Climate controls over the net carbon uptake period and amplitude of net ecosystem production in temperate and boreal ecosystems

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ABSTRACT

The seasonal and interannual variability of the terrestrial carbon cycle is regulated by the interactions of climate and ecosystem function. However, the key factors and processes determining the interannual variability of net ecosystem productivity (NEP) in different biomes are far from clear. Here, we quantified yearly anomalies of seasonal and annual NEP, net carbon uptake period (CUP), and the maximum daily NEP (NEP_{max}) in response to climatic variables in 24 deciduous broadleaf forest (DBF), evergreen forest (EF), and grassland (GRA) ecosystems that include at least eight years of eddy covariance observations. Over the 228 site-years studied, interannual variations in NEP were mostly explained by anomalies of CUP and NEP_{max}. CUP was determined by spring and autumn net carbon uptake phenology, which were sensitive to annual meteorological variability. Warmer spring temperatures led to an earlier start of net carbon uptake activity and higher spring and annual NEP values in DBF and EF, while warmer autumn temperatures in DBF, higher autumn radiation in EF, and more summer and autumn precipitation in GRA resulted in a later ending date of net carbon uptake and associated higher autumn and annual NEP. Anomalies in NEP_{max} s were determined by summer precipitation in DBF and GRA, and explained more than 50% of variation in summer NEP anomalies for all the three biomes. Results demonstrate the role of meteorological variability in controlling CUP and NEP_{max}, which in turn help describe the seasonal and interannual variability of NEP.

1. Introduction

Climate controls the terrestrial carbon cycle by regulating plant physiological processes, including phenology. Climate thus determines both ecosystem carbon uptake capacity as well as the length of the carbon uptake period, which are important determinants of ecosystem carbon sequestration (Falge et al., 2002b; Gu et al., 2009; Xia et al., 2015; Zhou et al., 2016). It is far from clear how climatic or meteorological changes impact net ecosystem production (NEP) by changing carbon uptake phenology and physiology, given that models are largely unable to simulate the interaction between climate and ecosystem carbon dynamics to date (IPCC, 2013).

Previous studies on the relationship between carbon uptake phenology and NEP primarily focus on growing season length (GSL). A longer GSL due to climate warming (Delpierre et al., 2015; Linderholm, 2006; Peñuelas and Filella, 2001) usually stimulates NEP (Baldocchi, 2008; Baldocchi and Wilson, 2001; Churkina et al., 2005; Dragoni et al., 2011; Richardson et al., 2013). Yet other studies have found no relationship between GSL and NEP (Dunn et al., 2007), or lower NEP with longer GSL (Hu et al., 2010b; Piao et al., 2007; Sacks et al., 2007). The reasons for this disparity are twofold; gross ecosystem productivity may be offset by concurrent increases in ecosystem respiration as NEP is the difference between the two, and longer GSLs may increase the likelihood of drought limitations to productivity.

With the advantage of quasi-continuous measurements of the net CO_2 exchange by the eddy covariance method, strong relationships between net carbon uptake period (CUP) and annual NEP have been characterized (Baldocchi et al., 2001; Baldocchi et al., 2005; Richardson et al., 2010; Richardson et al., 2013; Wu and Chen, 2013; Wu et al., 2013). Overall, annual NEP is more strongly correlated with CUP than GSL (Piao et al., 2007; White and Nemani, 2003; Wu et al., 2013). While climate controls on GSL have been well studied (Chmielewski and Rötzer, 2001; Delpierre et al., 2015; Matsumoto et al., 2003; Richardson et al., 2013), our understanding of climate controls over CUP and thus NEP across different ecosystems is still limited.

In addition to the CUP, the maximum daily ecosystem NEP (NEP_{max}, Fig. 1A) is another strong predictor of annual NEP, especially in temperate and boreal ecosystems that have obvious seasonal dynamics (Falge et al., 2002b; Xia et al., 2015; Zhou et al., 2016). With the same CUP, ecosystems that have a higher NEP_{max} tend to have larger annual NEP (Fig. 1D) (Churkina et al., 2005). Although a longer CUP may increase annual NEP, associated warmer and drier summers may suppress summer NEP_{max}, potentially offsetting any annual NEP increase (e.g. Fig. 1E) (Angert et al., 2005; Ciais et al., 2005; Cleland et al., 2007). Moreover, a longer CUP may decrease annual NEP because an earlier onset of the growing season may result from a shallow snowpack or increased transpiration, leaving less available water in the soil in summer and limiting plant growth later in the growing season (Hu et al., 2010a; Kljun et al., 2006; Sacks et al., 2007).

Niemand et al. (2005) linked phenology observations to flux measurements in a Norway spruce forest and found that earlier spring phenology correlated well with increased NEP only when the drought year of 2003 was excluded, suggesting that water availability influences the relationship between CUP and annual NEP. These results indicate that the effects of summer water limitation on NEP_{max} may potentially offset positive spring warming influences on spring NEP, leading to smaller changes in annual NEP than otherwise expected (Fig. 1E). In addition, autumn warming may also advance the ending of carbon uptake and decrease autumn NEP, resulting in a small change in annual NEP in response to climate warming (Fig. 1F). We tested the hypothesis that, by separating annual NEP variability into CUP and NEP_{max}, we can better disentangle how meteorological drivers impact NEP variability in deciduous broadleaf forests (DBF), evergreen forests (EF), and grasslands (GRA) that experience pronounced seasonality in temperate and boreal climate zones.

In this study, we analyzed eddy covariance-measured CO_2 flux and micrometeorological variables from 24 flux tower sites that have long-term (multi-year) quasi-continuous measurements. The specific questions addressed in this study include: (1) how are CUP and NEP_{max} related to annual NEP in different biomes; (2) what are the climate factors that determine NEP_{max} and the beginning (BDOY) and end (EDOY) of the CUP; and (3) how are seasonal NEP anomalies related to annual NEP anomalies?

2. Data and methods

2.1. Site selection and data processing

Surface-atmosphere CO_2 flux and micrometeorological data used in this analysis were downloaded from standardized files of the FLUXNET LaThuille database released in 2007 (Baldocchi, 2008; Baldocchi et al., 2001). The data have been quality-controlled and gap-filled by consistent methods (Moffat et al., 2007; Papale et al., 2006; Reichstein et al., 2005). From the available 253 sites, we identified and examined temperate and boreal ecosystems (38–62°N, −125 to 24°E; Table A1) that have clear seasonal dynamics. We only chose sites that have eight or more years of data for a total of 24 sites with 228 site-
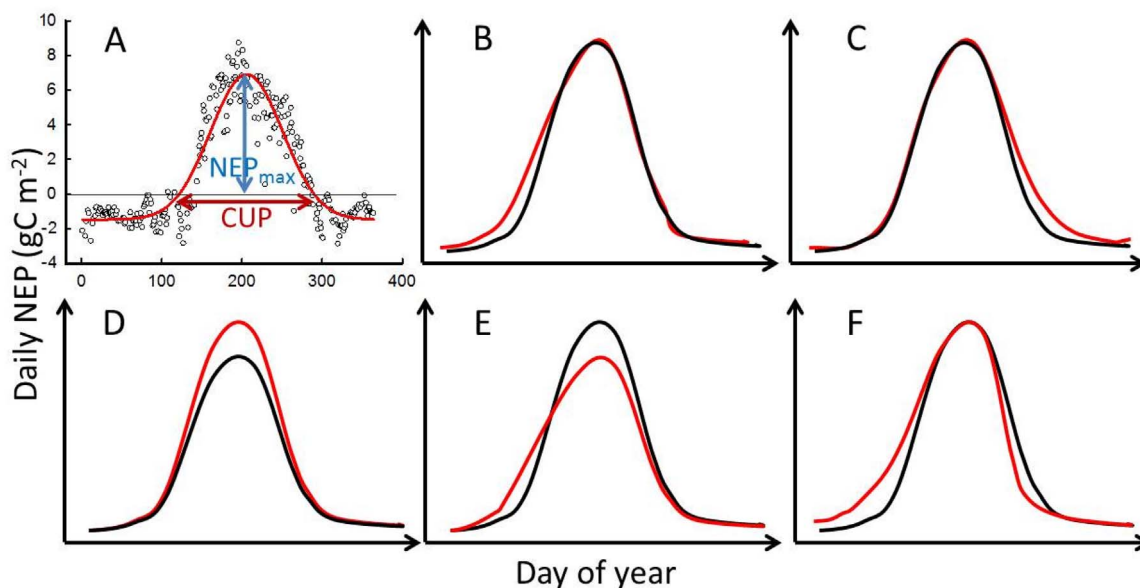

Fig. 1. Hypothesized changes in the regulation of annual NEP by net carbon uptake period (CUP) and the maximum daily net ecosystem productivity (NEP_{max}), and their roles in regulating annual NEP changes. Panel A defines the terminology used throughout the manuscript. Red lines in subsequent panels represent the change in a hypothetical warmer year versus the mean seasonal pattern in black. Panels (B) and (C) represent the phenological regulations by advancing net carbon sink beginning day (BDOY) or by delaying net carbon sink ending day (EDOY); (D) represents a change in NEP_{max}; (E) represents the larger spring NEP with an advancing BDOY but smaller summer NEP by decreasing NEP_{max}; and (F) represents larger spring NEP by early beginning of BDOY, but smaller autumn NEP with earlier EDOY. We only showed the representative scenarios rather than all possible interactions between NEP_{max}, BDOY and EDOY.
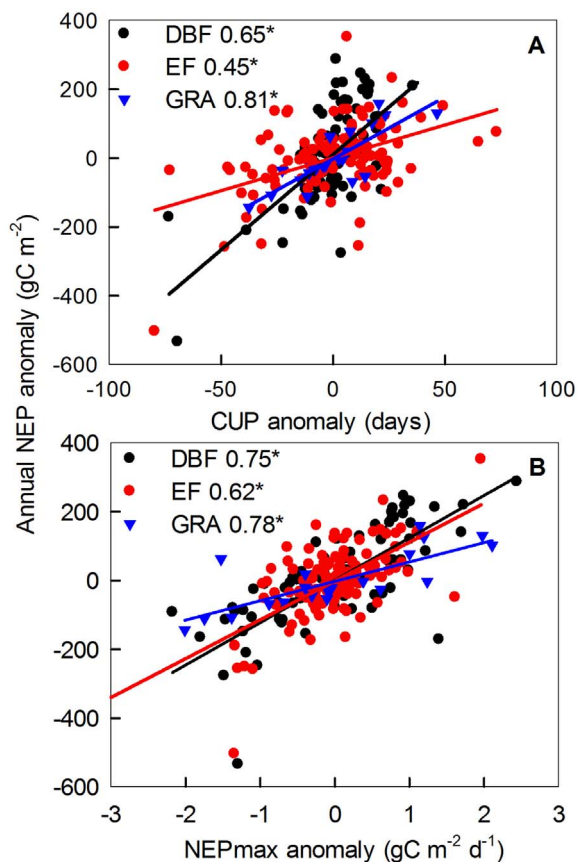
Fig. 2. (A) The changes in annual NEP anomalies with the anomalies of net carbon uptake period (CUP), and (B) the anomalies of maximum daily net ecosystem productivity (NEP_{max}) in temperate and boreal deciduous broadleaf (DBF), evergreen forest (EF) and grassland (GRA) ecosystems. The numbers in the legends are r values; all are significant at $P < 0.001$.

years to investigate the interannual variability of climate and CUP and NEP_{max}, as well as seasonal and annual NEP (Table A1). Daily data for each site were used to calculate the seasonal and annual values of incoming solar global radiation (R_g), air temperature (T_a), precipitation (PPT), and daily CO_2 fluxes (i.e., NEP, also called the net ecosystem exchange, NEE). These sites were divided into three groups based on International Geosphere-Biosphere Programme (IGBP) land cover classifications: deciduous broadleaf forests (DBF), evergreen forests (EF), and grasslands (GRA).

For each year, we calculated the seasonal and annual mean values of T, PPT, R_g, and NEP. The whole year was separated into the climatological seasons of winter (December–February), spring (March–May), summer (June–August), and autumn (September–November) in order to study seasonal changes in NEP in response to changes in CUP and NEP_{max}. When the missing daily data exceeded 10% of the entire season (or year), the seasonal (or yearly) value was indicated as missing. On average, for the 24 sites, 8% of the years were rejected due to insufficient data. The years rejected varied from 7% (US-Ha1) to 45% (IT-Col) among sites.

2.2. Definition and analysis

We used a 10-day moving average to determine the beginning (BDOY) and ending (EDOY) day of positive ecosystem NEP for each year for each site (Fig. 1A, Table A2). Consistently, BDOY occurred in spring and EDOY appears in autumn at all the sites. We defined the net carbon uptake period (CUP) as the number of days between the BDOY and EDOY (Fig. 1A). Daily ecosystem carbon uptake exceeds carbon release during the CUP. CUP is related to, but need not be identical to,

GSL. For example, the beginning of CUP may start later than leaf onset when the leaves photosynthesize at a rate that outweighs ecosystem respiration. The CUP ends when ecosystem respiration is higher than photosynthesis although plant growth and CO_2 uptake may continue. GSL in most cases will be longer than CUP because the balance between total ecosystem respiration and photosynthesis determines CUP (Churkina et al., 2005). The maximum daily NEP (NEP_{max}) is defined as the maximum value of daily NEP, which was derived from the moving average curves of NEP seasonal dynamics (Fig. 1A). Interannual variation as a yearly anomaly was calculated for each site-year for each variable.

2.3. Data analysis

To examine the relationships between climate anomalies and the anomalies of BDOY, EDOY, and NEP_{max}, as well as the anomalies in seasonal and annual NEP, we analyzed the data using simple linear regression. For testing the inequality of regression slopes among different vegetation types, the slopes between BDOY and EDOY anomalies, and seasonal or annual NEP anomalies for different seasons, we calculated t* using $t* = (b_1 - b_2)/\sqrt{(s_1^2 + s_2^2)}$, where b_1 and b_2 are regression slopes, and s_1 and s_2 are the standard errors of regression slopes for the vegetation types or different seasons. The null hypothesis is that the slopes b_1 and b_2 are not significantly different at $\alpha = 0.05$. We also used structural equation models to partition the total effect of variables on annual NEP into direct and indirect effects (Schumacker and Lomax, 2004; Vargas et al., 2010). A path model was developed to relate the anomalies of NEP to the anomalies of CUP and NEP_{max}, as well as the anomalies of seasonal climate factors in different ecosystems. The model was fitted using the 'lavaan' package (Rosseel, 2012) in R3.0.2 for Windows.

3. Results

3.1. CUP and NEP_{max} in controlling NEP

Across all the site-years, annual NEP anomalies were positively correlated with anomalies of CUP and NEP_{max} across all three ecosystem types ($P < 0.001$, Fig. 2A). The slope between CUP and NEP was significantly higher in DBF (5.5 g C m^{-2} per day) and GRA (3.6 g C m^{-2} per day) than in EF (1.9 g C m^{-2} per day, Fig. 2A). Across all site-years, annual NEP increased by 107 g C m^{-2} per unit increase of NEP_{max} (g C m^{-2} d^{-1}) (Fig. 2B). The relationship between NEP_{max} and NEP was similar between DBF (123.2 g C m^{-2}) and EF (112.9 g C m^{-2}) per unit increase of NEP_{max} (g C m^{-2} d^{-1}), and both were higher than that in GRA (56.3 g C m^{-2}) (Fig. 2B). NEP_{max} and CUP in combination explained 73, 54, 63% of the variation in annual NEP anomalies in DBF, EF, and GRA, respectively, as quantified using the structural equation models (Fig. A1).

3.2. Spring phenology and NEP

BDOY was significantly correlated with spring temperature in DBF and EF (Fig. 3A), but not with spring precipitation or radiation in any biome ($P > 0.05$). BDOY advanced by 2.6 and 3.7 days per degree increase of spring temperature for DBF and EF, respectively (Fig. 3A). Early BDOY led to an increase in spring NEP in the three biomes, and annual NEP in DBF and EF (Fig. 3B and C). For example, spring NEP increased by 4.0, 0.8 and 1.6 g C m^{-2} per day advance of BDOY for DBF, EF, and GRA, respectively (Fig. 3B), while annual NEP increased by 6.6 and 2.1 g C m^{-2} per day advance of BDOY for DBF and EF, respectively (Fig. 3C). All the spring climate factors in combination explained 37% and 16% of the variation in BDOY in DBF and EF, respectively, but explained only 3% in GRA (Fig. A1).
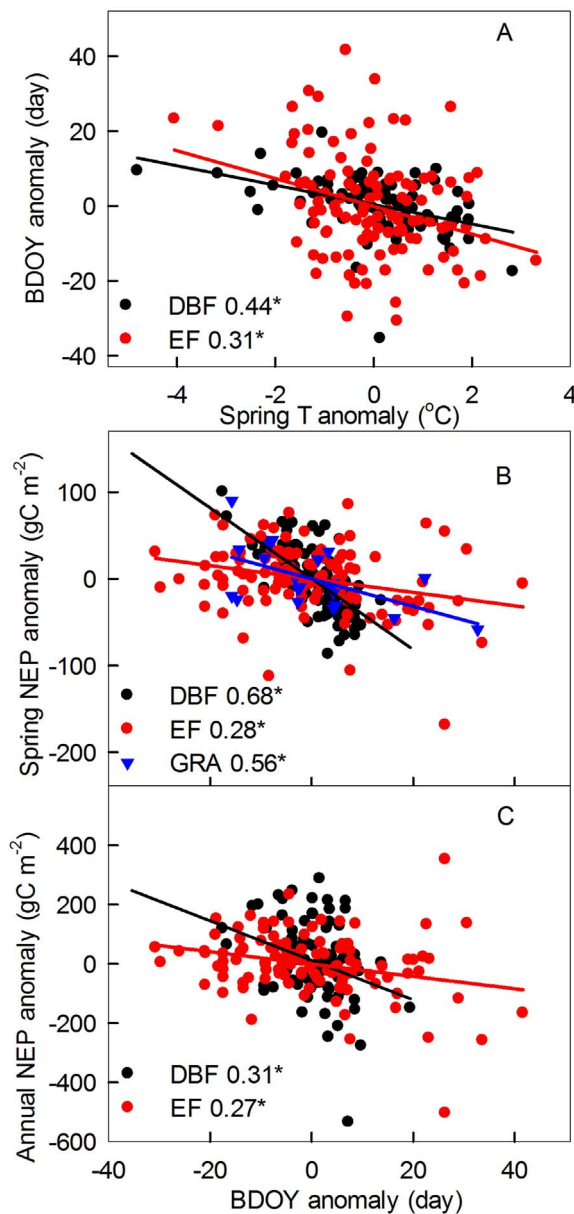
Fig. 3. (A) Spring phenology (net carbon sink beginning day, BDOY) in response to spring temperature change, and its contribution to spring (B) and annual (C) NEP anomalies in temperate and boreal deciduous broadleaf (DBF), evergreen forest (EF) and grassland (GRA) ecosystems. The numbers in the legends are r values; all are significant at $P < 0.01$.

3.3. Autumn phenology and NEP

EDOY anomalies were positively correlated with autumn temperature anomalies in DBF ($P < 0.001$, Fig. 4A), with autumn radiation anomalies in EF ($P < 0.01$, Fig. 4B), and with summer and autumn precipitation anomalies in GRA ($P < 0.01$, Fig. 4C). EDOY was later by 4.1 days per degree increase of autumn temperature in DBF (Fig. 4A), by 8 days per 100 MJ m^{-2} increase of radiation in EF, and by 2.3 days per 10 mm increase of summer or autumn precipitation in GRA. Later EDOY led to an increase of autumn and annual NEP in the three biomes (Fig. 4D, E). Autumn NEP increased by 2.8, 0.8 and 0.5 g C m^{-2} per extra day of EDOY for DBF, EF and GRA, respectively (Fig. 4D), while annual NEP increased by 6.2, 1.6 and 2.6 g C m^{-2} per day, respectively (Fig. 4E). The autumn climate factors in combination explained 21% and 48% of the variation in EDOY in DBF and GRA, respectively, but explained only 10% in EF (Fig. A1).

3.4. NEP$_{max}$ and NEP

NEP$_{max}$ had no significant relationship with summer temperature or radiation in any biome ($P > 0.05$), but was negatively correlated with summer precipitation anomalies in DBF and positively correlated with summer precipitation anomalies in GRA (Fig. 5A). NEP$_{max}$ anomalies were related to summer NEP anomalies for all the three biomes with similar slopes (Fig. 5B). Summer climate factors in combination explained most (62%) of the variation of NEP$_{max}$ in GRA but explained only 12% and 5% in DBF and EF (Fig. A1).

3.5. Relationships among seasonal NEP

Spring NEP anomalies were positively correlated with the summer, autumn, and winter NEP anomalies in DBF and EF, and the slope of this relationship did not differ between biomes (Fig. 6A–C). Summer NEP anomalies were correlated with autumn NEP anomalies in DBF and EF, and with winter NEP anomalies in EF (Fig. 6D, E). Autumn NEP anomalies were positively correlated with winter NEP anomalies only in EF (Fig. 6F). There were no significant relationships between seasonal NEP anomalies in GRA.

4. Discussion

We first discuss relationships between meteorological variables and the CUP, followed by a discussion of the relationships between CUP, NEP$_{max}$, and NEP on the annual and seasonal bases.

4.1. The relationship between climate and the beginning of the net carbon uptake period

Our results show that interannual variability in ecosystem net carbon uptake phenology was sensitive to climate factors. Spring temperature drives the variability in BDOY, with an average advance of $2.6 − 4.5$ days °C^{-1} in warmer years (Fig. 3). The advancement of vegetation phenology in response to temperature is well documented in previous studies (Jeong et al., 2011; Julien and Sobrino, 2009; Keenan et al., 2014; Menzel and Fabian, 1999; Menzel et al., 2006; Piao et al., 2006; Schwartz et al., 2006). In an analysis of direct observations of plant phenology over Europe for 1971–2000, Menzel et al. (2006) detected an average advance of 0.25 days year^{-1} in spring onset. Using satellite-measured normalized difference vegetation index, Jeong et al. (2011) demonstrated that the start of the growing season advanced by 5.2 days during 1982–1999 over the Northern Hemisphere due to observed warming. Most of these previous studies used satellite-derived data to directly infer vegetation phenological parameters (Jeong et al., 2011; Julien and Sobrino, 2009).

Vegetation phenology may not necessarily reflect ecosystem net carbon uptake phenology (Bauerle et al., 2012; White and Nemani, 2003), but we found that BDOY responded to temperature anomalies in DBF and EF (Fig. 3). The phenology of DBF emerged to be more sensitive to the spring air temperature anomalies when compared with EF and GRA, likely because of the fundamental differences in phenological strategies among the biomes. For example, leaf flush in deciduous trees can occur rapidly compared to the reestablishment of photosynthetic mechanisms in conifers (Gu et al., 2008; Monson et al., 2005; Richardson et al., 2010), resulting in a smaller sensitivity of BDOY in response to a warmer spring in EF than in other biomes.

4.2. The relationship between climate and the end of the net carbon uptake period

Previous studies examining autumn phenology often focus on the impact of temperature on autumn phenology of vegetation. For example, Keenan et al. (2014) reported that warmer autumn temperatures lead to later senescence. The sensitivity of autumn phenology to a
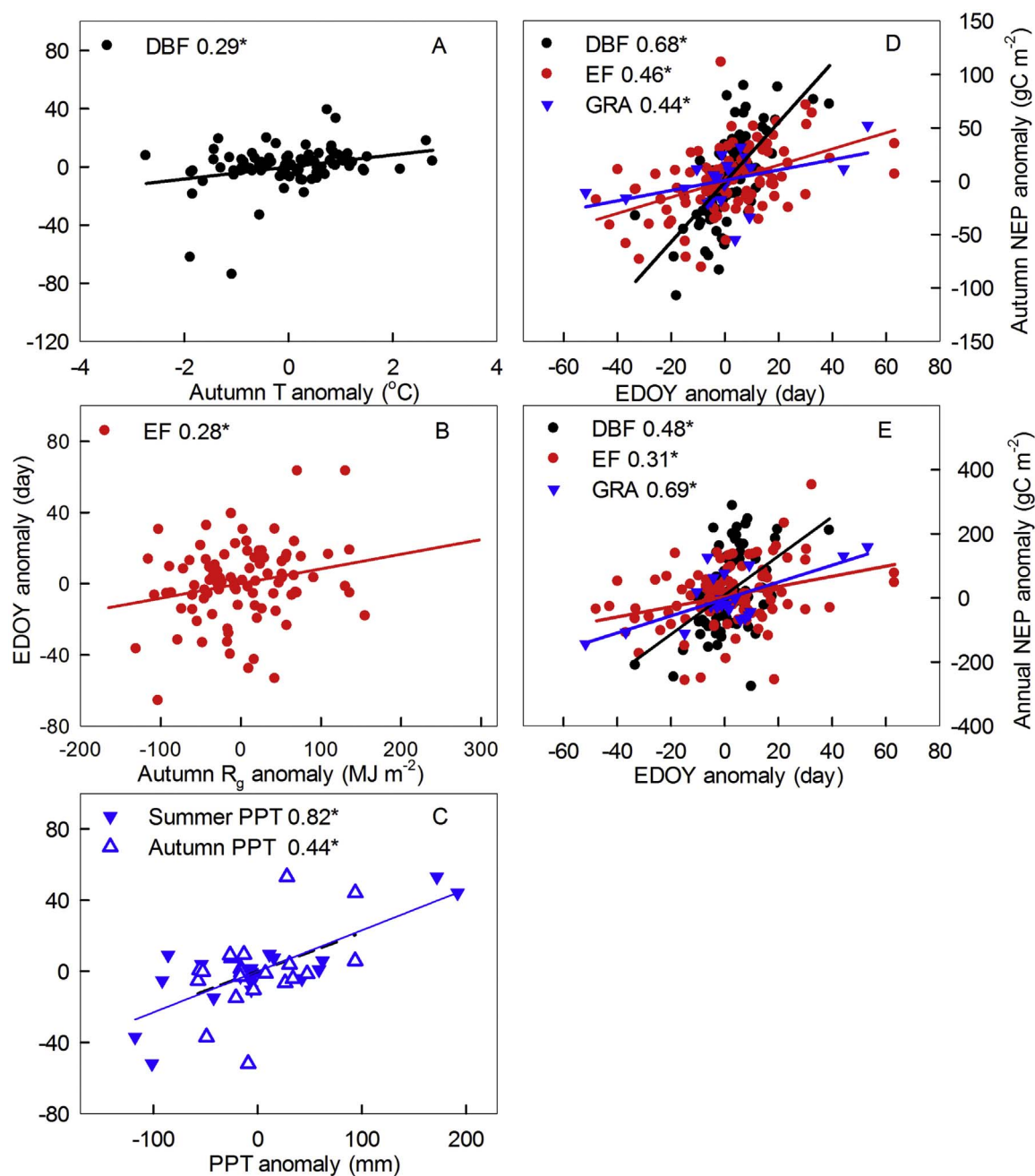
Fig. 4. (A–C) Significant relationships between meteorological variables and the day at which ecosystem net CO_2 uptake ends (EDOY) in temperate and boreal deciduous broadleaf (DBF), evergreen forest (EF) and grassland (GRA) ecosystems. The contributions of EDOY anomalies to autumn (D) and annual (E) NEP anomalies. The numbers in the legends are r values; all are significant at $P < 0.05$.

change from the mean temperature was similar across forest types, with a 1 °C difference from the mean temperature leading to a 1.8 day change in autumn senescence for DBF and a 6.3 day change in EF (Keenan et al., 2014). Using satellite NDVI data, Stockli and Vidale (2004) reported a delay of senescence in autumn by an average of 0.42 days year^{-1} over Europe with observed climate warming, while Tucker et al. (2001) found an earlier onset of autumn in Eurasia in a warmer environment. The above-mentioned results suggest large uncertainties in estimating the key climate factors for vegetation phenology changes in autumn (Menzel et al., 2006).

Vegetation phenology does not necessarily reflect net carbon uptake phenology, and we found that the variability of EDOY was determined by different environmental factors in different biomes. EDOY occurred later with higher autumn temperature in DBF, higher radiation in EF,

and more summer and autumn precipitation in GRA (Fig. 5). Our results indicate that precipitation and radiation, in addition to temperature, play important roles in regulating the EDOY in temperate and boreal ecosystems. More precipitation could improve soil water supply that enables longer carbon gain into autumn, while higher radiation may enable more net carbon gain as days are getting shorter and radiation is often limiting in autumn (Niu et al., 2011).

4.3. The joint roles of CUP and NEP$_{max}$ in regulating NEP

The interannual variation in NEP was attributed to yearly anomalies in CUP and NEP$_{max}$ (Fig. 2), which in combination explained 54–73% of changes in annual NEP in the three biomes (Fig. A1). In line with our findings, Xia et al. (2015) and Zhou et al. (2016) recently proposed that
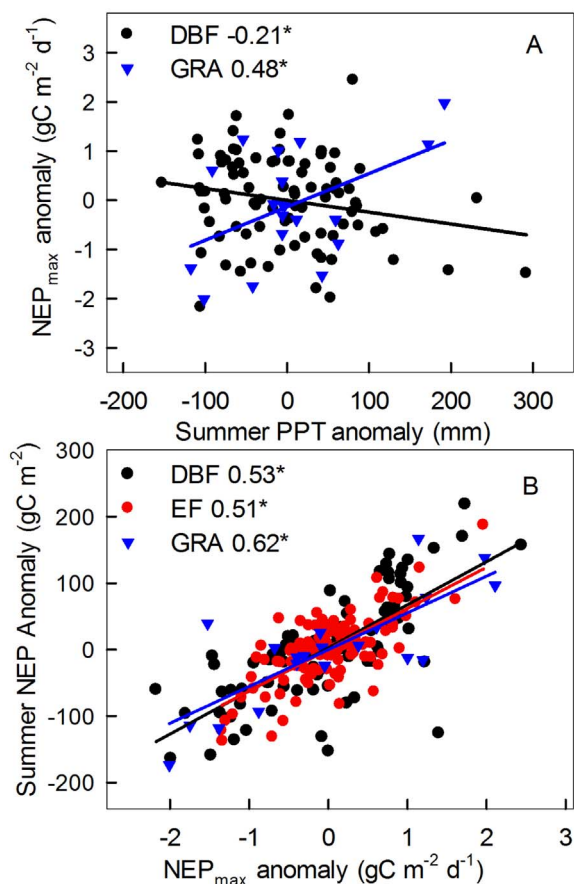
Fig. 5. (A) The relationship between summer precipitation (PPT) and maximum daily net ecosystem productivity (NEP$_{max}$) in temperate and boreal deciduous broadleaf (DBF) and grassland (GRA) ecosystems. (B) The contribution of NEP$_{max}$ anomalies to summer NEP anomalies at all three study biomes. The numbers in the legends are r values; all are significant at $P < 0.05$.

luxury of shedding leaves in winter. DBF are well known for having a higher maximum photosynthetic capacity, which is be offset by a shorter vegetation period (Roser et al., 2002; Schulze et al., 1977). The observed differences between EF and DBF in phenology-productivity relationships have ecological implications, especially in the light of climate change effects on phenology, as phenology models should predict ecosystem response to climate change in different ways for different biomes.

In addition to CUP, NEP$_{max}$ also contributed to the interannual variability of ecosystem NEP, especially during summer (Fig. 5). Our results showed that summer precipitation was related to NEP$_{max}$ in GRA and DBF, indicating that increases in annual NEP due to increases in CUP may be offset by the influence of summer precipitation on NEP$_{max}$. These results suggest that CUP and NEP$_{max}$ may play different roles in regulating the variability of annual NEP, depending on their interactions.

4.4. Seasonal NEP contributions to annual NEP anomalies

NEP anomalies in different seasons were related to annual NEP anomalies as expected (Fig. 6). Spring phenology was more strongly related to spring NEP than to annual NEP, suggesting that annual fluxes are much more variable because they are affected by weather events in other seasons. For example, in grasslands, although early onset of BDOY led to an increase of spring NEP, annual NEP showed no relationship with BDOY anomalies (Fig. 3). This is possibly due to the limitations of summer precipitation, which led to lower summer NEP (Fig. 1E). The insignificant relationship between spring NEP anomalies and NEP anomalies in other seasons in GRA (Fig. 6) also indicates that the depression of NEP in other seasons may exceed the legacy effects of spring NEP on later seasons. DBF and EF showed strong lag effects of spring NEP on the summer/autumn NEP (Fig. 6), suggesting that spring phenology plays an important role in determining the seasonal and annual NEP in these two biomes. Flux anomalies in other seasons may also partly contribute additional variability to the annual NEP.

The various relationships between NEP anomalies in different seasons indicate that the interannual variability of NEP can only be better understood by fully addressing the different responses of seasonal NEP to climate and meteorological variability. If we connect annual NEP anomalies to climate factors only at annual time scales, we might miss many significant relationships between seasonal NEP and climate factors at the ecosystem scale. Temperature is the main factor controlling the interannual variability of terrestrial NEP at the global scale (Jung et al., 2017; Wang et al., 2013; Wang et al., 2014), as the ecosystem and regional effects of precipitation compensate for each other (Ahlström et al., 2015; Poulter et al., 2014; Zeng et al., 2005). Understanding the links between ecosystem and global scale responses to climate variability is an important avenue of future research, and we must extend our understanding of the controls over NEP to tropical and subtropical ecosystems to do so from the "bottom up" using ecosystem-scale observations.

5. Conclusions

By analyzing eddy covariance CO_2 fluxes from 24 flux tower sites, this study examined the responses of CUP and NEP$_{max}$ to climate factors in temperate and boreal ecosystems with pronounced seasonality. Spring temperature was the primary controlling factor for BDOY, but the controlling factors for EDOY were different among biomes. Summer precipitation was the main factor effecting NEP$_{max}$ for DBF and GRA. Because these critical phenology and physiology-relevant variables were controlled by different seasonal environmental factors, there existed complex relationships among NEP anomalies in different seasons. This study provides a fundamental understanding of the role of ecosystem level phenology and physiology in regulating ecosystem carbon sequestration across temperate and boreal ecosystems, and
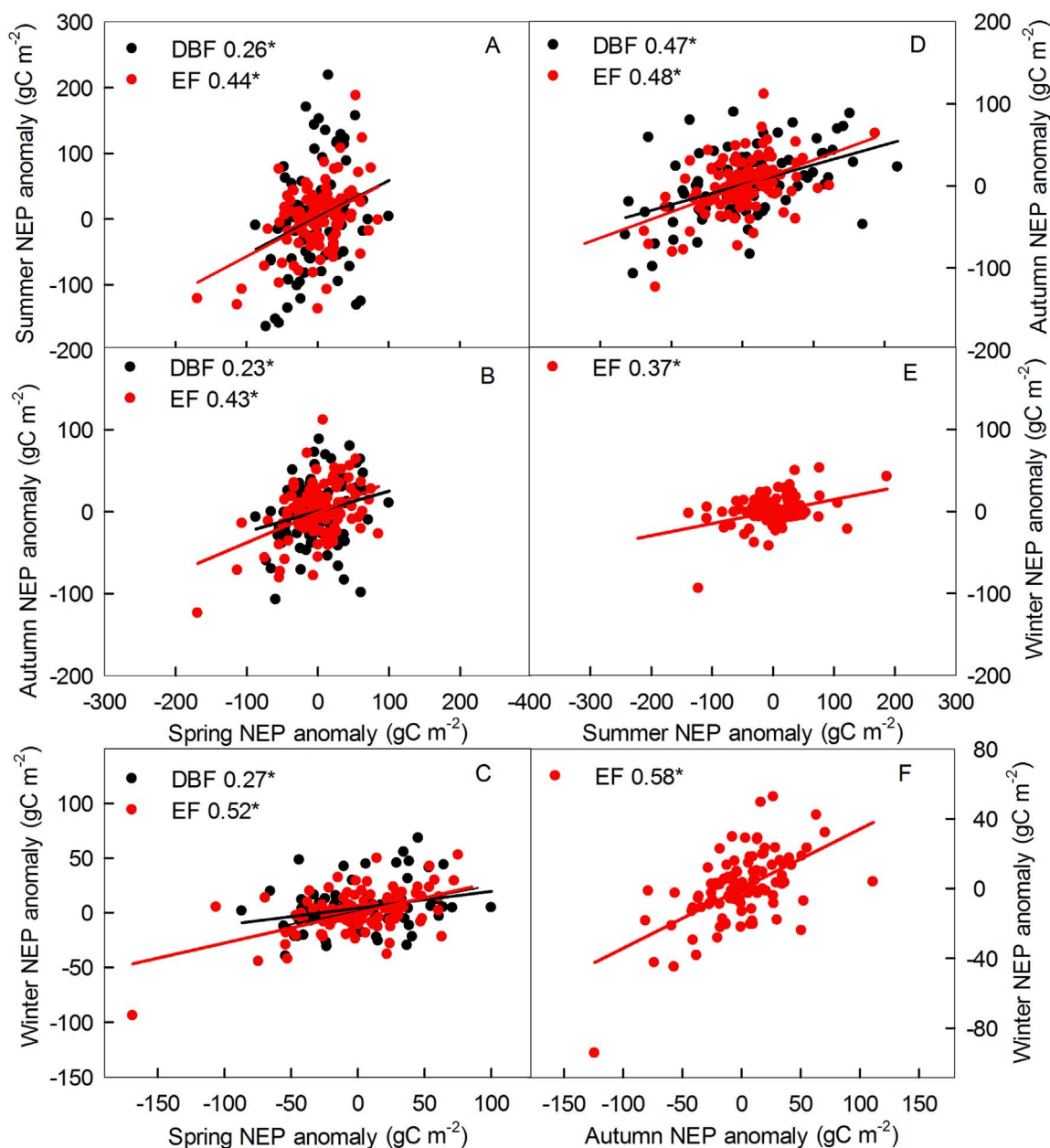
more than 90% of annual gross primary productivity (GPP) can be explained by the combination of growing season length and the maximum daily GPP in temperate, boreal, and arctic ecosystems. These findings highlighted the important role of GPP$_{max}$ and phenology in controlling production and emphasize the importance of extending such an analysis to account for NEP in addition to GPP.

We found that an early onset of net carbon uptake enhanced spring and annual NEP (Fig. 3), while a delay of EDOY increased autumn and annual NEP (Fig. 4), indicating the importance of CUP in regulating carbon sequestration in temperate and boreal ecosystems. The observed link between CUP and annual NEP in temperate and boreal ecosystems are consistent with the results of Baldocchi et al. (2001), Baldocchi (2008), and Wu and Chen (2013). Compared to previous studies, this study emphasized different sensitivities between climate and NEP among biomes and between seasons. Spring, autumn, and annual NEP changed more in DBF than in EF and GRA with the same change in BDOY or EDOY. This suggests a higher sensitivity of NEP to phenology changes in DBF than other biomes. Some previous studies also reported that ecosystem productivity in DBF was more sensitive than EF to carbon uptake period (Churkina et al., 2005; Wu et al., 2013). Using flux data, Wu et al. (2013) quantified that a one-day increase in CUP led to a 3.3 and 1.5 g C m^{-2} y^{-1} increase in annual NEP in DBF and EF, respectively. These results indicate that DBF tends to have a higher productivity during the growing season than EF due to the fundamental differences in physiological strategies between the two biomes (Barr et al., 2009; Falge et al., 2002a; Givnish, 2002; Richardson et al., 2009). Deciduous broadleaf tree species evolved millions of years after conifers and are much more efficient in assimilation per unit leaf surface—the

Fig. 6. Relationships among the seasonal net ecosystem productivity (NEP) anomalies in temperate and boreal deciduous broadleaf (DBF), evergreen forest (EF) and grassland (GRA) ecosystems. (A) The relationships between spring NEP anomaly and summer NEP anomaly; (B) the relationships between spring NEP anomaly and autumn NEP anomaly; (C) the relationships between spring NEP anomaly and winter NEP anomaly; (D) the relationships between summer NEP anomaly and autumn NEP anomaly; (E) the relationships between summer NEP anomaly and winter NEP anomaly; (F) the relationships between autumn NEP anomaly and winter NEP anomaly. The numbers in the legends are r values; all are significant at $P < 0.05$.

future studies should extend our understanding to regions with less-pronounced seasonality to improve our understanding of the relationship between climate and ecosystem carbon exchange.

Appendix A

See

Table A1
Site characteristics, climatic index, and studied period of eddy covariance research sites in this analysis.

Site name	Veg[1]	Lat[*]	Lon[**]	PPT[2](mm)	Ta (°C)	Period	References
AT-Neu	GRA	47.12	11.32	1040.4	6.3	2002–2009	(Wohlfahrt et al., 2008)
BE-Bra	EF	51.31	4.52	742.7	10.0	2000–2009	(Gielen et al., 2010)
BE-Vie	EF	50.31	6.00	1065.1	7.4	1996–2007	(Aubinet et al., 2001)
CA-Ca1	EF	49.87	−125.33	1369.2	9.9	1998–2005	(Humphreys et al., 2006)
CA-Let	GRA	49.71	−112.94	349.9	6.2	1998–2005	(Flanagan et al., 2002)
CA-Man	EF	55.88	−98.48	515	−1.2	1995–2003	(Dunn et al., 2007)
CA-Oas	DBF	53.63	−106.2	428.5	0.3	1997–2005	(Black et al., 2000)
DE-Hai	DBF	51.08	10.45	780.3	7.2	2000–2007	(Knohl et al., 2003)
DE-Tha	EF	50.96	13.57	643.1	8.1	1997–2008	(Grunwald and Bernhofer, 2007)
DK-Sor	DBF	55.49	11.65	952	8.7	1998–2009	(Pilegaard et al., 2003)
FI-Hyy	EF	61.85	24.29	620.2	2.2	1997–2008	(Suni et al., 2003)
FR-Pue	EF	43.74	3.59	734.5	12.9	2001–2008	(Rambal et al., 2004)
FR-Hes	DBF	48.67	7.06	793.3	9.2	1997–2008	(Granier et al., 2000)
IT-Ren	EF	46.59	11.43	964.7	6.2	2001–2009	(Montagnani et al., 2009)
IT-Col	DBF	41.85	13.59	970.9	7.3	1997–2007	(Van Dijk and Dolman, 2004)
US-Blo	EF	38.9	−120.63	1630	12.5	1999–2006	(Goldstein et al., 2000)
US-MMS	DBF	39.32	−86.41	1031.6	10.8	1999–2006	(Schmid et al., 2000)
IT-Ro1	DBF	42.41	11.93	763.7	15.3	2001–2008	(Rey et al., 2002)
NL-Loo	EF	52.17	5.74	786.2	9.4	1997–2009	(Dolman et al., 2002)
US-Ha1	DBF	43.54	−72.17	1071	6.6	1993–2006	(Urbanski et al., 2007)
US-Ho1	EF	45.2	−68.74	1070.3	5.3	1996–2004	(Hollinger et al., 2004)
US-UMB	DBF	45.56	−84.71	803.4	5.8	1999–2006	(Gough et al., 2008)
US-NR1	EF	40.03	−105.54	595.2	0.4	1999–2007	(Monson et al., 2002)
US-Var	GRA	38.41	−120.95	543.9	15.9	2001–2008	(Xu and Baldocchi, 2004)

*Positive value indicates north latitude. **Negative value indicates west longitude. 1vegetation, 2precipitation. DBF: deciduous broadleaf forest; EF: evergreen forest; GRA: grassland.

Table A2
The mean and variability of the beginning date (BDOY) and ending date (EDOY) of net carbon uptake for each study site during the study period.

| Sites	Vegetation	BDOY		EDOY	
		Mean	SD	Mean	SD
CA-Oas	DBF	135.6	10.8	251.4	4.2
DE-Hai	DBF	116.0	4.5	280.3	5.6
DK-Sor	DBF	108.7	6.4	262.8	8.3
FR-Hes	DBF	18.4	23.0	337.3	19.5
IT-Col	DBF	53.3	12.7	322.3	11.5
US-MMS	DBF	31.3	9.9	277.8	21.3
IT-Ro1	DBF	30.7	21.6	306.4	31.7
US-Ha1	DBF	77.2	5.1	294.0	18.9
US-UMB	DBF	110.0	8.1	285.9	5.1
BE-Bra	EF	91.3	16.2	267.7	7.7
BE-Vie	EF	45.9	16.3	292.6	10.9
CA-Ca1	EF	12.9	6.4	290.8	54.1
CA-Man	EF	98.8	17.8	247.6	16.7
DE-Tha	EF	42.0	17.1	314.7	13.4
FI-Hyy	EF	85.8	10.1	260.8	11.4
FR-Pue	EF	108.1	4.3	277.9	16.0
IT-Ren	EF	111.4	12.7	278.9	12.8
US-Blo	EF	91.3	11.6	269.0	35.7
NL-Loo	EF	133.2	5.3	274.5	4.1
US-Ho1	EF	109.6	3.7	279.0	5.9
US-NR1	EF	132.3	7.5	267.4	5.3
AT-Neu	GRA	89.7	4.5	255.1	4.0
CA-Let	GRA	110.7	13.8	219.2	35.3
US-Var	GRA	16.7	15.8	134.4	7.1
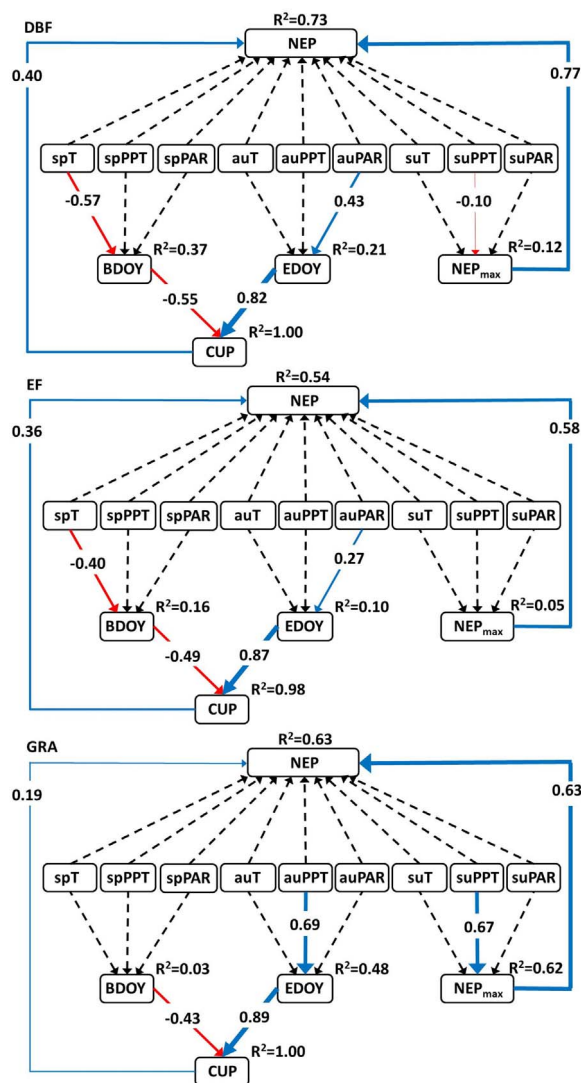
Fig. A1. The structure equation modeling results of the relationship between the anomalies in environmental factors and the anomalies in net carbon uptake period (CUP) and the maximum daily net ecosystem productivity (NEP_{max}) attributes of NEP in temperate and boreal deciduous broadleaf (DBF), evergreen forest (EF) and grassland (GRA) ecosystems. Blue arrows indicate significant positive relationships while red arrows indicate significant negative relationships ($P < 0.05$). Black dashed arrows indicate insignificant relationships ($P > 0.05$). Arrow width is proportional to the strength of the relationship. Numbers adjacent to arrows are path coefficients and indicative of the effect size of the relationship. The proportion of variance explained (R^2) appears alongside every response variable in the model. BDOY and EDOY indicate the beginning and ending date of net carbon uptake, respectively. T, PPT, and PAR indicate temperature, precipitation, and radiation, respectively. Sp, su, and au indicate spring, summer, and autumn, respectively.

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