global models we found no evidence that NPP in eastern China was associated with elevation.

Our best climatic models indicated that energy input in winter was important in explaining forest NPP in eastern China. The most important climatic factors were the negative influence of winter temperature and sunshine duration time, as indicated by climatic and global models, respectively. Our result substantiate the hypothesis that anomalously warm winter climate can result in a loss of frost resistance during a prolonged thaw period, at a time that the tree is normally dormant and fully frost hardy (Auclair and others 1996). This thaw period increases the probability that a subsequent severe freezing event will damage the forests (Yin and others 1994), which will deplete the pool of the stored carbohydrates and reduce a forest's potential for future growth. One extreme example is China's snow disaster in 2008, which broke 57-year records for freezing days and minimum temperatures and had severe negative impacts on natural and agricultural ecosystems, and resulted in serious human and economic losses (Wang and other 2008; Hui 2009). Winter temperatures also constrain tree growth in different temperate forest ecosystems in eastern North American (Pederson and others 2004). The importance of winter climate on forest NPP is further emphasized by the strong positive effect of

Table 3 Most supported spatial autocorrelation regression models for four categories of effects hypothesized to affect forest net primary productivity (NPP) based on 221 forest sites (1989–1994) in eastern China

Model	R^2	Adjusted R^{2a}	P value	AIC[b]
Physical model				
$Y = -27.3 \times \mathrm{Lat}^* + 12.19 \times \mathrm{Long}^* - 129.57$	0.408	0.395	<0.001	3035.9
Climatic model				
$Y = 1.98 \times \mathrm{PRE}^*_{\mathrm{WIN}} + 87.47 \times \mathrm{TEM}^*_{\mathrm{SPR}} - 63.44 \times \mathrm{TEM}^*_{\mathrm{SUM}} - 25.78 \times \mathrm{TEM}^*_{\mathrm{WIN}} + 920.69$	0.433	0.415	<0.001	3039.6
NDVI model				
$Y = 812.11 \times \mathrm{NDVI}_{\mathrm{SPR}} - 593.84 \times \mathrm{NDVI}_{\mathrm{SUM}} - 389.24 \times \mathrm{NDVI}^*_{\mathrm{WIN}} + 611.1$	0.333	0.314	<0.001	3047.5
Global model				
$Y = -34.21 \times \mathrm{Lat}^* + 23.27 \times \mathrm{Long}^* - 2.32 \times \mathrm{SUN}^*_{\mathrm{WIN}} + 77.61 \times \mathrm{TEM}^*_{\mathrm{SPR}} - 83.48 \times \mathrm{TEM}^*_{\mathrm{AUT}} - 419.3$	0.466	0.448	<0.001	3039.9

* Significant level of < 0.01 in Student's t test between NPP and its driving variables

[a] Adjusted R^2: adjusted to account for the number of terms in the model

[b] AIC: Akaike information criterion for model comparison

winter precipitation in the climatic models, and this can be also related to a direct physiological influence. Forest growth benefits from the previous winter's precipitation, as the latter works to enrich soil moisture storage, which is crucial for the coming year tree growth. Precipitation throughout the dormant season might likewise control water availability in early spring (Oberhuber and others 1998).

Climatic models also indicated a positive relationship of forest NPP with spring temperature. In conditions where temperature strongly limits the radial growth of trees, especially in northern part of eastern China, the temperature must be higher than some threshold for the thawing of the upper soil layer so that radial growth can commence (Goldstein and others 1985; Vaganov and others 1999). High spring temperatures also lead to the breaking of dormancy and the resumption of physiological activity in the tree, and thus increase the duration of the current growing season (Lebourgeois and others 2005). Furthermore, a warm spring will speed the snowmelt and have a subsequent positive effect on soil moisture in early forest growth season.

We also found support for negative effects of summer (climatic model) and autumn (global model) temperatures. Trees divide and enlarge cells most actively during the warmest period of the growing season, and the climate conditions during this period determine the amount of photosynthates available for radial growth (Raftoyannis and Radoglou 2002; Deslauriers and others 2003). High temperatures and strong solar radiation in summer and autumn seasons can intensify evaporation rates thus decreasing moisture content (Körner 1998; Granier and others 2000). A water deficit results in a higher loss of assimilated carbon as a source of energy thus should be detrimental to tree growth (Aranda and others 2000; Lebourgeois and others 2005). In contrast, a cool, moist summer and autumn can result in rapid tree growth because evapotranspiration losses are smaller and water stress reduced (Kienast and others 1987). A similar trend was found by Clark and others (2003), who observed daily minimum temperatures were negatively related to large interyear variations in forest-wide aboveground biomass increment of tropical forests. There is a large and well-established body of literature describing the temperature inducing drought stress is one possible explanation for a late-twentieth century decrease in the positive relationship of temperature and forest growth at high northern latitudes across the Northern Hemisphere (Briffa and others 1998; Barber and others 2000; Büntgen and others 2008; D'Arrigo 2008). Based on weather station data in Asia-Pacific Network (APN) countries examined for the 1955–2007 period, Choi and others (2009) have confirmed the fact that summer warm nights and days are changing more rapidly per unit change in mean temperatures than the corresponding frequencies for cool nights and days. Under recent climate warming (Kerr 2007), temperature-induced drought stress may become the dominant factor limiting the future capacity of forests in eastern China to sequester carbon.

NDVI is a useful tool for assessing extent and condition of vegetation (Tucker 1979; Myneni and others 1995) and NPP has been frequently predicted by NDVI. For example, Fang and others (2001) used an annual mean NDVI dataset over China to quantify temporal NPP variability relative to precipitation variation for five biome groups across China. Nemani and others (2003) used a biome-specific production efficiency model that combined photosynthetically active radiation (FPAR) and leaf area index (LAI) derived

from NDVI with climate data to estimate the annual estimated NPP across the world. We found a positive relationship between NPP and NDVI in spring, but a negative relationship in summer and winter. This result is generally concordant with the response patterns of NPP to temperature. The advancement of forest growing season primarily led by an elevated spring temperature is suggestive of an increase in forest growth associated with a lengthening of the active growing season (Keeling and others 1996; Myneni and others 1997; Nemani and others 2003). This might be employed as a potential interpretation of positive link between spring NDVI and NPP. Based on a time series NDVI and corresponding ground-based information in China, Piao and others (2003) also emphasized that the regions with the largest increase in spring NPP appeared mainly in eastern China. The detrimental impacts on forest growth of high temperature in winter (loss of frost resistance) and summer (drought stress) should be the plausible explanations for negative relationships of NPP with NDVI in winter and summer. In sum, the relationships between forest NPP and seasonal NDVI are complicated, and the direction of the effects can change among the different seasons. The assumption of a uniform positive relationship between NDVI and NPP models, based on annual data, might lead to biased results if seasonal effects are not adequately considered.

Conclusion

Study of the responses of terrestrial net primary production (NPP) to climate changes can help scientists understand feedback between climate systems and terrestrial ecosystems and be one of key focuses for global scientific community (Cramer and others 1999). We developed four categories of NPP models (Physical, Climatic, NDVI and Global) based factors hypothesized to affect NPP. We used data for 221 sites in eastern China from the EMDI project and successfully fit regression models for all model categories and identified strong predictors of NPP in eastern China. Based on our most supported models that considered all categories of effects (global models), the best predictors of NPP were latitude (−), longitude (+), winter sunshine duration (−), spring temperature (+), and autumn temperature (−). In addition the important seasonal effects on NPP included summer and autumn drought stress (as indicated by temperature) and spring NDVI (+), summer NDVI (−) and winter NDVI (−) seasons. Most studies of NPP have focused on annual climate data (Fang and others 2001; Knapp and Smith 2001; Nemani and others 2003; Schuur 2003). We suggest more investigation of seasonal climate effects on NPP are needed to understand the relationship between NPP and climate and to develop better climate-vegetation models (Hicke and others 2002; Piao and others 2003; Yu and others 2008).

Acknowledgments Funding support for this study was provided by the National Basic Research Program of China (Grant No. 2009CB421104) and The "Strategic Priority Research Program-Climate Change: Carbon Budget and Relevant Issues" of the Chinese Academy of Sciences (Grant No. XDA05060104). We would like to thank Xiaoming Feng and Nan lü for assisting with the design and application of the survey, Yu liu for providing valuable assistance on data analysis, and two anonymous reviewers for valuable remarks on an early version of the manuscript.

References

Akaike H (1973) Information theory and extension of the likelihood ratio principle. In: Pietrov BN, Csaki F (eds) Proceedings of the second international symposium of information theory. Akademiai Kiado, Budapest, pp 257–281

Aranda I, Gil L, Pardos JA (2000) Water relations and gas exchange in *Fagus sylvatica* L. and *Quercus petraea* (Mattuschka) Liebl. in a mixed stand at their southern limit of distribution in Europe. Trees-Structure and Function 14(6):344–352

Auclair AND, Lill JT, Revenga C (1996) The role of climate variability and global warming in the dieback of Northern hardwoods. Water, Air, and Soil Pollution 91(3–4):163–186

Barber VA, Juday GP, Finney BP (2000) Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. Nature 405(6787):668–673

Bini LM, Diniz JAF, Rangel TFLVB, Akre TSB, Albaladejo RG, Albuquerque FS, Aparicio A, Araujo MB, Baselga A, Beck J, Bellocq MI, Bohning-Gaese K, Borges PAV, Castro-Parga I, Chey VK, Chown SL, de Marco P, Dobkin DS, Ferrer-Castan D, Field R, Filloy J, Fleishman E, Gomez JF, Hortal J, Iverson JB, Kerr JT, Kissling WD, Kitching IJ, Leon-Cortes JL, Lobo JM, Montoya D, Morales-Castilla I, Moreno JC, Oberdorff T, Olalla-Tarraga MA, Pausas JG, Qian H, Rahbek C, Rodriguez MA, Rueda M, Ruggiero A, Sackmann P, Sanders NJ, Terribile LC, Vetaas OR, Hawkins BA (2009) Coefficient shifts in geographical ecology: an empirical evaluation of spatial and non-spatial regression. Ecography 32(2):193–204

Briffa KR, Schweingruber FH, Jones PD, Osborn TJ, Shiyatov SG, Vaganov EA (1998) Reduced sensitivity of recent tree-growth to temperature at high northern latitudes. Nature 391(6668): 678–682

Büntgen U, Frank D, Wilson R, Carrer M, Urbinati C (2008) Testing for tree-ring divergence in the European Alps. Global Change Biology 14(10):2443–2453

Burnham KP, Anderson DR (2002) Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York

Chatterjee S, Hadi AS, Price B (2000) Regression analysis by example. Wiley, New York

Cheng C (1993) Climate and agriculture in China. China Meteorological Press, Beijing

Choi G, Collins D, Ren GY, Trewin B, Baldi M, Fukuda Y, Afzaal M, Pianmana T, Gomboluudev P, Huong PTT, Lias N, Kwon WT, Boo KO, Cha YM, Zhou YQ (2009) Changes in means and extreme events of temperature and precipitation in the Asia-Pacific Network region, 1955–2007. International Journal of Climatology 29(13):1906–1925

Clark DA, Piper SC, Keeling CD, Clark DB (2003) Tropical rain forest tree growth and atmospheric carbon dynamics linked to

interannual temperature variation during 1984–2000. Proceedings of the National Academy of Sciences of the United States of America 100(10):5852–5857

Cramer W, Kicklighter DW, Bondeau A, Moore B, Churkina C, Nemry B, Ruimy A, Schloss AL (1999) Comparing global models of terrestrial net primary productivity (NPP): overview and key results. Global Change Biology 5(S1):1–15

D'Arrigo R (2008) On the 'Divergence Problem' in Northern Forests: a review of the tree-ring evidence and possible causes. Global and Planetary Change 60(3–4):289–305

Del Grosso S, Parton W, Stohlgren T, Zheng DL, Bachelet D, Prince S, Hibbard K, Olson R (2008) Global potential net primary production predicted from vegetation class, precipitation, and temperature. Ecology 89(8):2117–2126

Deslauriers A, Morin H, Begin Y (2003) Cellular phenology of annual ring formation of Abies balsamea in the Quebec boreal forest (Canada). Canadian Journal of Forest Research 33(2):190–200

Diallo O, Diouf A, Hanan NP, Naliaye A, Prevost Y (1991) AVHRR monitoring of savanna primary production in Senegal, West Africa: 1987–1988. International Journal of Remote Sensing 12(6):1259–1279

Dormann CF (2007) Effects of incorporating spatial autocorrelation into the analysis of species distribution data. Global Ecology and Biogeography 16(2):129–138

Editorial Committee for Vegetation of China (1980) Vegetation of China Science Press, Beijing

Etien N, Daux V, Masson-Delmotte V, Mestre O, Stievenard M, Guillemin MT, Boettger T, Breda N, Haupt M, Perraud PP (2009) Summer maximum temperature in northern France over the past century: instrumental data versus multiple proxies (tree-ring isotopes, grape harvest dates and forest fires). Climatic Change 94(3–4):429–456

Fang JY, Wang GG, Liu GH, Xu SL (1998) Forest biomass of China: an estimate based on the biomass-volume relationship. Ecological Applications 8(4):1084–1091

Fang JY, Chen AP, Peng CH, Zhao SQ, Ci L (2001) Changes in forest biomass carbon storage in China between 1949 and 1998. Science 292(5525):2320–2322

Fang JY, Song YC, Liu HY, Piao SL (2002) Vegetation–climate relationship and its application in the division of vegetation zone in China. Acta Botanica Sinica 44(9):1105–1122

Fang JY, Piao SL, Zhou LM, He JS, Wei FY, Myneni RB, Tucker CJ, Tan K (2005) Precipitation patterns alter growth of temperate vegetation. Geophysical Research Letters 32(21):L21411. doi: 21410.21029/22005GL024231

Gao Q, Yu M, Yang XS (2000) An analysis of sensitivity of terrestrial ecosystems in China to climatic change using spatial simulation. Climatic Change 47(4):373–400

Goldstein GH, Brubaker LB, Hinckley TM (1985) Water relations of white spruce (*Picea glauca* (Moench) Voss) at tree line in north Alaska. Canadian Journal of Forest Research 15(6):1080–1087

Goward SN, Turner S, Dye DG, Liang S (1994) The University-of-Maryland improved global vegetation index product. International Journal of Remote Sensing 15(17):3365–3395

Graham MH (2003) Confronting multicollinearity in ecological multiple regression. Ecology 84(11):2809–2815

Granier A, Biron P, Lemoine D (2000) Water balance, transpiration and canopy conductance in two beech stands. Agricultural and Forest Meteorology 100(4):291–308

Hawkins BA, Diniz JAF, Bini LM, De Marco P, Blackburn TM (2007) Red herrings revisited: spatial autocorrelation and parameter estimation in geographical ecology. Ecography 30(3):375–384

Hicke JA, Asner GP, Randerson JT, Tucker C, Los S, Birdsey R, Jenkins JC, Field C, Holland E (2002) Satellite-derived increases in net primary productivity across North America, 1982–1998. Geophysical Research Letters 29(10):L1427. doi: 1410.1029/2001GL013578

Hu ZM, Fan JW, Zhong HP, Yu GR (2007) Spatiotemporal dynamics of aboveground primary productivity along a precipitation gradient in Chinese temperate grassland. Science in China Series D-Earth Sciences 50(5):754–764

Hui G (2009) China's snow disaster in 2008, who is the principal player? International Journal of Climatology 29(14):2191–2196

James ME, Kalluri S (1994) The Pathfinder AVHRR land data set: an improved coarse resolution data set for terrestrial monitoring. International Journal of Remote Sensing 15(17):3347–3364

Justice CO, Townshend JRG, Holben BN, Tucker CJ (1985) Analysis of the phenology of global vegetation using meteorological satellite data. International Journal of Remote Sensing 6(8):1271–1318

Keeling CD, Chin JFS, Whorf TP (1996) Increased activity of northern vegetation inferred from atmospheric CO_2 measurements. Nature 382(6587):146–149

Kerr RA (2007) Climatic change: global warming is changing the world. Science 316(5822):188–190

Kienast F, Schweingruber FH, Braker OU, Schar E (1987) Tree-ring studies on conifers along ecological gradients and the potential of single-year analyses. Canadian Journal of Forest Research 17(7):683–696

Kissling WD, Carl G (2008) Spatial autocorrelation and the selection of simultaneous autoregressive models. Global Ecology and Biogeography 17(1):59–71

Knapp AK, Smith MD (2001) Variation among biomes in temporal dynamics of aboveground primary production. Science 291(5503):481–484

Körner C (1998) A re-assessment of high elevation treeline positions and their explanation. Oecologia 115(4):445–459

Kumar M, Monteith JL (1982) Remote sensing of plant growth. In: Smith H (ed) Plants and the daylight spectrum. Academic Press, London

Lebourgeois F, Breda N, Ulrich E, Granier A (2005) Climate-tree-growth relationships of European beech (*Fagus sylvatica* L.) in the French Permanent Plot Network (RENECOFOR). Trees-Structure and Function 19(4):385–401

Leemans R, Cramer W (1991) The IIASA database for mean monthly values of temperature, precipitation and cloudiness of a global terrestrial grid. RR-91-18. International Institute for Applied Systems Analysis (IIASA)

Lennon JJ (2000) Red-shifts and red herrings in geographical ecology. Ecography 23(1):101–113

Li ZQ, Yu GR, Xiao XM, Li YN, Zhao XQ, Ren CY, Zhang LM, Fu YL (2007) Modeling gross primary production of alpine ecosystems in the Tibetan Plateau using MODIS images and climate data. Remote Sensing of Environment 107(3):510–519

Lieth H (1975) Modeling the primary productivity of the world. In: Lieth H, Whittaker RH (eds) Primary productivity of the biosphere. Springer-Verlag, New York, pp 237–264

Liu GH, Fu BJ, Fang JY (2000) Carbon dynamics of Chinese forests and its contribution to global carbon balance. Acta Ecologica Sinica 20(5):733–740

Lucht W, Prentice IC, Myneni RB, Sitch S, Friedlingstein P, Cramer W, Bousquet P, Buermann W, Smith B (2002) Climatic control of the high-latitude vegetation greening trend and Pinatubo effect. Science 296(5573):1687–1689

Luo TX (1996) Patterns of biological production and its mathematical models for main forest types of China. PhD dissertation, Committee of Synthesis Investigation of Natural Resources, Chinese Academy of Sciences, Beijing

Malingreau JP (1986) Global vegetation dynamics—satellite-observations over Asia. International Journal of Remote Sensing 7(9):1121–1146

Myneni RB, Hall FG, Sellers PJ, Marshak AL (1995) The interpretation of spectral vegetation indexes. IEEE Transactions on Geoscience and Remote Sensing 33(2):481–486

Myneni RB, Keeling CD, Tucker CJ, Asrar G, Nemani RR (1997) Increased plant growth in the northern high latitudes from 1981 to 1991. Nature 386(6626):698–702

Myneni RB, Dong J, Tucker CJ, Kaufmann RK, Kauppi PE, Liski J, Zhou L, Alexeyev V, Hughes MK (2001) A large carbon sink in the woody biomass of Northern forests. Proceedings of the National Academy of Sciences of the United States of America 98(26):14784–14789

Nemani RR, Keeling CD, Hashimoto H, Jolly WM, Piper SC, Tucker CJ, Myneni RB, Running SW (2003) Climate-driven increases in global terrestrial net primary production from 1982 to 1999. Science 300(5625):1560–1563

Neter J, Kutner MH, Nachtsheim CJ, Wasserman W (1996) Applied linear statistical models. Irwin, Chicago

New M, Hulme M, Jones P (1999) Representing twentieth-century space-time climate variability. Part I. Development of a 1961–90 mean monthly terrestrial climatology. Journal of Climate 12(3):829–856

New M, Hulme M, Jones P (2000) Representing twentieth-century space-time climate variability. Part II. Development of 1901–96 monthly grids of terrestrial surface climate. Journal of Climate 13(13):2217–2238

Ni J (2004) Estimating net primary productivity of grasslands from field biomass measurements in temperate northern China. Plant Ecology 174(2):217–234

Ni J, Zhang XS, Scurlock JMO (2001) Synthesis and analysis of biomass and net primary productivity in Chinese forests. Annals of Forest Science 58(4):351–384

Oberhuber W, Stumbock M, Kofler W (1998) Climate tree-growth relationships of Scots pine stands (*Pinus sylvestris* L.) exposed to soil dryness. Trees-Structure and Function 13(1):19–27

Olson RJ, Johnson K, Zheng D, Scurlock JMO (2001) Global and regional ecosystem modeling: databases of model drivers and validation measurements. ORNL/TM-2001/196. Oak Ridge National Laboratory, Oak Ridge

Pederson N, Cook ER, Jacoby GC, Peteet DM, Griffin KL (2004) The influence of winter temperatures on the annual radial growth of six northern-range-margin tree species. Dendrochronologia 22(1):7–29

Piao SL, Fang JY, Chen AP (2003) Seasonal dynamics of terrestrial net primary production in response to climate changes in China. Acta Botanica Sinica 45(3):269–275

Piao SL, Ciais P, Friedlingstein P, Peylin P, Reichstein M, Luyssaert S, Margolis H, Fang JY, Barr A, Chen AP, Grelle A, Hollinger DY, Laurila T, Lindroth A, Richardson AD, Vesala T (2008) Net carbon dioxide losses of northern ecosystems in response to autumn warming. Nature 451(7174):49–53

Piao SL, Fang JY, Ciais P, Peylin P, Huang Y, Sitch S, Wang T (2009) The carbon balance of terrestrial ecosystems in China. Nature 458(7241):1009–1014

Raftoyannis Y, Radoglou K (2002) Physiological responses of beech and sessile oak in a natural mixed stand during a dry summer. Annals of Botany 89(6):723–730

Rangel TF, Diniz JAF, Bini LM (2010) SAM: a comprehensive application for spatial analysis in Macroecology. Ecography 33(1):46–50

Rosenzweig C, Karoly D, Vicarelli M, Neofotis P, Wu QG, Casassa G, Menzel A, Root TL, Estrella N, Seguin B, Tryjanowski P, Liu CZ, Rawlins S, Imeson A (2008) Attributing physical and biological impacts to anthropogenic climate change. Nature 453(7193):353–357

Schuur EAG (2003) Productivity and global climate revisited: the sensitivity of tropical forest growth to precipitation. Ecology 84(5):1165–1170

Sellers PJ, Los SO, Tucker CJ, Justice CO, Dazlich DA, Collatz GJ, Randall DA (1996) A revised land surface parameterization (SiB2) for atmospheric GCMs.2. The generation of global fields of terrestrial biophysical parameters from satellite data. Journal of Climate 9(4):706–737

Sherry RA, Zhou XH, Gu SL, Arnone JA, Schimel DS, Verburg PS, Wallace LL, Luo YQ (2007) Divergence of reproductive phenology under climate warming. Proceedings of the National Academy of Sciences of the United States of America 104(1):198–202

Tao SY, Chen LX (1987) A review of recent research on the east Asian summer monsoon in China. In: Chang CP, Krishnamurti TN (eds) Monsoon meteorology. Oxford University Press, London, pp 60–92

Tucker CJ (1979) Red and photographic infrared linear combinations for monitoring vegetation. Remote Sensing of Environment 8(2):127–150

Vaganov EA, Hughes MK, Kirdyanov AV, Schweingruber FH, Silkin PP (1999) Influence of snowfall and melt timing on tree growth in subarctic Eurasia. Nature 400(6740):149–151

Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin JM, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. Nature 416(6879):389–395

Wang ZY, Zhang Q, Chen Y, Zhao S, Zeng H, Zhang Y, Liu Q (2008) Characters of meteorological disasters caused by the extreme synoptic process in early 2008 over China. Advances in Climate Change Research 4(2):63–67

Yin XW, Foster NW, Morrison IK, Arp PA (1994) Tree-ring based growth analysis for a Sugar Maple stand—relations to local climate and transient soil properties. Canadian Journal of Forest Research 24(8):1567–1574

Yu GR, Zhang LM, Sun XM, Fu YL, Wen XF, Wang QF, Li SG, Ren CY, Song X, Liu YF, Han SJ, Yan JH (2008) Environmental controls over carbon exchange of three forest ecosystems in eastern China. Global Change Biology 14(11):2555–2571

Zhou BH, Zheng BH (2008) Research on aquatic ecoregions for lakes and reservoirs in China. Environmental Monitoring and Assessment 147(1–3):339–350