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Approaches of climate factors affecting the spatial variation of annual gross primary productivity among terrestrial ecosystems in China

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ABSTRACT

Analyzing the approaches that climatic factors affect the spatial variation of annual gross primary productivity (GPP_{yr}) would improve our understanding on its spatial pattern. Based on network eddy covariance measurements and published data in literature, we separated GPP_{yr} into radiation use efficiency (RUE) and annual absorbed photosynthesis active radiation ($APAR_{yr}$), where $APAR_{yr}$ can be regarded as the product of the fraction of absorbed annual photosynthesis active radiation ($FPAR_{yr}$) and annual PAR (PAR_{yr}). Given that PAR_{yr} affects the spatial variation of GPP_{yr} directly through itself, we investigated factors affecting the spatial variations of RUE and $FPAR_{yr}$, to reveal how climatic factors affect the spatial variation of GPP_{yr}. Results suggest that the spatial variation of RUE was directly affected by annual mean air temperature (MAT) and annual mean CO_2 mass concentration (ρ_{cyr}). The increasing MAT and ρ_{cyr} directly enhanced RUE. The increasing annual precipitation (MAP) directly prompted $FPAR_{yr}$. Therefore, MAT and ρ_{cyr} affected the spatial variation of GPP_{yr} through altering RUE while the effect of MAP was achieved through altering $FPAR_{yr}$. Our study could also provide an alternative way for regional GPP_{yr} assessment.

1. Introduction

Gross primary productivity (GPP) is the amount of CO_2 that is taken up by plants from the atmosphere through photosynthesis (Chen et al., 2012), serving as the largest carbon flux between terrestrial ecosystems and the atmosphere (Beer et al., 2010). Along with ecosystem respiration, GPP controls the CO_2 exchange between terrestrial ecosystems and the atmosphere (Beer et al., 2010), which is of significant importance in regulating the terrestrial carbon budget (Chapin et al., 2006; Yuan et al., 2010) and then climate change (Ciais et al., 2013; Hilker et al., 2008; Li et al., 2013). Additionally, as the start of biogeochemical cycles, GPP drives several ecosystem functions (Beer et al., 2010) and contributes to ecosystem services such as food and wood production. Therefore, it is worthwhile to quantify the magnitude of GPP and its spatial variation at the regional scale.

Based on network eddy covariance measurements, many investigations have analyzed the spatial variation of annual GPP (GPP_{yr}) and its affecting factors (Baldocchi, 2008; Chen et al., 2013b; Kato and Tang, 2008; Law et al., 2002; Luyssaert et al., 2007; Wang et al., 2008b; Yu et al., 2013). Many factors, especially climatic variables such as annual mean air temperature (MAT) (Chen et al., 2013b; Kato and Tang, 2008; Luyssaert et al., 2007; Magnani et al., 2007; Reichstein et al., 2007; Yu et al., 2013) and annual precipitation (MAP) (Chen et al., 2013b; Kato and Tang, 2008; Luyssaert et al., 2007; Yu et al., 2013), were found to strongly affect the spatial

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variation of GPP_{yr}. However, how these climatic factors affect the spatial variation of GPP_{yr} was not well documented, which impeded our fully understanding on the spatial variation of GPP_{yr}.

Radiation use efficiency theory is widely used to describe the dynamics of GPP over the world (Running et al., 2004; Wang et al., 2010; Wu et al., 2010a; Zhao and Running, 2010), which provides a solid basis for revealing how climatic factors affect the spatial variation of GPP_{yr}. According to the radiation use efficiency theory (Monteith, 1972), GPP_{yr} can be considered as the product of radiation use efficiency (RUE) and absorbed annual photosynthesis active radiation ($APAR_{yr}$), where $APAR_{yr}$ was the fraction of $APAR_{yr}$ ($FPAR_{yr}$) multiplying annual photosynthesis active radiation (PAR_{yr}). Given that PAR_{yr} affects the spatial variation of GPP_{yr} by itself, analyzing factors affecting the spatial variations of RUE and $FPAR_{yr}$ would thus underpin our understanding on how factors affect that of GPP_{yr}. Factors affecting the spatial variation of RUE have been extensively investigated. For example, the spatial variation of RUE was found to be affected by that of MAT (Schwalm et al., 2006) or MAP (Garbulsky et al., 2010), while most of these studies were conducted among European (Garbulsky et al., 2010) or American ecosystems (Schwalm et al., 2006), which covered a limited range of altitude. Though climatic and global change were found to influence the interannual variation of $FPAR_{yr}$ (Ciais et al., 2005; Nemani et al., 2003), little attention was paid to factors affecting the spatial variation of $FPAR_{yr}$ as it can be directly calculated from satellite products. Therefore, our current understandings on how climatic factors affect the spatial variation of RUE and $FPAR_{yr}$ thus GPP_{yr} may be insufficient, which impeded our understanding on GPP_{yr} spatial variation.

Situated in the eastern of Asia, China experiences a unique climate and huge altitude gradient because of the uplift of Qinghai-Tibetan Plateau and Asian monsoon (Wu et al., 2007). Therefore, analyzing the spatial variations of RUE and $FPAR_{yr}$ in China would help to reveal how various factors affect the global variation of GPP_{yr}, which would also provide an alternative tool to assess the spatiotemporal variation of GPP_{yr}, the basis for carbon management policy aiming at mitigating climate change (Houghton, 2007; Piao et al., 2009). Chinese scientists have conducted eddy covariance measurements, which simultaneously measured CO_2 fluxes and meteorological variables, for many years (Yu et al., 2013), making it possible to conduct such an analysis.

Therefore, based on radiation use efficiency theory and eddy covariance measurements in China (Fig. 1), we first separated GPP_{yr} into RUE, $FPAR_{yr}$, and PAR_{yr}. Then factors affecting the spatial variations of RUE and $FPAR_{yr}$ were detailed investigated. The specific objectives of our study were to: 1) reveal factors affecting the spatial variations of RUE and $FPAR_{yr}$ in terrestrial ecosystems of China, and 2) further clarify how climatic factors affect the spatial variation of GPP_{yr}.

2. Material and methods

2.1. Site information

By integrating ChinaFLUX observations and other measurements in literature, we built a dataset containing 55-site GPP_{yr} data (Fig. 1). This dataset covered most ecosystem types (Fig. 1) and fully represented the spatial distribution of typical ecosystems in China. The detailed site information was provided in Table 1.

2.2. GPP_{yr} and climatic data processing

In this study, GPP_{yr} was estimated from eddy covariance measurements, which was collected from literature. When collecting GPP_{yr} data, we simultaneously gathered geographical information and main climatic variables, including latitude, longitude, altitude, MAT, MAP, and PAR_{yr}, most of which were thought to potentially affect the spatial variation of GPP_{yr}. If the site missed MAT and MAP, we used its multi-year average as the substitution. If there were no PAR_{yr} observations, we obtained its value from the interpolated PAR_{yr} (Zhu et al., 2010).

In addition, CO_2 was found to affect the seasonal and interannual variation of instaneous GPP (Norby et al., 2005). Therefore, we introduced annual mean CO_2 mass concentration (ρ_{cyr}) as another climatic variable. Given that no ρ_{cyr} was directly reported at most sites, we calculated ρ_{cyr} based on the CO_2 mole fraction (b_c) from Mauna Loa (Keeling et al., 1976; Thoning et al., 1989), CO_2 mole mass (M_c, 44 g mol^{-1}), and mole volume at the current state (V_1) as:

$$\rho_{cyr} = \frac{b_c \times M_c}{V_1} \tag{1}$$

Where V_1 can be calculated based on the ideal gas state equation as:

$$\begin{aligned} V_1 &= \frac{P_0 \times V_0}{(273.15 + T_{a0})} \times \frac{(273.15 + T_{a1})}{P_1} \\ &= \frac{101325 \times 22.4 \times 10^{-3}}{298.15} \times \frac{(273.15 + T_{a1})}{P_1} \end{aligned} \tag{2}$$

where P_1 and T_{a1} are the atmospheric pressure and MAT at the current state, respectively. While P_0, V_0, and T_{a0} are the atmosphere pressure, mole volume, and MAT at the normal state, respectively, which equal to 101325 Pa, 22.4×10^{-3} m^3 mol^{-1}, and 25 °C, respectively.

According to the pressure-height formula, we calculated P_1 from altitude (Alt, with the unit of m) and MAT (with the unit of °C) as:

$$P_1 = 1013.25/10^{\left(\frac{\text{Alt}}{18400\times(1+\frac{\text{MAT}}{273})}\right)} \tag{3}$$

In addition, if the site had multiyear observations, we calculated the mean GPP_{yr} and climatic variables among the measuring period, which may exclude the effect of inter-annual variation.

2.3. Leaf area index data processing

At each site, we extracted LAI data with 8-day temporal resolution from the global land surface satellite dataset (Liang et al., 2013) and calculated the annual mean LAI (LAI_{yr}) for the year that GPP_{yr} was observed as:

$$LAI_{yr} = \frac{1}{46}\sum_{i=1}^{46} LAI_i \tag{4}$$

where LAI_i is the 8-day LAI values.

If the site had multiyear observations, we also used the mean LAI_{yr} for the measuring period to represent its biotic factor.

2.4. RUE calculation

According to the radiation use efficiency theory, GPP_{yr} is the product of RUE, $FPAR_{yr}$, and PAR_{yr}. $FPAR_{yr}$ can be calculated from LAI_{yr} based on Beer-lambert law as:

$$FPAR_{yr} = 1 - \exp(-k \times LAI_{yr}) \tag{5}$$

where k is the extinction coefficient, which is set to 0.5 according to Yuan et al. (2010). Therefore, RUE (gC MJ^{-1}) was calculated as

$$RUE = \frac{GPP_{yr}}{FPAR_{yr} \times PAR_{yr}} \tag{6}$$

Table 1
Site information used in this study.

Observation period	Site code	Latitude (°N)	Longitude (°E)	Altitude (m.a.s.l)	Ecosystem types	IGBP classification[1]	MAT (°C)[2]	MAP (mm)	GPP_{yr} (gC m^{-2} yr^{-1})	Reference
2003–2008	XSBN	21.95	101.20	750	Forest	EBF	19.25 ± 0.23	1416.75 ± 201.09	2342.67 ± 174.10	(Zhang et al., 2010)
2003–2008	DHS	23.17	112.53	300	Forest	MF	20.37 ± 0.32	1481.67 ± 353.56	1367.26 ± 78.42	ChinaFLUX
2009–2010	ALS	24.53	101.02	2476	Forest	EBF	11.63	1374.4	1848.34	(Tan et al., 2011)
2003–2008	QYZ	26.73	115.05	100	Forest	EBF	18.19 ± 0.41	1094.03 ± 204.91	1798.74 ± 100.44	ChinaFLUX
2008	HT	26.83	109.75	330	Forest	ENF	16.8	1214.9	1272	(Zhang, 2010)
2003	TY	28.92	111.45	92	Cropland	CRO	17	1050	1598.54	(Zhu, 2005)
2006–2007	YY	29.53	112.86	30	Forest	EBF	17.85	1502.99	1974.8	(Han, 2008)
2004–2008	DX	29.67	91.33	4250	Grassland	GRA	2.51 ± 0.49	468.44 ± 155.61	197.47 ± 58.14	ChinaFLUX
2006–2007	AQ	30.47	116.99	10	Forest	EBF	17.41	1500	1859.2	(Han, 2008)
2005–2007	DTG	31.52	121.96	4	Wetland	WET	16.33 ± 0.47	864.67 ± 50.16	1829.67 ± 193.54	(Guo, 2010a)
2005–2007	DTD	31.52	121.97	4	Wetland	WET	16.33 ± 0.47	864.67 ± 50.16	1570 ± 218.09	(Guo, 2010a)
2005	DTZ	31.58	121.90	4	Wetland	WET	15.56	817	1512.63	FLUXNET
2010	XP	33.35	113.91	49	Forest	DBF	14.8	529.5	1288.1	(Geng, 2011)
2006	SJY	34.35	100.55	3980	Grassland	GRA	-2	461	480.27	(Wu et al., 2010b)
2007–2008	WS	36.65	116.05	30	Cropland	CRO	13.45	470.55	1838	(Lei and Yang, 2010)
2003–2008	YC	36.83	116.57	28	Cropland	CRO	12.91 ± 0.78	575.35 ± 174.75	1746.62 ± 139.35	ChinaFLUX
2002–2004	HB	37.62	101.30	3250	Grassland	GRA	-1.03 ± 0.45	609.37 ± 31.47	634.5 ± 54.15	(Kato et al., 2006)
2003–2008	HBGC	37.67	101.33	3293	Grassland	GRA	-1.77 ± 0.74	473.9 ± 65.45	574.64 ± 45.22	ChinaFLUX
2004–2008	HBSD	37.68	101.31	3160	Wetland	WET	-1.35 ± 0.49	438.9 ± 110.40	489.12 ± 40.61	ChinaFLUX
2006	DXF	39.53	116.25	30	Forest	DBF	11.5	444.2	1525	(Zha, 2007)
2006	KBQG	40.38	108.55	1170	Grassland	GRA	7.5	180	270.18	FLUXNET
2005–2006	KBQF	40.54	108.69	1020	Forest	DBF	9.38	153.06	162.78	FLUXNET
2005	PJ	41.13	121.90	7	Wetland	WET	8.97	590	1298.16	(Zhou et al., 2009)
2005–2006	DLC	42.05	116.67	1350	Cropland	CRO	3.02	411.4	306.76	(Zhang et al., 2007)
2005–2006	DLG	42.05	116.28	1350	Grassland	GRA	2.77	550.08	324.16	(Zhang et al., 2007)
2003–2008	CBS	42.40	128.10	736	Forest	MF	4.42 ± 0.57	465.65 ± 35.78	1338.84 ± 108.86	ChinaFLUX
2006	XLF	43.55	116.67	1250	Grassland	GRA	1.45	202	148.71	(Chen et al., 2009), FLUXNET
2006	XLD	43.55	116.67	1250	Grassland	GRA	1.51	202	294.45	(Chen et al., 2009), FLUXNET
2004–2006	XLHT	44.13	116.33	1030	Grassland	GRA	1.9 ± 1.49	241.67 ± 63.07	130.02 ± 25.53	(Wang et al., 2008c)
2004–2006	FK	44.28	87.93	475	Grassland	GRA	6.5	153.23 ± 23.25	218.25 ± 125.49	(Liu et al., 2012)
2004–2008	NM	44.53	116.67	1189	Grassland	GRA	1.16 ± 1.24	252.46 ± 89.25	231.66 ± 111.13	ChinaFLUX
2004–2006	TYC	44.57	122.92	159	Cropland	CRO	6.37	311.7	444.33 ± 56.36	(Du et al., 2012)
2007–2008	CL	44.58	123.50	150	Grassland	GRA	7.5	296.05	488.15	(Dong et al., 2011)
2004–2006	TYG	44.59	122.52	168	Grassland	GRA	6.37	311.7	304.67 ± 22.81	(Du et al., 2012)
2004	LS	45.33	127.67	340	Forest	DNF	1.79	552	1351	(Wang et al., 2008a)
2004	MES	45.42	127.67	340	Forest	DBF	2.8	772.9	1176	(Wang, 2008)
2004–2006	SJS	47.58	133.52	56	Wetland	WET	2	549.33	497	(Song, 2007)
2006	SJD	47.58	133.52	56	Cropland	CRO	2	544	689	(Song, 2007)
2006	SJC	47.58	133.52	56	Cropland	CRO	2	544	568	(Song, 2007)
2007–2008	HZ	51.78	123.02	773	Forest	DNF	-4.4	655	739.03	ChinaFLUX
2008–2009	REG	33.93	102.87	3430	Wetland	WET	1.1	650	630.95	(Hao et al., 2011)
2010	GQ	21.57	109.76	0	Wetland	WET	22.9	1770	1952.6	(Chen, 2013; Xiao et al., 2013)
2009–2011	YX	23.92	117.42	65	Wetland	WET	21.3	992.57 ± 99.51	1855.33 ± 84.24	(Chen, 2013; Xiao et al., 2013)
2011	LA	30.18	119.34	185	Forest	EBF	16	1201.72	1235.15	(Sun et al., 2013)
2005	HN	33.00	117.00	15	Forest	DBF	17.68	1500	1700.94	FLUXNET
2008	YK	38.86	100.41	1519	Cropland	CRO	7	67.4	1567	(Wang et al., 2012)
2007–2009	XLD	35.020	112.47	410	Forest	DBF	15.08 ± 0.35	395.4 ± 95.22	1332.14 ± 44.18	(Guo, 2010b)
2009–2010	DG	22.97	113.74	40	Forest	EBF	22.7	2033.5	1482	(Sun et al., 2012)
2007–2008	HG	35.95	104.13	1961	Grassland	GRA	8.3	250	204	(Du et al., 2012)
2006–2009	JFL	18.61	108.84	890	Forest	EBF	19.8	2348.75	1970	(Chen, 2010)
2011	AJ	30.48	119.67	380	Forest	EBF	14	1518.8	1595	(Yang, 2012)
2010	HY	36.95	100.75	3140	Grassland	GRA	1	354.2	611.43	(Zhang et al., 2012)
2008	AR	38.04	100.46	3032	Grassland	GRA	-0.67	450	853	(Wang et al., 2012)
2012	BDL	40.37	115.94	535	Forest	DBF	8.6	354.4	694	(Tang et al., 2013)
2012	ALP	40.02	116.38	51	Forest	DBF	10.8	716	1192	(Chen et al., 2013a)

Note: 1. Vegetation class according to the classification of International Geosphere-Biosphere Program (MF = mixed forest, EBF =evergreen broad-leaved forest, ENF = evergreen needle-leaved forest, DBF = deciduous broad-leaved forest, DNF = deciduous needle-leaved forest, GRA = grassland, OSH = open shrubland, CRO =cropland, WET = wetland).
2. The error interval means the standard deviation of annual mean air temperature (MAT), annual precipitation (MAP), and annual gross primary productivity (GPP_{yr}) during the observation period. Limited to the observation years, some sites with <3 observations do not have the error interval.

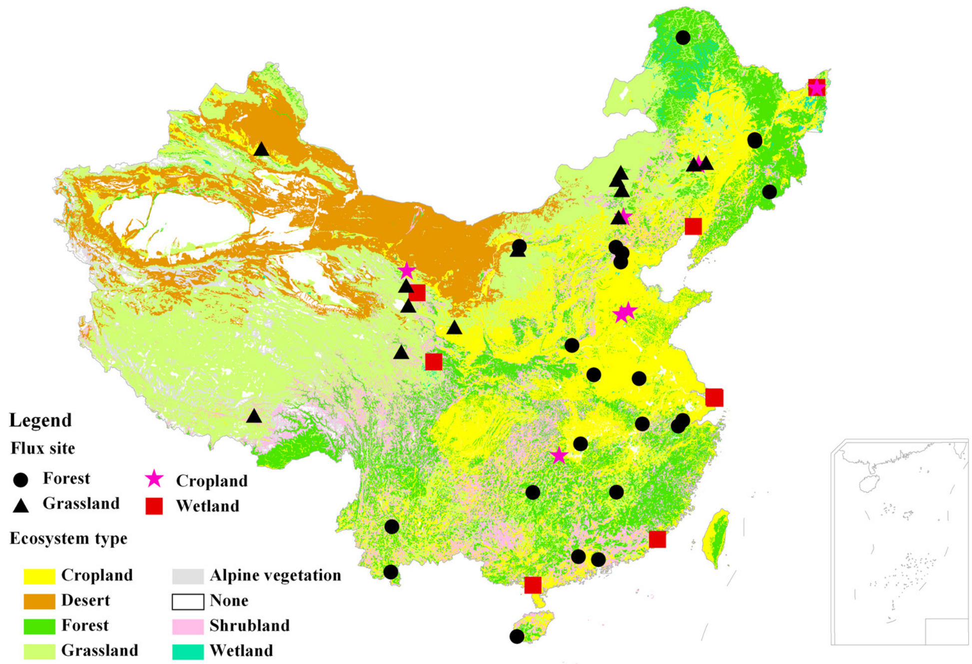

Fig. 1. Spatial distribution of sites used in this study. The background was the vegetation map of China according to Editorial Committee of Vegetation Map of China (2007).

2.5. Statistical analyses

Under Matlab 7.7 (Math Works Inc., Natick, MA, USA), we employed the linear regression to separately analyze the effects of various factors such as MAT, MAP, PAR_{yr}, ρ_{cyr}, and LAI_{yr} on the spatial variations of RUE and $FPAR_{yr}$, respectively. Based on the significant factors, the stepwise regression was used to build a multivariable regression. Path analysis was then explored to distinguish the direct factors affecting the spatial variation of RUE.

3. Results

3.1. Factors affecting the spatial variation of RUE

Many factors were found to significantly affect the spatial variation of RUE but their effects distinctly differed (Fig. 2). MAT, whose increase significantly raised RUE, inserted the strongest effect on the spatial variation of RUE, with an R^2 of 0.35 and an RMSE of 0.69 gC MJ^{-1} (Fig. 2a), while MAP played the weakest role in the spatial variation of RUE, only 10% of which was explained (Fig. 2b).

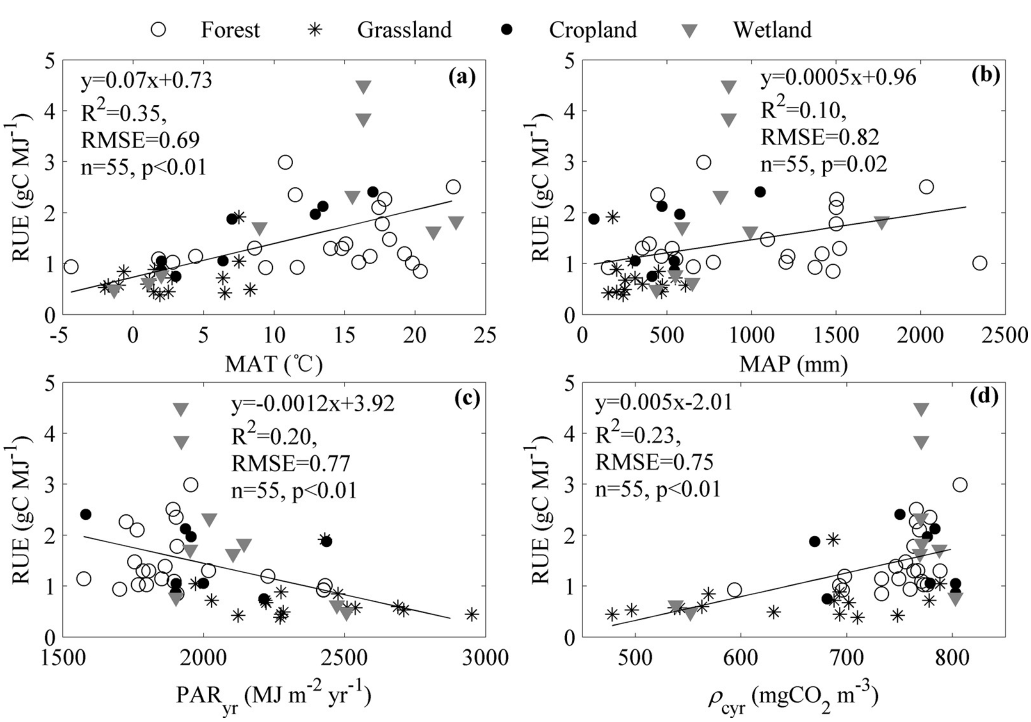

Fig. 2. Effects of factors on the spatial variation of radiation use efficiency (RUE) among terrestrial ecosystems in China. (a–d) were the effects of annual mean air temperature (MAT, a), annual precipitation (MAP, b), annual photosynthesis active radiation (PAR_{yr}, c), and annual mean CO_2 mass concentration (ρ_{cyr}, d), respectively.

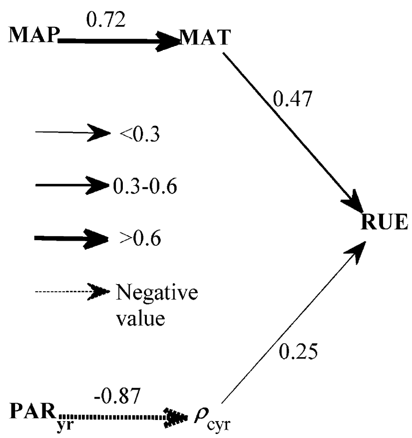

Fig. 3. Path diagram of factors affecting the spatial variation of radiation use efficiency (RUE). The abbreviations of factors were as follows: annual mean air temperature (MAT), annual precipitation (MAP), annual photosynthesis active radiation (PAR_{yr}), and annual mean CO_2 mass concentration (ρ_{cyr}).

PAR_{yr} exhibited a negative effect on the spatial variation of RUE, with an R^2 of 0.20 and an RMSE of 0.77 gC MJ^{-1} (Fig. 2c), whereas the increasing ρ_{cyr} significantly prompted RUE, with an R^2 of 0.23 and an RMSE of 0.75 gC MJ^{-1} (Fig. 2d). However, there was no significant correlation between LAI_{yr} and RUE (data were not shown).

The multivariable regression equation, which was developed from stepwise regression, only contained MAT and ρ_{cyr} (Eq. 7) and explained 40% of the spatial variation of RUE, with an RMSE of 0.67 gC MJ^{-1}.

$$RUE = 0.052MAT + 0.0024_{\rho cyr} - 0.887,$$
$$R^2 = 0.40,\ RMSE = 0.67,\ n = 55 \quad (7)$$

Path analysis results validated that the spatial variation of RUE was jointly affected by the direct effects of MAT and ρ_{cyr} (Fig. 3). The increasing MAT and ρ_{cyr} had positive direct effects on the spatial variation of RUE. In addition, the effect of MAP was reflected by the direct effect of MAT, while that of PAR_{yr} was represented by the direct effect of ρ_{cyr}.

3.2. Factors affecting the spatial variation of $FPAR_{yr}$

The spatial variation of $FPAR_{yr}$ was also found to be affected by many factors (Fig. 4). The increasing MAT prompted $FPAR_{yr}$ in spatial, with an R^2 of 0.19 and an RMSE of 0.19. MAP, whose increase enhanced $FPAR_{yr}$, served as the strongest climatic factor affecting the spatial variation of $FPAR_{yr}$, with an R^2 of 0.43 and an RMSE of 0.16 (Fig. 4b). However, with the increasing PAR_{yr}, $FPAR_{yr}$ exhibited a decreasing trend (Fig. 4c).

The developed regression equation by the stepwise regression just contained MAP, suggesting that the spatial variation of $FPAR_{yr}$ sourced from the direct effect of MAP.

In addition, $FPAR_{yr}$ was the function of LAI_{yr} (Eq. 5), whose spatial variation was primarily affected by the direct effect of MAP (Supplementary Material 1). Therefore, MAP affected the spatial variation of $FPAR_{yr}$ through altering LAI_{yr}.

3.3. Approaches of climatic factors affecting the spatial variation of GPP_{yr}

Based on above analyses, we can infer the approaches that climatic factors affect the spatial variation of GPP_{yr} in China (Fig. 5). GPP_{yr} was the product of RUE, $FPAR_{yr}$, and PAR_{yr}. The spatial variation of RUE was controlled by the joint effects of MAT and ρ_{cyr}, whose increase made RUE significantly increase (Fig. 5a and 5b). The spatial variation of $FPAR_{yr}$ was primarily affected by MAP, which dominated the spatial variation of LAI_{yr} (Fig. 5c), the foundation for calculating $FPAR_{yr}$ (Eq. 5). Therefore, MAT and ρ_{cyr} affected the spatial variation of GPP_{yr} primarily by altering RUE, while the effect of MAP was primarily achieved through altering $FPAR_{yr}$.

4. Discussion

4.1. Mechanisms underlying how climatic factors affect the spatial variation of GPP_{yr}

Following the radiation use efficiency theory, we separated GPP_{yr} into RUE, $FPAR_{yr}$, and PAR_{yr}. Then factors affecting the spatial variations of RUE and $FPAR_{yr}$ were investigated to reveal how climatic factors affect the spatial variation of GPP_{yr}. However, radiation use efficiency theory is developed from describing daily GPP and deems it as the product of RUE and APAR, where APAR was the multiplication of PAR and FPAR (Running et al., 2004; Wang et al., 2010; Wu et al., 2010a; Zhao and Running, 2010). RUE used in this study differed from that in describing the daily GPP. Therefore, based on the radiation use efficiency theory describing the daily GPP, we speculated the relationship between RUE used in our study and that in describing the daily GPP, which aimed to clarify mechanisms underlying the approaches that factors affect the spatial variation of GPP_{yr}.

GPP_{yr} is also the product of growing-season mean GPP (GPP_{gs}) and growing-season length (GSL), where GPP_{gs} may approximate to the product of growing-season mean RUE (RUE_{gs}) and growing-season mean APAR ($APAR_{gs}$), which may approximate to the multiplication of growing-season mean FPAR ($FPAR_{gs}$) and growing-season mean PAR (PAR_{gs}) (Stoy et al., 2008). In addition, RUE is the results of maximum RUE (mRUE) multiplying the limiting effects of various factors and mRUE varies little among season (Monteith, 1972; Running et al., 2004). Therefore, GPP_{yr} may approximate to the product of mRUE, $FPAR_{gs}$, PAR_{gs}, GSL, and limiting effects of various factors. Additionally, the seasonal variation of PAR was smaller than its spatial variation (Zhu et al., 2010), which may make the spatial variation of PAR_{gs} be similar to that of PAR_{yr}. Meanwhile, growing-season LAI (LAI_{gs}) dominated the LAI_{yr} in sites used in this study, which may make the spatial variation of $FPAR_{gs}$ be similar to that of $FPAR_{yr}$. Our calculated RUE may thus be proportional to the product of mRUE, GSL, and limiting effects of various factors.

Therefore, the effect of MAT on the spatial variation of RUE may be through the following two approaches. First, MAT, whose increases lengthened the GSL (Liu et al., 2010), dominated the spatial variation of GSL thus RUE. Second, the increasing MAT may smooth the limiting effect of T_a thus improved RUE (Yuan et al., 2010). The effect of ρ_{cyr} on RUE may be achieved through altering mRUE as the increase of ρ_{cyr} supplied more substrate for photosynthesis and improved the carboxylation efficiency (Norby et al., 2005).

MAP dominated the spatial variation of LAI_{yr} (Supplementary Information 1), which was consistent with the model results (Shao and Zeng, 2011). Given that $FPAR_{yr}$ is calculated from LAI_{yr}, the effect of MAP on the spatial variation of $FPAR_{yr}$ was achieved through altering LAI_{yr}.

Additionally, our results may somewhat differ from previous studies focusing on the spatial variation of RUE (Garbulsky et al., 2010; Schwalm et al., 2006), which may primarily stem from the unique climate gradients of China as few Chinese sites were included in their studies (Garbulsky et al., 2010; Schwalm et al., 2006).

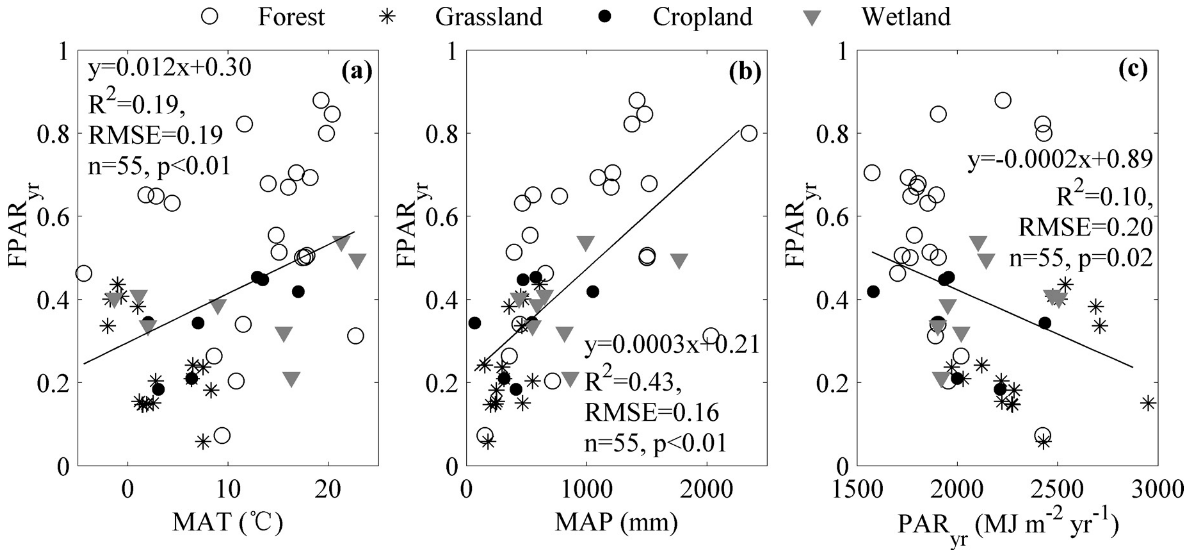

Fig. 4. Effects of climatic factors on the spatial variation of fraction of absorbed annual photosynthesis active radiation ($FPAR_{yr}$) in China. (a–c) were the effects of annual mean air temperature (MAT, a), annual precipitation (MAP, b), and annual photosynthesis active radiation (PAR_{yr}, c), respectively.

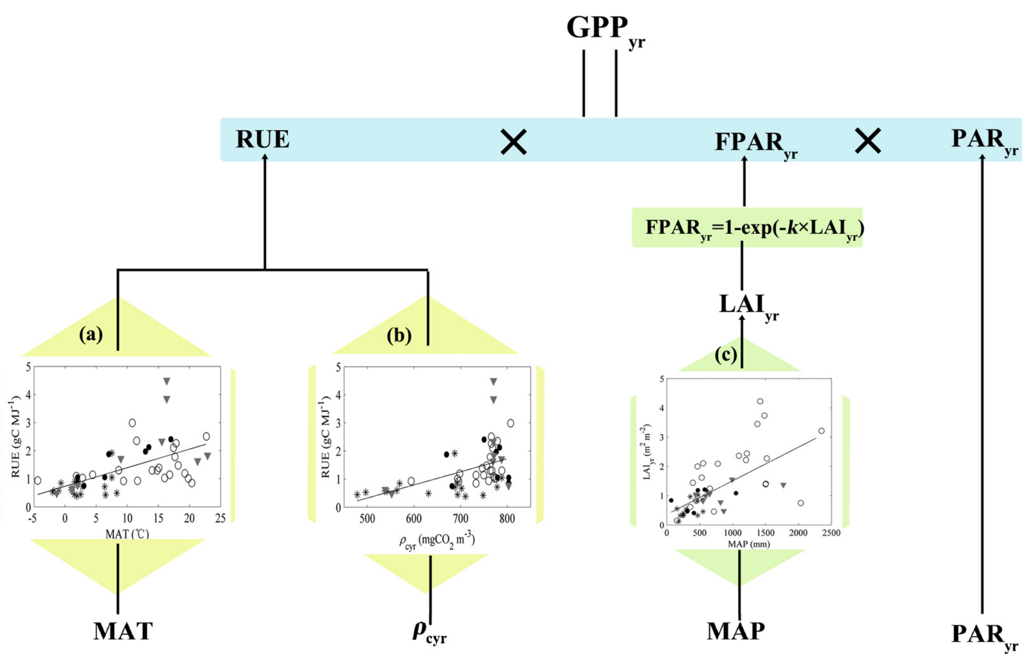

Fig. 5. Approaches that various factors affect the spatial variation of annual gross primary productivity (GPP_{yr}) across terrestrial ecosystems in China. The abbreviations of each item were as follows: annual mean air temperature (MAT), annual precipitation (MAP), annual photosynthesis active radiation (PAR_{yr}), annual mean leaf area index (LAI_{yr}), annual mean CO_2 mass concentration (ρ_{cyr}), fraction of absorbed annual photosynthesis active radiation ($FPAR_{yr}$), and radiation use efficiency (RUE). Panel (a) reflected the relationship between MAT and RUE, which was drawn based on Fig. 2(a), while panel (b) reflected that between ρ_{cyr} and RUE, which was drawn based on Fig. 2(d). Panel (c) reflected the relationship between MAP and LAI_{yr}, which was drawn based on the Supplementary Material 1.

4.2. Uncertainties analyses

In this study, we analyzed the approaches that climatic factors affect the spatial variation of GPP_{yr} based on the radiation use efficiency theory. Our results not only validated the dominating role of climatic factors such as MAT and MAP (Kato and Tang, 2008; Yu et al., 2013) but also found the role of ρ_{cyr} in the spatial variation of GPP_{yr}. Most importantly, we revealed how these climatic factors affect the spatial variation of GPP_{yr}. Our results would therefore improve our understanding on the spatial variation of GPP_{yr} and provide an alternative approach to the regional GPP_{yr} assessment.

However, there were some uncertainties in this study, which can be summarized into the following two aspects. First, the mechanisms underlying the approaches that factors affect the spatial variation of GPP_{yr} should be deeply investigated. Though we speculated how climatic factors affect the spatial variations of RUE and $FPAR_{yr}$ from the radiation use efficiency theory, we still needed more data especially daily data to support our speculation, such as GPP_{gs} was proportional to the product of RUE and $APAR_{gs}$, which would also benefit for revealing other potential factors affecting the spatial variation of RUE. Second, only using MAP to infer the spatial variation of $FPAR_{yr}$ was uncertain. Though MAP was found to be the direct factor affecting the spatial variation of $FPAR_{yr}$, there were many other factors such as human disturbance may influence the value of $FPAR_{yr}$ besides MAP (Chapin et al., 2012). However, our analysis on the relationship between MAP and $FPAR_{yr}$

primarily aimed to illustrate how MAP affects the spatial variation of GPP_{yr} but not to infer $FPAR_{yr}$ from MAP.

5. Conclusions

From the viewpoint of radiation use efficiency theory, we revealed how various factors affect the spatial variation of GPP_{yr} through investigating the factors affecting the spatial variations of RUE and $FPAR_{yr}$ based on network eddy covariance measurements. Results suggest that MAT and ρ_{cyr} affected the spatial variation of GPP_{yr} primarily through altering RUE while the effect of MAP was achieved through altering $FPAR_{yr}$. Our results improved our understanding on the spatial variation of GPP_{yr} and provided an alternative approach for regional carbon budget assessment.

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Appendix A. Supplementary Material

Supplementary material associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2015.11.028.

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