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Original Articles

Interannual and spatial variability of net ecosystem production in forests explained by an integrated physiological indicator in summer

Ying Liu^{a,b}, Chaoyang Wu^{a,b,*}, Lin Liu^{c,*}, Chengyan Gu^d, T. Andrew Black^e, Rachhpal S. Jassal^e, Lukas Hörtnagl^f, Leonardo Montagnani^{g,h}, Fernando Moyanoⁱ, Andrej Varlagin^j, M. Altaf Arain^k, Ajit Govind^l

^a The Key Laboratory of Land Surface Pattern and Simulation, Institute of Geographical Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, China

^b University of the Chinese Academy of Sciences, Beijing 100049, China

^c Hebei GEO University, Shijiazhuang 050031, China

^d Planning and Design Institute of Forestry Product Industry, National Forestry and Grassland Administration, Beijing 100010, China

^e University of British Columbia, 136-2357 Main Mall, Vancouver, BC V6T 1Z4, Canada

^f ETH Zurich, Department of Environmental Systems Sciences, 8092, Zurich, Switzerland

^g Forest Services of Autonomous Province of Bolzano, via Bolzano 6, 39100, Italy

^h Faculty of Science and Technology, Free University of Bolzano, Piazza Università 5, 39100 Bolzano, Italy

ⁱ University of Goettingen, Bioclimatology, Büsingenweg 2, 37077 Göttingen, Germany

^j A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, 119071, Leninsky pr.33, Moscow, Russia

^k School of Geography and Earth Sciences and McMaster Centre for Climate Change, McMaster University, Hamilton, Ontario L8S4K1, Canada

^l INRA, UMR 1391 ISPA, F-33140 Villenave d'Ornon, Bordeaux, France



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ABSTRACT

Understanding the feedback of ecosystem carbon uptake on climate change at temporal and spatial scales is crucial for developing ecosystem models. Previous studies have focused on the role of spring and autumn phenology in regulating carbon sequestration in forest stands, but few on the impact of physiological status in summer. However, plant accumulated the most carbon in summer compared with spring and autumn, therefore, it is of great significance to explore the role of summer phenological metrics on the variability of carbon sequestration. Using 514 site-years of flux data obtained at 40 FLUXNET sites including three forest ecosystems (i.e. evergreen needleleaf forest (ENF), deciduous broadleaf forest (DBF) and mixed forest (MF)) in Europe and North America, we compared the potential of physiological and phenological metrics of Gross Primary Production (GPP) and Ecosystem Respiration (RECO) in explaining the interannual and spatial variability (IAV and SV) of forest net ecosystem production (NEP). In view of the better performance of physiological metrics, we developed the maximum carbon uptake index (MCUI), which integrated the physiology metrics of photosynthesis and respiration in summer, and further explored its ability in explaining the IAV and SV of NEP. The results suggest that the MCUI had a better ability than respiration-growth length ratio (RGR) in predicting NEP for all three forest types. The interpretation of MCUI based on meteorological variables illustrated that the controlling meteorological factors of MCUI differed substantially among ecosystems. The summer shortwave radiation had the greatest influence on MCUI at DBF sites, while the soil water content played an important but opposite role at ENF and DBF sites, and no significant meteorological driver was found at MF sites. The higher potential of MCUI in explaining IAV and SV of NEP highlights the importance of summer physiology in controlling the forest carbon sequestration, and further confirms the significant role of peak plant growth in regulating carbon cycle of forest ecosystems. Understanding the drivers of peak plant growth is therefore of a great significance for further improving the precision of ecosystem model in the future.

* Corresponding authors at: The Key Laboratory of Land Surface Pattern and Simulation, Institute of Geographical Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, China (C. Wu).

E-mail addresses: liuy.19b@igsrr.ac.cn (Y. Liu), wucy@igsrr.ac.cn (C. Wu), liulin7801@126.com (L. Liu).

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1. Introduction

Forest ecosystem is the dominant terrestrial ecosystem on Earth and plays an important role in global carbon sequestration (Pan et al., 2013; Shiga et al., 2018). Net ecosystem productivity (NEP), which represents the net gain of carbon (C) at the ecosystem level and is the result of the difference between C uptake through photosynthesis and C released through respiration, determines the capacity of an ecosystem to act as carbon source or sink (Ryu et al., 2019; Woodwell et al., 1978; Yatskov et al., 2019). In the context of global climate change, understanding the interannual and spatial variability (IAV and SV) of NEP in forest helps to improve the simulation accuracy of carbon uptake, thus providing a better understanding of how forest functions as part of the global carbon cycle (Ballantyne et al., 2012; Luo et al., 2015; Wu et al., 2012).

Photosynthesis and respiration are the two main processes affecting carbon sequestration at the ecosystem level. Using the long-term continuous eddy-covariance (EC) technique, NEP can be well measured within the footprint ($NEP = -NEE$), and partitioned into Gross Primary Production (GPP) and Ecosystem Respiration (RECO) (Baldocchi, 2003; Papale et al., 2006). Vegetation phenology describes the recurring seasonal changes of plant development status in response to environmental changes (Lieth, 1974), and includes key events such as sprouting, leaf development, flowering, and defoliation (Ivits et al., 2012; Walther et al., 2002). Plant summer physiology (e.g., leaf pigmentation, leaf mass per unit area, water and nutrient content, etc. (Ma et al., 2011; McKown et al., 2013)), which can be indicated by summer flux, reflect the greatest potential of canopy assimilation and respiratory potential (Hilker et al., 2011; Keenan et al., 2014). Accordingly, several phenological and physiological metrics derived from GPP and RECO have been proposed for tracking changes of the vegetation growth process, using the time series of carbon flux or vegetation indices (Garrity et al., 2011; Gonsamo et al., 2013; Huang et al., 2018; Richardson et al., 2010; Wohlfahrt et al., 2005; Wu and Chen, 2013; Xia et al., 2015; Zhou et al., 2016). Given that phenology and physiology are important processes in controlling vegetation carbon accumulation, evaluations of phenological and physiological metrics are of great significance to improve our understanding of the feedbacks of ecosystem processes to climate change (Baldocchi et al., 2001; Pan et al., 2013; Wilkinson et al., 2012; Yu et al., 2008).

Previous studies focused on the effect of GPP-derived phenology on carbon sequestration, and found that prolonged growing season lengths (GSL) usually increase annual cumulative NEP across and within sites (Baldocchi, 2008; Churkina et al., 2005; Dragoni et al., 2011; Richardson et al., 2009). However, there are also several studies showing different or even diametrically contrary conclusions. For example, the prolongation of GSL caused by autumn warming may reduce carbon sequestration in high latitude ecosystems, because the loss of respiration far exceeds the benefit of photosynthesis in the late growing season (Piao et al., 2008; Wu et al., 2013). Besides, although a warm spring increases NEP in the early growing season, it can also lead to soil moisture deficits in summer, and thus reduce the annual cumulative NEP (Buermann et al., 2013; Hu et al., 2010; Sacks et al., 2007). Moreover, the NEP shows great interannual variability with the same GSL because of the effect of summer drought (Angert et al., 2005). The relationship between the GSL and NEP is not necessarily linear and predictable (Richardson et al., 2013), and consequently, taking into account the physiological status of vegetation in summer, when drought periods most often happens (David et al., 2007; Eisenhauer et al., 2012; Peichl et al., 2015), could be of great importance to better interpret the variability of carbon sequestration. Previous studies have confirmed that summer physiology (e.g. the maximum of GPP, GPP_{max}) is highly relevant to the IAV of GPP (Xia et al., 2015; Xu et al., 2019; Zhou et al., 2016) and an increasing trend of peak growth of vegetation was observed at the global scale in the context of climate change (Gonsamo et al., 2018; Huang et al., 2018). However, the potential of GPP_{max} in explaining the variability of NEP has not been studied at the interannual

and spatial scales across forest types.

Ecosystem respiration, which describes the process of gross CO_2 release from the ecosystem, is an essential component of the terrestrial carbon cycle (Luyssaert et al., 2007; Waring et al., 1998). Concurrent enhancement of RECO typically tends to offset about 50% of the increased GPP that results from a longer GSL (Richardson et al., 2010). However, the effects of seasonal characteristics of respiration (i.e. the start, end, length and maximum of RECO) on carbon sequestration have not been systematically studied among different forest types.

An integrated indicator considering both photosynthesis and respiration is better for understanding the role of phenology and physiology in regulating carbon sequestration (Piao et al., 2008). Combining the phenological metrics of photosynthesis and respiration, Wu et al. (2012) derived a respiration–growth length ratio indicator (RGR) at three forest sites in Canada and found that RGR performed better in explaining the IAV of NEP than the single phenological metrics. However, this metric lacks validation at more tower stations and plant functional types. In addition, an integrated physiological indicator considering both respiration and photosynthesis has not been developed and tested across forest types yet.

Using 514 sites-years of flux data observed at 40 sites across three forest types (i.e. evergreen needleleaf forest (ENF), deciduous broadleaf forests (DBF) and mixed forest (MF)) in northern temperate and boreal regions (30°–70° N), we investigated the role of phenological and physiological metrics derived from GPP and RECO in controlling the IAV and SV of NEP. The specific objectives were (1) to compare the potential of single phenological metrics (the start, end, and length of GPP and RECO) and physiological metrics (the maximum of GPP and RECO) in interpreting IAV and SV of NEP, (2) to explore the ability of integrated indicators considering both GPP and RECO for a better explanation of NEP, and (3) to understand the control of meteorological variables on the new indicator.

2. Material and methods

2.1. Study sites

We selected 40 forest sites from the Fluxnet community including 20 evergreen needleleaf forests, 14 deciduous broadleaf forests and 6 mixed forests (Fig. 1). The selection criteria were as follows. First, we used the sites which have at least 5 years of complete data records, with these being less than 20% gap-filled each year. Second, the selected sites had a complete set of meteorological variables, including air temperature, precipitation, shortwave radiation. Third, mature and undisturbed forests were given preference. All sites are distributed in North America and Europe, covering various climate types. The descriptions of these sites are shown in Supplementary Table 1.

2.2. Flux and meteorological data

Flux and meteorological data at all study sites were obtained from the FLUXNET2015 Dataset (<https://fluxnet.fluxdata.org/data/fluxnet2015-dataset/>). This dataset collects the continuous half-hourly eddy covariance measurements at FLUXNET sites and includes several improvements to the data quality control protocols and the data processing pipeline (Pastorello et al., 2020, 2014). Net ecosystem exchange ($NEE = -NEP$) is filtered with an ensemble of USTAR thresholds calculated with two different methods (Barr et al., 2013; Papale et al., 2006), and then gap-filled with the marginal distribution sampling (MDS) method (Reichstein et al., 2005), and partitioned into Gross Primary Production (GPP) and Ecosystem Respiration (RECO) using both the nighttime based (Reichstein et al., 2005) and daytime based approach (Lasslop et al., 2010). GPP and RECO based on nighttime approach were used in this study. RECO estimated from nighttime data (Reichstein et al., 2005) were used in this study.

Air temperature (T_a), shortwave radiation (SW), vapor pressure

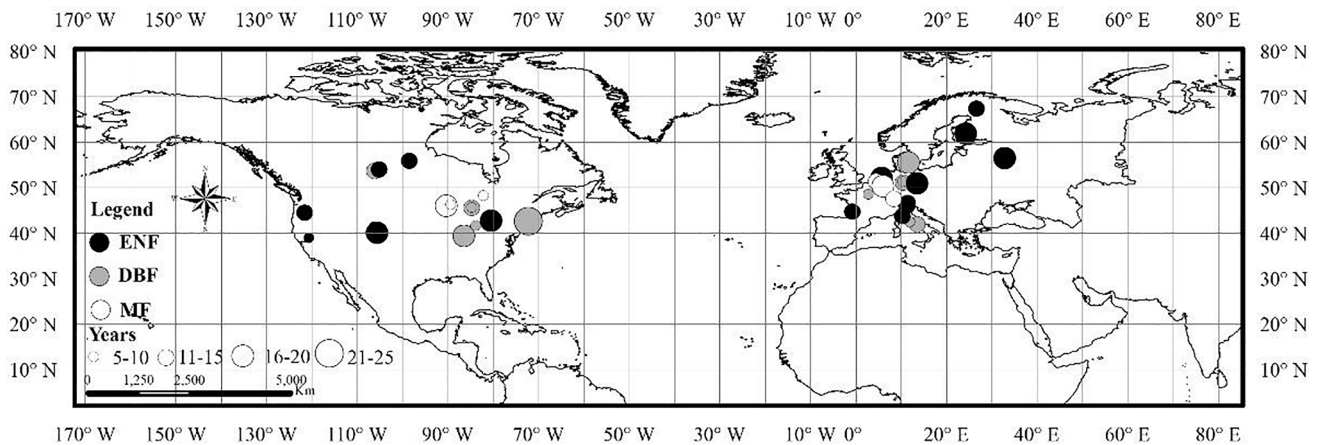


Fig. 1. Spatial distribution of study sites in this study. ENF (●), DBF (●) and MF (○) represent evergreen needleleaf forests, deciduous broadleaf forests and mixed forests, respectively. The circle size represents the data years of these sites.

deficit (VPD) and precipitation were obtained from field measurement of flux towers. To ensure data measurement consistency across flux sites, the gridded daily soil water content (SWC) (CCI SM v04.2, <http://www.esa-soilmoisture-cci.org>) with 0.25° spatial resolution and monthly soil temperature (Ts) (FLDAS_NOAH01_C_GL_M, https://disc.gsfc.nasa.gov/datasets/FLDAS_NOAH01_C_GL_M_001/summary?keywords=FLDAS_NOAH01_C_GL_M) data records with 0.1° spatial resolution and a depth of 0–10 cm were obtained (An et al., 2016; Dorigo et al., 2017). The mean values of these meteorological variables in early summer (from June 1 to July 31) were calculated from daily record in each site-year. The reason for the selection of this time duration is that most of days of year (DOYs) for the peak of GPP and RECO were appeared in June and July in the three forest types (GPP_{max}: DOY 185 ± 23 for ENF, DOY 181 ± 15 for DBF and DOY 184 ± 15 for MF; RECO_{max}: DOY 199 ± 24 for ENF, DOY 184 ± 26 for DBF and DOY 206 ± 36 for MF) (supplementary Fig. 1).

2.3. Physiological and phenological metrics

Several physiological and phenological metrics derived from daily GPP and RECO were used in this study. The summer physiological metrics were the maximum value of GPP and RECO (GPP_{max} and RECO_{max}). The phenological metrics included the start, end and length of the photosynthesis (GPP_{start}, GPP_{end}, and GPP_{GSL}) and respiration (RECO_{start} and RECO_{end} and RECO_{RSL}), and we also counted the days when GPP_{max} and RECO_{max} appeared.

The following methods were used to calculate these metrics for each site-year. We derived the smoothed time series estimates of GPP and RECO using the Savitzky-Golay (SG) filter, which is based on local polynomial least square fitting and widely used in data smoothing and denoising (Chen et al., 2004; Savitzky and Golay, 1964) (Fig. 2). The smoothing window and iteration time were set as 4 and 20, respectively (Peng et al., 2019). GPP_{max} and RECO_{max} can be determined as the maximum value of smoothed daily GPP and RECO. Then, 10% of the difference between annual maximum and minimum RECO was adopted to define RECO_{start} and RECO_{end} (Wu and Chen, 2013). Finally, we fitted a seven-parameter double logistic function (Eq. (1)) to derive fitted curves for daily GPP estimates (Gonsamo et al., 2012). GPP_{start} and GPP_{end} can be estimated by the extreme points of the third derivative of the fitted curve of equation (1).

$$GPP(t) = \alpha_1 + \frac{\alpha_2}{1 + e^{-\delta_1(t-\beta_1)}} - \frac{\alpha_3}{1 + e^{-\delta_2(t-\beta_2)}} \quad (1)$$

where GPP (t) is daily GPP at day of year (DOY) t, α_1 is the background of

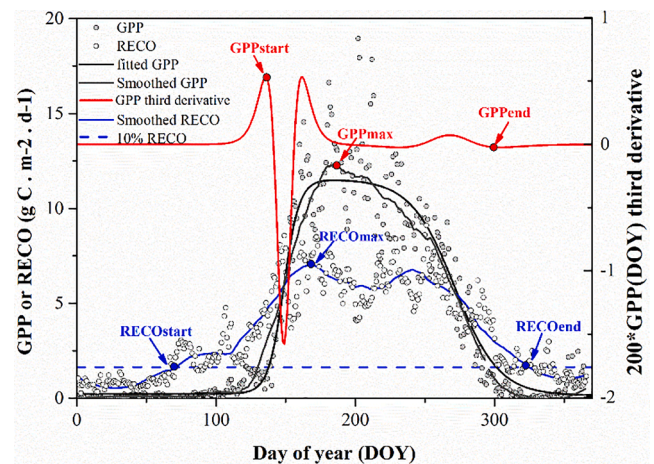


Fig. 2. Example of calculating the metrics in this study using daily gross primary productivity (GPP) and respiration (RECO) data of Ontario-Turkey Point 1974 Plantation White Pine (CA-TP3) in 2012. The growing season start (GPP_{start}) and end (GPP_{end}) are defined by the extremes of the third derivatives (GPP (DOY)) of the fitted logistic function. RECO_{start} and RECO_{end} are respectively determined by the days when smoothed daily RECO first reaches and leaves 10% of the annual RECO value range. GPP_{max} and RECO_{max} are defined as the maximum of smoothed GPP and RECO curves.

GPP in the year, α_2 is the early summer plateau, α_3 is the amplitude of late summer plateau, δ_1 and δ_2 are the transition in slope coefficients, and β_1 and β_2 are the midpoints in the day of year (DOY) of these transitions for GPP increase and decrease, respectively. GPP_{start} is the DOY at the beginning of the slope of the rising curve. Similarly, GPP_{end} is the DOY at the end of the falling curve (Fig. 2).

2.4. Modeling NEP using physiological metrics

After obtaining phenological metrics, we can determine the phenological indicator of the respiration–growth length ratio (RGR) (Wu and Chen, 2013):

$$RGR = \frac{RECO_{end} - RECO_{start}}{GPP_{end} - GPP_{start}} \times 100\% \quad (2)$$

After obtaining phenological metrics, considering the important and opposite roles of physiological metrics (GPP_{max} and RECO_{max}) in regulating annual carbon uptake, we derived two new integrated

physiological indicators: the photosynthesis-respiration maximum ratio (PRMR) and the maximum carbon uptake index (MCUI).

PRMR was proposed to explain the IAV of NEP, since both GPP_{max} and $RECO_{max}$ showed higher correlation with NEP anomaly than phenological metrics for all forest types (Fig. 3). Thus, PRMR was selected as a candidate for temporal-scale factor ($Scale_{temporal}$) of MCUI.

$$PRMR = \frac{GPP_{max}}{RECO_{max}} \quad (3)$$

Given the great potential of GPP_{max} in explaining the spatial variability of NEP (Fig. 4), we defined GPP_{max} as the spatial-scale factor ($Scale_{spatial}$) of MCUI. Accordingly, MCUI (unit: grams C meter⁻²day⁻¹) was finally defined as followed (see Eq. (4)).

$$MCUI = Scale_{temporal} * Scale_{spatial} = \frac{GPP_{max} * GPP_{max}}{RECO_{max}} \quad (4)$$

2.5. Statistical analysis strategy

We calculated the yearly anomalies of all variables, which have been verified as a reliable method in evaluating IAV between variables across sites (Richardson et al., 2010). (Richardson et al., 2010). The yearly anomalies of physiological indicators, phenological indicators, meteorological variables in early summer and NEP were calculated using this method. The yearly anomaly was defined as the difference between the annual observations and the multi-year mean value of the study period.

$$A_i = x_i - X_{mean} \quad (5)$$

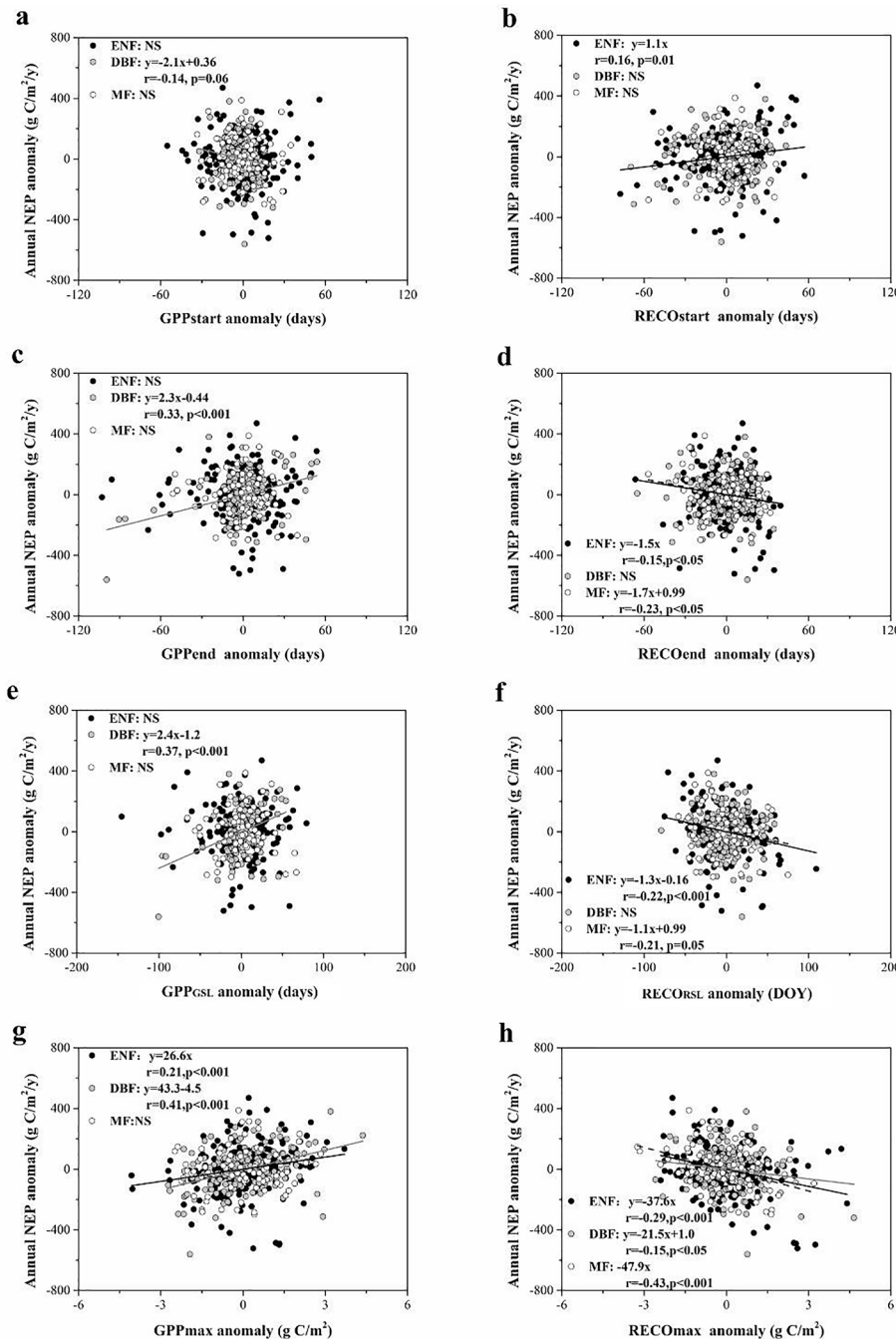


Fig. 3. Relationship between the interannual net ecosystem productivity (NEP) anomalies and metrics anomalies: (a) the start of the growing season (GPP_{start}), (b) the start of respiration ($RECO_{start}$), (c) the end of the growing season (GPP_{end}), (d) the end of respiration ($RECO_{end}$), (e) the length of the growing season (GPP_{GSL}), (f) the length of respiration ($RECO_{RSL}$), (g) the maximum of gross primary production (GPP_{max}) and (h) the maximum of respiration ($RECO_{max}$) in evergreen needleleaf forests (ENF), deciduous broadleaf forests (DBF) and mixed forests (MF) ecosystem.

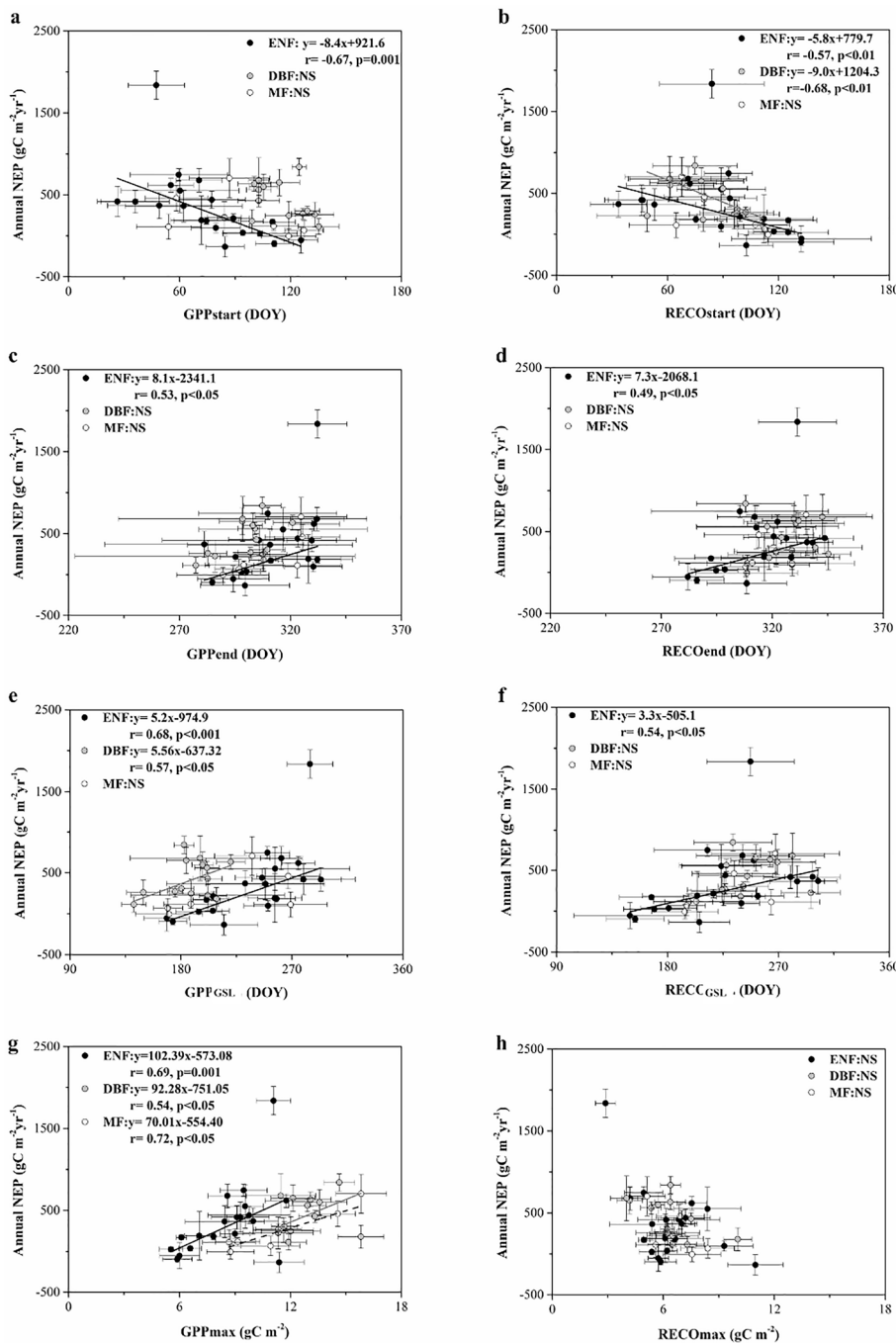


Fig. 4. Relationship between annual net ecosystem productivity (NEP) and metrics: (a) the start of growing season (GPP_{start}), (b) the start of respiration (RECO_{start}), (c) the end of growing season (GPP_{end}), (d) the end of respiration (RECO_{end}), (e) the length of growing season (GPP_{GSL}), (f) the length of respiration (RECO_{RSL}), (g) the maximum of gross primary production (GPP_{max}) and (h) the maximum of respiration (RECO_{max}) in evergreen needleleaf forests (ENF), deciduous broadleaf forests (DBF) and mixed forests (MF) ecosystem.

where A_i is the yearly anomaly of a variable in the year i , x_i represents the observation of the variable in the year i , and X_{mean} is the multi-year mean value of the variable in specific site during the study period.

In addition to the IAV, we compared the ability of phenological and physiological indicators to explain the SV of NEP across sites for a particular forest type (i.e. DBF, ENF, MF). First, the mean values and standard errors of these indicators were calculated for each site. Then, a simple linear regression was used to analyze the relationship between these indicators and NEP across each of three forest types. All correlations in this study were evaluated by the Pearson correlation coefficient (r) and a p -value threshold of 0.05. Furthermore, these correlations were divided into DBF, ENF and MF forest functional types, considering their large differences in carbon sequestration characteristics and responses to climate change.

3. Results

3.1. Explaining variability of NEP using single physiological and single phenological metrics

We found that physiological metrics (GPP_{max} and RECO_{max}) and phenological metrics (GPP_{start}, GPP_{end}, GPP_{GSL}, RECO_{start}, RECO_{end} and RECO_{RSL}) differed in their ability in explaining the IAV of NEP among these three forest types. Besides, opposite correlations were observed between the IAV of NEP and GPP-based and RECO-based metrics (Fig. 3).

Phenological metrics showed relatively weak relationships with the annual NEP. The GPP-derived phenological metrics were only significantly correlated with annual NEP at DBF sites. Among them, GPP_{GSL}

and GPP_{end} showed higher ability than GPP_{start} , with Pearson's r of 0.33 ($p < 0.001$) and 0.37 ($p < 0.001$), respectively (Fig. 3a, c, e). However, the phenological metrics derived from RECO showed no significant correlation with the NEP at DBF sites, but significant correlations at MF and ENF sites. Similar to the phenological metrics of photosynthesis, $RECO_{end}$ and $RECO_{RSL}$ performed relatively better than the $RECO_{start}$, with negative r of -0.15 ($p < 0.05$) and -0.22 ($p < 0.001$) for ENF sites and r of -0.23 ($p < 0.05$) and -0.21 ($p = 0.05$) for MF sites (Fig. 3b, d, f).

Physiological metrics (GPP_{max} and $RECO_{max}$) exhibited a higher correlation than corresponding phenological metrics in interpreting the IAV of NEP. GPP_{max} performed better than any other GPP-derived phenological metrics (GPP_{start} , GPP_{end} and GPP_{GSL}), with higher correlations at DBF sites ($r = 0.41$, $p < 0.001$) and ENF sites ($r = 0.21$, $p < 0.001$) (Fig. 3g). Similarly, we found that $RECO_{max}$ was more tightly correlated with annual NEP than RECO-derived phenological metrics ($RECO_{start}$, $RECO_{end}$ and $RECO_{RSL}$), with r of -0.29 ($p < 0.001$), -0.15 ($p < 0.05$) and -0.43 ($p < 0.001$) for ENF, DBF and MF sites, respectively (Fig. 3h).

The impacts of physiological and phenological metrics on SV of NEP were also analyzed among different forest types. We found that, in contrast to IAV of NEP, consistent correlations were observed between SV of NEP and GPP-based and RECO-based metrics (Fig. 4).

The RECO-derived phenological metrics, including $RECO_{start}$,

$RECO_{end}$, and $RECO_{RSL}$, were significantly correlated with SV of NEP at ENF sites, with comparable Pearson's r of -0.57 ($p < 0.01$), 0.49 ($p < 0.05$) and 0.54 ($p < 0.05$). $RECO_{start}$ was the only metric that was significantly correlated with NEP at DBF sites ($r = -0.68$, $p < 0.01$). However, no significant correlation was observed between the SV of NEP and $RECO_{max}$ of these three forest types.

Compared with RECO-derived metrics, all GPP-derived metrics exhibited higher correlations with the SV of NEP for ENF sites (Fig. 4), and GPP_{start} , GPP_{end} , GPP_{GSL} and GPP_{max} had overall similar performances with high Pearson's r of -0.67 ($p = 0.001$), 0.53 ($p < 0.05$), 0.68 ($p < 0.001$), 0.69 ($p < 0.001$) (Fig. 4a, c, e, g), respectively. Among them, GPP_{GSL} and GPP_{max} were also reliable in interpreting the SV of NEP at DBF sites ($r = 0.57$, $p < 0.05$ and $r = 0.54$, $p < 0.05$) (Fig. 4e, g). GPP_{max} was the only metric that was significantly correlated with the SV of NEP of MF ($r = 0.72$, $p < 0.05$) (Fig. 4g).

3.2. Explaining the variability of NEP using integrated physiological and integrated phenological indicators

The PRMR was proposed with a better performance of single physiological metrics (GPP_{max} and $RECO_{max}$) in explaining the IAV of NEP (as presented in Fig. 3), and MCUI aimed to further improve the ability of PRMR in interpreting the SV of NEP (as presented in Fig. 4). We compared these two indicators with RGR, which is the phenological

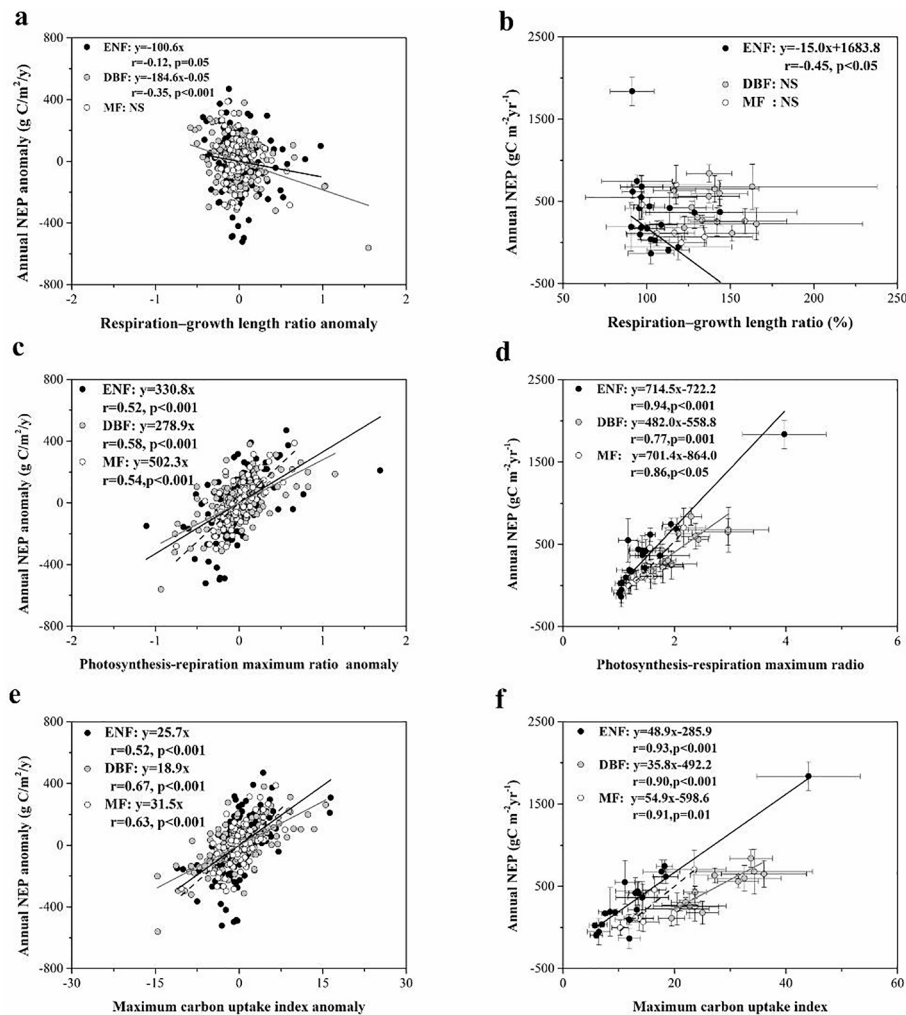


Fig. 5. Relationship between the interannual net ecosystem productivity (NEP) anomalies and indicator anomalies: (a) Respiration-growth length ratio (RGR), (c) Photosynthesis-respiration maximum ratio (PRMR), (e) Maximum carbon uptake index (MCUI). Relationship between annual NEP and (b) RGR, (d) PRMR, (f) MCUI in evergreen needleleaf forests (ENF), deciduous broadleaf forests (DBF) and mixed forests (MF) ecosystem.

indicator integrating the length of GPP and RECO.

We found that RGR showed limited potential in interpreting the IAV and SV of NEP. RGR was slightly negatively correlated with NEP at ENF and DBF sites ($r = -0.12$, $p = 0.05$ and $r = -0.35$, $p < 0.001$) (Fig. 5a), and no significant correlation was observed at MF sites. Besides, RGR only had a significant correlation with spatial NEP at ENF sites ($r = -0.45$, $p < 0.05$) (Fig. 5b).

In comparison, PRMR and MCUI performed better in explaining both IAV and SV of NEP, especially at ENF and MF ecosystems where RGR failed to provide reliable NEP estimates (Fig. 5). Both PRMR and MCUI were significantly correlated with IAV and SV of NEP for all three forest types (Fig. 5c, d, e, f). MCUI improved the accuracy of PRMR in interpreting SV of NEP, with a higher r of 0.90 ($p < 0.001$) for DBF and 0.91 ($p = 0.01$) for MF, and a comparable r of 0.93 ($p < 0.001$) for ENF (Fig. 5 d, f). Moreover, compared with PRMR, MCUI showed a higher correlation with the IAV of NEP in the DBF ecosystem, with a high Pearson's r of 0.67 ($p < 0.001$) (Fig. 5c, e).

We further compared the performances of MCUI and RGR in explaining the variability of NEP at each study site (Table 1). RGR still showed limited potential with significant correlations observed only at two ENF sites (CZ-BK1 and DE-Tha) and two DBF sites (IT-Ro1 and IT-Ro2). By comparison, MCUI was more tightly linked to IAV of NEP for all three forest types, both in the number of significant sites (12 out of 20 for ENF, 10 out of 14 for DBF sites and 3 out of 6 for DBF sites) and in the value of the correlation coefficient with r ranged from 0.53 ($p = 0.033$) at US-NR1 to 0.96 ($p = 0.000$) at US-GLE. In addition, we found that, for significant correlations, the mean slope of MCUI and NEP regressions at ENF and MF sites were steeper than that of DBF sites (38.8 for ENF, 36.9 for MF and 20.1 for DBF).

3.3. Controls of meteorological variables on MCUI

We found that relationships between MCUI and meteorological variables, including T_a , SW, VPD, precipitation, T_s and SWC, differed substantially among forest types (Table 2 and Fig. 6).

For ENF ecosystem, SWC was the only meteorological variable that was significantly correlated with MCUI anomalies, with a positive r of 0.20 ($p < 0.01$) (Table 2). The same result was also confirmed at the site level. In contrast with other meteorological drivers, SWC was significantly correlated with MCUI anomalies at most ENF sites, with more significantly positive than negative correlations (15.0%, $p < 0.05$ vs. 5.0%, $p < 0.05$) (Fig. 6). More significant correlations were observed at DBF sites. SW, VPD, Precipitation and SWC were all significantly correlated with MCUI. Among them, SW and VPD showed positive correlations, but precipitation and SWC exhibited negative correlations. SW was the most important factor affecting MCUI with r of 0.34 ($p < 0.001$) (Table 2). Similar results were observed at each single site, where the MCUI of 78.57% of DBF sites was positively correlated with SW (Fig. 6). No significant correlation was found between MCUI and meteorological variables anomalies at MF sites. The result was consistent with the statistics at the site level as shown in Fig. 6.

4. Discussion

4.1. The role of phenology in regulating NEP among forest types

Phenological metrics seemed to show relatively limited potential in predicting the IAV of NEP (Fig. 3). Among three forest types, the significant correlation between photosynthesis phenology and NEP was only found at DBF sites, and GPP_{GSL} and GPP_{end} performed slightly better than GPP_{start} (Fig. 3a, c, e). These results are in line with a previous study that found higher correlations of NEP to phenological metrics (the start, end and length of carbon uptake) at DBF sites than that of ENF sites (Fu et al., 2017). Deciduous forest adopts the survival strategy of higher rate of photosynthesis in a shorter growing season, and reduces carbon loss in winter by defoliation. Therefore, phenology showed

Table 1

Relationship between annual cumulative net ecosystem production (NEP) and respiration-growth length ratio (RGR) and the maximum carbon uptake index (MCUI) for each site.

Site_ID	PFT	RGR		MCUI	
		R (P-value)	Slope (g Cm ⁻² day ⁻¹)	R (P-value)	Slope (g Cm ⁻² day ⁻¹)
CA-Man	ENF	NS		NS	
CA-Obs	ENF	-0.46 (0.142)	-198.81	NS	
CA-TP1	ENF	NS		0.86 (0.063)	26.61
CA-TP3	ENF	NS		0.69 (0.028)	18.26
CA-TP4	ENF	NS		0.59 (0.042)	14.84
CH-Dav	ENF	NS		0.55 (0.021)	76.85
CZ-BK1	ENF	-0.97 (0.007)	-343.71	0.83 (0.081)	42.90
DE-Tha	ENF	-0.53 (0.029)	-673.16	NS	
FI-Hyy	ENF	-0.43 (0.075)	-237.30	0.70 (0.001)	23.18
FI-Sod	ENF	-0.46 (0.096)	-136.75	0.52 (0.058)	16.94
FR-LBr	ENF	NS		0.67 (0.034)	40.03
IT-Lav	ENF	NS		0.86 (0.000)	16.06
IT-Ren	ENF	NS		0.87 (0.000)	37.48
IT-SRo	ENF	NS		0.70 (0.008)	68.49
NL-Loo	ENF	NS		0.65 (0.006)	52.38
RU-Fyo	ENF	NS		0.63 (0.009)	39.14
US-Blo	ENF	NS		NS	
US-GLE	ENF	-0.54 (0.137)	-226.75	0.96 (0.000)	75.09
US-Me2	ENF	NS		NS	
US-NR1	ENF	NS		0.53 (0.033)	25.75
CA-Oas	DBF	-0.44 (0.105)	-378.15	0.44 (0.104)	18.20
DE-Hai	DBF	NS		0.51 (0.079)	10.57
DE-Lnf	DBF	NS		0.75 (0.033)	17.53
DK-Sor	DBF	NS		0.70 (0.001)	34.02
FR-Fon	DBF	-0.51 (0.166)	-406.05	0.90 (0.000)	18.95
IT-Col	DBF	NS		0.70 (0.008)	14.80
IT-Ro1	DBF	-0.86 (0.029)	-199.49	0.68 (0.095)	23.01
IT-Ro2	DBF	-0.81 (0.008)	-297.57	0.81 (0.008)	21.18
US-Ha1	DBF	-0.41 (0.085)	-375.09	0.55 (0.012)	22.39
US-	DBF	-0.42 (0.102)	-246.15	0.50 (0.051)	17.45
US-Oho	DBF	NS		0.85 (0.002)	23.79
US-	DBF	NS		0.78 (0.001)	15.55
US-UMB	DBF	NS		NS	
US-Umd	DBF	NS		NS	
US-WCr	DBF	NS		0.64 (0.026)	14.95
BE-Bra	MF	NS		0.57 (0.028)	32.50
BE-Vie	MF	NS		0.59 (0.010)	43.52

(continued on next page)

Table 1 (continued)

Site_ID	PFT	RGR		MCUI	
		R (P-value)	Slope (g Cm ⁻² day ⁻¹)	R (P-value)	Slope (g Cm ⁻² day ⁻¹)
CA-Gro	MF	NS		NS	
CH-Lae	MF	-0.49 (0.150)	-461.82	0.77 (0.060)	32.42
US-PFa	MF	NS		NS	
US-Syv	MF	NS		0.85 (0.007)	34.77

Note: ENF, DBF and MF represent evergreen needleleaf forest, deciduous broadleaf forests and mixed forest, respectively. NS indicate not significant.

higher sensitivity to carbon sequestration (Churkina et al., 2005; Givnish, 2002; Richardson et al., 2009; Roser et al., 2002). Other studies have discussed the importance of autumn phenology in regulating the inter-annual variability of NEP (Dragoni et al., 2011; Gallinat et al., 2015; Wu et al., 2013; Zhu et al., 2012). In addition, we found that the start, end and length of the respiration also played an underappreciated role in explaining the IAV of NEP at ENF and MF sites (Fig. 3b, d, f). These results confirmed the important role of the respiration in controlling annual NEP (Chen et al., 2015; Valentini et al., 2000).

4.2. The role of physiology in regulating NEP among forest types

We found that physiological indicators may be potentially more useful than phenological metrics to interpret the IAV of NEP (Fig. 3). Such a result is consistent with a previous study, given that the large fluxes rather than phenology could better help in understanding the variability of these fluxes (Zscheischler et al., 2016). The cumulative NEP in summer contributed more to annual NEP than its counterparts in spring and autumn (Supplementary Fig. 2). Since GPP_{max} and RECO_{max} are tightly correlated with summer NEP (Supplementary Fig. 3), they could provide relatively reliable NEP estimates (Musavi et al., 2017; Xia et al., 2015; Zhou et al., 2016).

GPP_{max} of DBF exhibited a higher correlation with NEP than that of ENF and MF, but RECO_{max} of DBF sites showed lower correlation than that of ENF and MF. We suggest that the summer photosynthetic rate of DBF is more crucial in controlling carbon sequestration than that of ENF and MF, while the maximum summer respiratory rate seems less important. At ENF sites, both GPP_{max} and RECO_{max} influenced the IAV of NEP, and RECO_{max} was more linked to IAV of NEP than GPP_{max}. Additionally, ENF is more sensitive to summer respiration and less sensitive to summer photosynthesis than DBF, as indicated by the different regression slopes. This performance might be interpreted by physiological characteristic of ENF, given that ENF ecosystems are more adaptable to seasonal changes with relatively low rates of photosynthesis and high rates of respiration continuing for longer periods than deciduous forests (Barr et al., 2009; Piao et al., 2007; Richardson et al., 2010; Wu and Chen, 2013). For MF, we found that the IAV of NEP was correlated with RECO_{max} but not with GPP_{max}. These results demonstrate the substantial differences of NEP controllers among forest types as well as that partitioning NEP into GPP and RECO could help to

Table 2

Relationships between the maximum carbon uptake index (MCUI) anomaly and meteorological variables anomaly across vegetation types.

Meteorological variables		T _a (°C)	SW (MJm ⁻² day ⁻¹)	VPD (hPa)	Precipitation (mm)	T _s (°C)	SWC (%)
ENF (N = 20)	r	-0.02	0.004	-0.12	0.05	0.03	0.20
	P-value	0.748.	0.947	0.078	0.514	0.714	0.004
DBF (N = 14)	r	0.05	0.34	0.17	-0.19	0.07	-0.12
	P-value	0.482	0.000	0.037	0.013	0.349	0.012
MF (N = 6)	r	-0.07	-0.11	-0.04	-0.10	-0.09	0.09
	P-value	0.523	0.327	0.753	0.444	0.420	0.450

Note: ENF = Evergreen Needleleaf forests, DBF = Deciduous Broadleaf forests, MF = mixed forests. T_a, SW, VPD, precipitation, T_s and SWC are average values of daily air temperature, shortwave radiation, vapor pressure deficit, precipitation, soil temperature and soil water content from June to July. Bold font indicated significant correlations were found.

understand the role of these two processes in controlling carbon uptake (Baldocchi et al., 2018; Fu et al., 2019; Niu et al., 2017; Schwalm et al., 2010).

4.3. Controls of meteorological factors on MCUI

Understanding the response of MCUI to meteorological factors can help to model NEP in forest ecosystem. MCUI is an integrated indicator that combines maximum respiratory and photosynthetic rates, thus any meteorological variables that affect these two processes will affect MCUI. Unfortunately, we found that there is no single meteorological driver for MCUI.

Precipitation can affect carbon sequestration by affecting SWC (Knapp et al., 2008), however, the effects of water regimes on the IAV of NEP are often ecosystem specific (Niu et al., 2017). We found that MCUI was not significantly correlated with summer precipitation but summer SWC at ENF sites, suggesting that SWC has a more direct impact on NEP than precipitation. The positive correlation between SWC and MCUI at ENF sites confirms that a higher SWC could probably lead to a higher NEP in a water limited ecosystem (Davidson et al., 1998; Quan et al., 2019; Reich et al., 2018). However, we found that both SWC and precipitation in summer are negatively correlated with MCUI at DBF sites. A similar result that summer precipitation is negatively correlated with the maximum of NEP at DBF sites (Fu et al., 2017), suggests that more water does not always lead to a higher NEP. More precipitation and high SWC

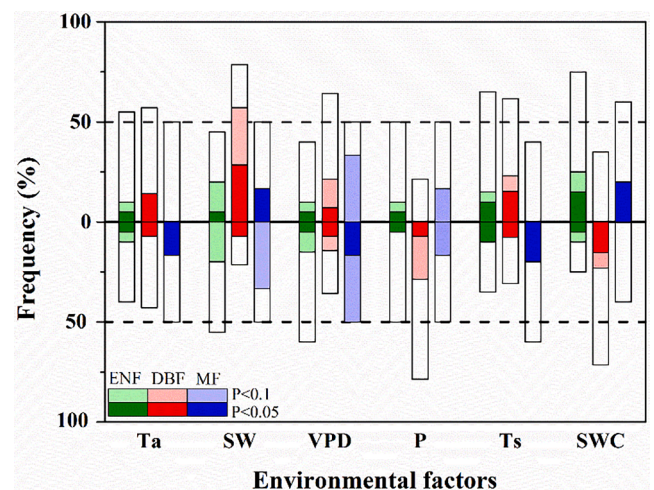


Fig. 6. The correlation coefficient between the maximum carbon uptake index (MCUI) and environment variables at all three types (20 evergreen needleleaf forest (ENF), 14 deciduous broadleaf forest (DBF) and 6 mixed forest (MF)) of study sites. Bars above and below the zero line represent the percentages of positive and negative correlations, respectively. Dark-colored parts indicate significant correlations at $p < 0.05$ and light-colored parts indicate significant correlations at $p < 0.1$. T_a, SW, VPD, precipitation, T_s and SWC are average values of daily air temperature, global shortwave radiation, vapor pressure deficit, precipitation, soil temperature and soil water content from June to July.

are always associated with less incoming PAR, which leads to less photosynthesis, and hence less NEP (Gonsamo et al., 2015; Oliphant et al., 2011). The significant positive correlation between SW and MCUI in DBF ecosystems also supported this view (Table 2). With climate change, the aggravated mismatch between water conditions and temperature may instead have opposite effects on productivity (Heisler-White et al., 2009; Thomey et al., 2011). In addition, MCUI was significantly correlated with VPD, but showed no preference for positive or negative correlation at the site level (Fig. 6).

Shortwave radiation has a more important role than other climate factors in regulating IAV of NEP at local scales (Jung et al., 2017; Niu et al., 2017), especially in light-sensitive ecosystems (Delpierre et al., 2012; Oliphant et al., 2011). We found that summer shortwave radiation was significantly positively correlated with MCUI at DBF sites (Table 2 and Fig. 6). Such a result is consistent with a previous study, given that the increasing of shortwave radiation is in line with increasing NEP in mature deciduous forests (Gonsamo et al., 2015). Gonsamo et al. (2018) also showed that the earlier occurrence of peak plant activity will result in increased plant productivity because of higher solar irradiance. However, in regions with long winters, the spring phenological activity and carbon uptake rely on cues other than the shortwave radiation (Zohner et al., 2016), which is consistent with the poor correlation between shortwave radiation and MCUI at ENF sites, and also suggest the complexity of shortwave radiation in controlling NEP among different temperate forest species.

4.4. The development of MCUI

The integrated indicator MCUI was developed because of the imperfect but complementary ability of GPP_{max} and $RECO_{max}$ in estimating the interannual variability of NEP (Fig. 3). First, we proposed the PRMR using the ratio of photosynthesis and respiration maximum, and PRMR did exhibit higher potential than single physiological metrics, confirming that respiration and photosynthesis are equally important in regulating NEP (Huang et al., 2012; Piao et al., 2008; Wu et al., 2013). Then, considering the better performance of GPP_{max} in predicting SV of NEP (Fig. 4g), MCUI was developed based on PRMR, and this helped to improve the ability of PRMR in explaining SV of NEP, especially at DBF sites (Fig. 5d, f). Furthermore, it should be noted that MCUI also performed better than PRMR in explaining the IAV of NEP at DBF sites (Fig. 5c, e), and the higher correlation between GPP_{max} and IAV of NEP at DBF sites may interpret the better performance (Fig. 3g). Moreover, MCUI showed a similar and powerful ability to indicate the variability of NEP among three forest types, especially at ENF and MF sites where the previously integrated phenological indicator (RGR) cannot provide reliable estimates. As an integrated physiological indicator, the better performance of MCUI is not surprising, given that the generally stronger abilities of single physiological metrics than single phenological metrics in explaining NEP. The better performance of integrated physiological indicator compared to integrated phenological indicators further illustrates that the summer physiology status (related to maximum potential) may be more valuable than phenology (related to time) in regulating forest NEP, which agrees with the previous finding that the maximum carbon uptake dominates the IAV of NEP more than the net carbon uptake period at the global scale (Fu et al., 2019).

In contrast with DBF, the MCUI of ENF and MF were more sensitive to IAV and SV of NEP, with higher slopes of regressions (Fig. 5e, f), indicating the more important role of summer physiology in regulating NEP for ENF and MF ecosystems than for DBF ecosystems. On the contrary, the phenology of DBF exhibited a relatively higher sensitivity to NEP, which is also supported by previous studies (Churkina et al., 2005; Piao et al., 2007; Richardson et al., 2010; Wu et al., 2013). The opposite sensitivity of physiology-NEP and phenology-NEP relationship confirmed that the sensitivity of ecophysiology-drivers of NEP is often ecosystem specific and depends on the characteristic of the ecosystem.

To the best of our knowledge, this is the first analysis to simulate NEP

merely using physiological metrics, which is a beneficial attempt and particularly significant for C sequestration. However, MCUI was mathematical and performance-based, rather than mechanistic and meteorological driven. We tried to interpret the variability of MCUI using the meteorological factors, but unfortunately, no single meteorological driver for MCUI was found among these forest types (Table 2 and Fig. 6). In addition, the MCUI still showed uncertainty, especially at several ENF sites. Although GPP_{max} and $RECO_{max}$ could represent photosynthesis and respiration to some extent (Huang et al., 2018; Xia et al., 2015; Xu et al., 2019; Zhou et al., 2017), using only these two metrics in summer might inevitably lead to certain uncertainties. For instance, the maximum carbon uptake depends on the relative strengths of photosynthesis and respiration, yet the largest difference between photosynthesis and respiration is not always around the day of GPP_{max} and $RECO_{max}$, which results in the inability of MCUI to accurately predict the NEP.

4.5. Limitations and challenges

Our study showed that the IAV and SV of NEP can be better explained by physiological indicator in summer rather than previously used phenological indicator. However, given that most of flux sites have less than 30 years measurements, and hence the NEP variability is strictly more sensitive to summer physiology rather than phenology in such a short period. Besides, the distribution of sampled flux towers may affect the result of the relative contributions of the phenology and physiology to SV of NEP.

In addition, the different forest managements may have impacts on annual cumulative NEP (Clay et al., 2019; Fahey et al., 2010; Hyvönen et al., 2007; Tong et al., 2020), especially considering that these sites are located in different geographical environments. When calculating the overall average over all years for a site, the average implies the management of the respective sites in all years was constant. However, the fact that management has always changed over times. Thus, it may affect the validity of the indicators proposed in this study under different forest management modes and methods.

Since the development of MCUI was based on GPP and RECO at tower stations, the application of MCUI is limited due to the lack of measured ecosystem respiration in large areas. Clarifying the relationship between MCUI and meteorological factors will help to select the useful meteorological variables to predict MCUI and thus NEP, but inconsistent correlations were observed among ENF, DBF and MF sites, which causes its difficulty to apply in a large area (Shen et al., 2014).

5. Conclusions

Our study explored the impact of summer physiology of photosynthesis and respiration in regulating the IAV and SV of NEP in forests, in contrast to previous studies of carbon sequestration mainly focused on the photosynthetic phenology or the metrics of NEP itself. Using 514 sites-years of flux data observed at 50 sites covering three forest types from North America and Europe, we found that the IAV and SV of NEP can be better explained by a new integrated physiological indicator, MCUI, highlighting the important role of physiological process in summer. This might be the first evidence of the importance of investigating the role of summer physiological indicators in controlling the variability of NEP based on both GPP and RECO. These results are of great significance for understanding the responses of the carbon uptake in forest ecosystem under future climate change.

CRediT authorship contribution statement

Ying Liu: Writing - original draft, Conceptualization, Data curation, Formal analysis. **Chaoyang Wu:** Writing - review & editing, Conceptualization, Funding acquisition, Visualization. **Lin Liu:** Project administration, Resources, Software. **Chengyan Gu:** Project administration,

Resources, Software, Supervision. **T. Andrew Black:** Writing - review & editing. **Rachhpal S. Jassal:** Writing - review & editing. **Lukas Hörtnagl:** Writing - review & editing. **Leonardo Montagnani:** Writing - review & editing. **Fernando Moyano:** Writing - review & editing. **Andrej Varlagin:** Writing - review & editing. **M. Altaf Arain:** Writing - review & editing. **Ajit Govind:** Writing - review & editing.

Declaration of Competing Interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2021.107982>.

References

- An, R., et al., 2016. Validation of the ESA CCI soil moisture product in China. *Int. J. Appl. Earth Obs. Geoinf.* 48, 28–36.
- Angert, A., et al., 2005. Drier summers cancel out the CO₂ uptake enhancement induced by warmer springs. *Proc. Natl. Acad. Sci. U.S.A.* 102 (31), 10823–10827.
- Baldocchi, D., 2008. Breathing of the terrestrial biosphere: lessons learned from a global network of carbon dioxide flux measurement systems. *Aust. J. Bot.* 56 (1), 1–26.
- Baldocchi, D., Chu, H., Reichstein, M., 2018. Inter-annual variability of net and gross ecosystem carbon fluxes: A review. *Agric. For. Meteorol.* 249, 520–533.
- Baldocchi, D., Falge, E., Gu, L., Olson, R., Hollinger, D., Running, S., Anthoni, P., Bernhofer, C.H., Davis, K., Evans, R., Fuentes, J., Goldstein, A., Katul, G., Law, B., Lee, X., Malhi, Y., Meyers, T., Munger, W., Oechel, W., Paw, K.T., Pilegaard, K., Schmid, H.P., Valentini, R., Verma, S., Vesala, T., Wilson, K., Wofsy, S., 2001. FLUXNET: a new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor, and energy flux densities. *B. Am. Meteorol. Soc.* 82 (11), 2415–2434.
- Baldocchi, D.D., 2003. Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: past, present and future. *Glob. Change Biol.* 9 (4), 479–492.
- Ballantyne, A.P., Alden, C.B., Miller, J.B., Tans, P.P., White, J.W.C., 2012. Increase in observed net carbon dioxide uptake by land and oceans during the past 50 years. *Nature* 488 (7409), 70–72.
- Barr, A., Black, T.A. and McCaughey, H., 2009. Phenology of ecosystem processes. *Climatic and Phenological Controls of the Carbon and Energy Balances of Three Contrasting Boreal Forest Ecosystems in Western Canada*. NY: Springer, New York.
- Barr, A.G., Richardson, A.D., Hollinger, D.Y., Papale, D., Arain, M.A., Black, T.A., Bohrer, G., Dragoni, D., Fischer, M.L., Gu, L., Law, B.E., Margolis, H.A., McCaughey, J.H., Munger, J.W., Oechel, W., Schaeffer, K., 2013. Use of change-point detection for friction-velocity threshold evaluation in eddy-covariance studies. *Agric. For. Meteorol.* 171–172, 31–45.
- Buermann, W., Bikash, P.R., Jung, M., Burn, D.H., Reichstein, M., 2013. Earlier springs decrease peak summer productivity in North American boreal forests. *Environ. Res. Lett.* 8 (2), 024027. <https://doi.org/10.1088/1748-9326/8/2/024027>.
- Chen, J., Jönsson, P., Tamura, M., Gu, Z., Matsushita, B., Eklundh, L., 2004. A simple method for reconstructing a high-quality NDVI time-series data set based on the Savitzky-Golay filter. *Remote Sens. Environ.* 91 (3–4), 332–344.
- Chen, Z., Yu, G., Zhu, X., Wang, Q., Niu, S., Hu, Z., 2015. Covariation between gross primary production and ecosystem respiration across space and the underlying mechanisms: a global synthesis. *Agric. For. Meteorol.* 203, 180–190.
- Churkina, G., Schimel, D., Braswell, B.H., Xiao, X., 2005. Spatial analysis of growing season length control over net ecosystem exchange. *Glob. Change Biol.* 11 (10), 1777–1787.
- Clay, L., Motallebi, M., Song, B.o., 2019. An Analysis of Common Forest Management Practices for Carbon Sequestration in South Carolina. *Forests* 10 (11), 949. <https://doi.org/10.3390/f10110949>.
- David, T.S., Henriques, M.O., Kurz-Besson, C., Nunes, J., Valente, F., Vaz, M., Pereira, J. S., Siegwolf, R., Chaves, M.M., Gazarini, L.C., David, J.S., 2007. Water-use strategies in two co-occurring Mediterranean evergreen oaks: surviving the summer drought. *Tree Physiol.* 27 (6), 793–803.
- Davidson, E.A., Belk, E., Boone, R.D., 1998. Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. *Glob. Change Biol.* 4 (2), 217–227.
- Delpierre, N., Soudani, K., François, C., Le Maire, G., Bernhofer, C., Kutsch, W., Misson, L., Rambal, S., Vesala, T., Dufréne, E., 2012. Quantifying the influence of climate and biological drivers on the interannual variability of carbon exchanges in European forests through process-based modelling. *Agric. For. Meteorol.* 154–155, 99–112.
- Dorigo, W., Wagner, W., Albergel, C., Albrecht, F., Balsamo, G., Brocca, L., Chung, D., Ertl, M., Forkel, M., Gruber, A., Haas, E., Hamer, P.D., Hirschi, M., Ikonen, J., de Jeu, R., Kidd, R., Lahoz, W., Liu, Y.Y., Miralles, D., Mistelbauer, T., Nicolai-Shaw, N., Parinussa, R., Pratola, C., Reimer, C., van der Schalie, R., Seneviratne, S.I., Smolander, T., Lecomte, P., 2017. ESA CCI Soil Moisture for improved Earth system understanding: State-of-the art and future directions. *Remote Sens. Environ.* 203, 185–215.
- Dragoni, D. et al., 2011. Evidence of increased net ecosystem productivity associated with a longer vegetated season in a deciduous forest in south-central Indiana, USA. *Global Change Biology*, 17(2): 886–897.
- Eisenhauer, N., Cesarz, S., Koller, R., Worm, K., Reich, P.B., 2012. Global change belowground: impacts of elevated CO₂, nitrogen, and summer drought on soil food webs and biodiversity. *Glob. Change Biol.* 18 (2), 435–447.
- Fahey, T.J., Woodbury, P.B., Battles, J.J., Goodale, C.L., Hamburg, S.P., Ollinger, S.V., Woodall, C.W., 2010. Forest carbon storage: ecology, management, and policy. *Front. Ecol. Environ.* 8 (5), 245–252.
- Fu, Z., Stoy, P.C., Luo, Y., Chen, J., Sun, J., Montagnani, L., Wohlfahrt, G., Rahman, A.F., Rambal, S., Bernhofer, C., Wang, J., Shirkey, G., Niu, S., 2017. Climate controls over the net carbon uptake period and amplitude of net ecosystem production in temperate and boreal ecosystems. *Agric. For. Meteorol.* 243, 9–18.
- Fu, Z., Stoy, P.C., Poulter, B., Gerken, T., Zhang, Z., Waktulcho, G., Niu, S., 2019. Maximum carbon uptake rate dominates the interannual variability of global net ecosystem exchange. *Glob. Change Biol.* 25 (10), 3381–3394.
- Gallinat, A.S., Primack, R.B. and Wagner, D.L., 2015. Autumn, the neglected season in climate change research (vol 30, pg 169, 2015). *Trends Ecol. Evol.*, 30(6): 364–364.
- Garrity, S.R., Bohrer, G., Maurer, K.D., Mueller, K.L., Vogel, C.S., Curtis, P.S., 2011. A comparison of multiple phenology data sources for estimating seasonal transitions in deciduous forest carbon exchange. *Agric. For. Meteorol.* 151 (12), 1741–1752.
- Givnish, T.J., 2002. Adaptive significance of evergreen vs. deciduous leaves: Solving the triple paradox. *Silva Fenn.* 36 (3), 703–743.
- Gonsamo, A., Chen, J.M., D’Odorico, P., 2013. Deriving land surface phenology indicators from CO₂ eddy covariance measurements. *Ecol. Ind.* 29, 203–207.
- Gonsamo, A., Chen, J.M., Ooi, Y.W., 2018. Peak season plant activity shift towards spring is reflected by increasing carbon uptake by extratropical ecosystems. *Glob. Chang. Biol.* 24 (5), 2117–2128.
- Gonsamo, A., Chen, J.M., Wu, C., Dragoni, D., 2012. Predicting deciduous forest carbon uptake phenology by upscaling FLUXNET measurements using remote sensing data. *Agr. Forest Meteorol.* 165, 127–135.
- Gonsamo, A., Croft, H., Chen, J.M., Wu, C., Froelich, N., Staebler, R.M., 2015. Radiation contributed more than temperature to increased decadal autumn and annual carbon uptake of two eastern North America mature forests. *Agric. For. Meteorol.* 201, 8–16.
- Heisler-White, J.L., Blair, J.M., Kelly, E.F., Harmoney, K., Knapp, A.K., 2009. Contingent productivity responses to more extreme rainfall regimes across a grassland biome. *Glob. Change Biol.* 15 (12), 2894–2904.
- Hilker, T., Gitelson, A., Coops, N.C., Hall, F.G., Black, T.A., 2011. Tracking plant physiological properties from multi-angular tower-based remote sensing. *Oecologia* 165 (4), 865–876.
- Hu, J., Moore, D.J.P., Burns, S.P., Monson, R.K., 2010. Longer growing seasons lead to less carbon sequestration by a subalpine forest. *Glob. Change Biol.* 16 (2), 771–783.
- Huang, K., Xia, J., Wang, Y., Ahlström, A., Chen, J., Cook, R.B., Cui, E., Fang, Y., Fisher, J.B., Huntzinger, D.N., Li, Z., Michalak, A.M., Qiao, Y., Schaefer, K., Schwalm, C., Wang, J., Wei, Y., Xu, X., Yan, L., Bian, C., Luo, Y., 2018. Enhanced peak growth of global vegetation and its key mechanisms. *Nat. Ecol. Evol.* 2 (12), 1897–1905.
- Huang, N.i., Niu, Z., Zhan, Y., Xu, S., Tappert, M.C., Wu, C., Huang, W., Gao, S., Hou, X., Cai, D., 2012. Relationships between soil respiration and photosynthesis-related spectral vegetation indices in two cropland ecosystems. *Agric. For. Meteorol.* 160, 80–89.
- Hyvönen, R., Ågren, G.I., Linder, S., Persson, T., Cotrufo, M.F., Ekblad, A., Freeman, M., Grelle, A., Janssens, I.A., Jarvis, P.G., Kellomäki, S., Lindroth, A., Loustau, D., Lundmark, T., Norby, R.J., Oren, R., Pilegaard, K., Ryan, M.G., Sigurdsson, B.D., Strömgren, M., van Oijen, M., Wallin, G., 2007. The likely impact of elevated [CO₂], nitrogen deposition, increased temperature and management on carbon sequestration in temperate and boreal forest ecosystems: a literature review. *New Phytol.* 173 (3), 463–480.

- Ivits, E., et al., 2012. Combining satellite derived phenology with climate data for climate change impact assessment. *88-89(May)*: p.85-97.
- Jung, M., Reichstein, M., Schwalm, C.R., Huntingford, C., Sitch, S., Ahlström, A., Arneeth, A., Camps-Valls, G., Ciais, P., Friedlingstein, P., Gans, F., Ichii, K., Jain, A.K., Kato, E., Papale, D., Poulter, B., Raduly, B., Rödenbeck, C., Tramontana, G., Viovy, N., Wang, Y.-P., Weber, U., Zaehle, S., Zeng, N., 2017. Compensatory water effects link yearly global land CO₂ sink changes to temperature. *Nature* 541 (7638), 516–520.
- Keenan, T.F., Darby, B., Felts, E., Sonnentag, O., Friedl, M.A., Hufkens, K., O'Keefe, J., Klosterman, S., Munger, J.W., Toomey, M., Richardson, A.D., 2014. Tracking forest phenology and seasonal physiology using digital repeat photography: a critical assessment. *Ecol. Appl.* 24 (6), 1478–1489.
- Knapp, A.K. et al., 2008. Consequences of more extreme precipitation regimes for terrestrial ecosystems. *Bioscience*, 58(9): 811–821.
- Lasslop, G. et al., 2010. Separation of net ecosystem exchange into assimilation and respiration using a light response curve approach: critical issues and global evaluation. *Global Change Biol.*, 16(1): 187–208.
- Lieth, H., 1974. Purposes of a phenology book. *Ecol. Stud. Anal. Synth.* 8, 3–19.
- Luo, Y., Keenan, T.F., Smith, M., 2015. Predictability of the terrestrial carbon cycle. *Glob. Change Biol.* 21 (5), 1737–1751.
- Luyssaert, S., et al., 2007. CO₂ balance of boreal, temperate, and tropical forests derived from a global database. *Glob. Change Biol.* 13 (12), 2509–2537.
- Ma, S., Baldocchi, D.D., Mambelli, S. and Dawson, T.E.J.F.E., 2011. Are temporal variations of leaf traits responsible for seasonal and inter-annual variability in ecosystem CO₂ exchange? , 25(1): 258–270.
- McKown, A.D., Guy, R.D., Azam, M.S., Drewes, E.C., Quamme, L.K., 2013. Seasonality and phenology alter functional leaf traits. *Oecologia* 172 (3), 653–665.
- Musavi, T., Migliavacca, M., Reichstein, M., Kattge, J., Wirth, C., Black, T.A., Janssens, I., Knohl, A., Loustau, D., Rouspard, O., Varlagin, A., Rambal, S., Cescatti, A., Gianelle, D., Kondo, H., Tamrakar, R., Mahecha, M.D., 2017. Stand age and species richness dampen interannual variation of ecosystem-level photosynthetic capacity. *Nat. Ecol. Evol.* 1 (2) <https://doi.org/10.1038/s41559-016-0048>.
- Niu, S., Fu, Z., Luo, Y., Stoy, P.C., Keenan, T.F., Poulter, B., Zhang, L., Piao, S., Zhou, X., Zheng, H., Han, J., Wang, Q., Yu, G., 2017. Interannual variability of ecosystem carbon exchange: from observation to prediction. *Glob. Ecol. Biogeogr.* 26 (11), 1225–1237.
- Oliphant, A.J., Dragoni, D., Deng, B., Grimmond, C.S.B., Schmid, H.-P., Scott, S.L., 2011. The role of sky conditions on gross primary production in a mixed deciduous forest. *Agric. For. Meteorol.* 151 (7), 781–791.
- Pan, Y., Birdsey, R.A., Phillips, O.L., Jackson, R.B., 2013. The structure, distribution, and biomass of the world's forests. *Annu. Rev. Ecol. Evol. S* 44 (1), 593–622.
- Papale, D., Reichstein, M., Aubinet, M., Canfora, E., Bernhofer, C., Kutsch, W., Longdoz, B., Rambal, S., Valentini, R., Vesala, T., Yakir, D., 2006. Towards a standardized processing of Net Ecosystem Exchange measured with eddy covariance technique: algorithms and uncertainty estimation. *Biogeosciences* 3 (4), 571–583.
- Pastorello, G., et al., 2020. The FLUXNET2015 dataset and the ONEFlux processing pipeline for eddy covariance data. *Sci. Data* 7 (1), 225.
- Pastorello, G.Z., et al., 2014. Observational Data Patterns for Time Series Data Quality Assessment, 10th IEEE International Conference on e-Science (e-Science'2014), Sao Paulo, pp. 271–278.
- Peichl, M., Sonnentag, O., Nilsson, M.B., 2015. Bringing Color into the picture: using digital repeat photography to investigate phenology controls of the carbon dioxide exchange in a boreal mire. *Ecosystems* 18 (1), 115–131.
- Peng, J., Wu, C., Zhang, X., Wang, X., Gonsamo, A., 2019. Satellite detection of cumulative and lagged effects of drought on autumn leaf senescence over the Northern Hemisphere. *Glob. Change Biol.* 25 (6), 2174–2188.
- Piao, S., Ciais, P., Friedlingstein, P., Peylin, P., Reichstein, M., Luyssaert, S., Margolis, H., Fang, J., Barr, A., Chen, A., Grelle, A., Hollinger, D.Y., Laurila, T., Lindroth, A., Richardson, A.D., Vesala, T., 2008. Net carbon dioxide losses of northern ecosystems in response to autumn warming. *Nature* 451 (7174), 49–52.
- Piao, S., Friedlingstein, P., Ciais, P., Viovy, N., Demarty, J., 2007. Growing season extension and its impact on terrestrial carbon cycle in the Northern Hemisphere over the past 2 decades. *Global Biogeochem. Cy* 21 (3), n/a–n/a.
- Quan, Q., Tian, D., Luo, Y., Zhang, F., Crowther, T.W., Zhu, K., Chen, H.Y.H., Zhou, Q., Niu, S., 2019. Water scaling of ecosystem carbon cycle feedback to climate warming. *Sci. Adv.* 5 (8), eaav1131. <https://doi.org/10.1126/sciadv.aav1131>.
- Reich, P.B., Sendall, K.M., Stefanski, A., Rich, R.L., Hobbie, S.E., Montgomery, R.A., 2018. Effects of climate warming on photosynthesis in boreal tree species depend on soil moisture. *Nature* 562 (7726), 263–267.
- Reichstein, M., Falge, E., Baldocchi, D., Papale, D., Aubinet, M., Berbigier, P., Bernhofer, C., Buchmann, N., Gilmanov, T., Granier, A., Grunwald, T., Havrankova, K., Ilvesniemi, H., Janous, D., Knohl, A., Laurila, T., Lohila, A., Loustau, D., Matteucci, G., Meyers, T., Miglietta, F., Ourcival, J.-M., Pumpanen, J., Rambal, S., Rotenberg, E., Sanz, M., Tenhunen, J., Seufert, G., Vaccari, F., Vesala, T., Yakir, D., Valentini, R., 2005. On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm. *Glob. Change Biol.* 11 (9), 1424–1439.
- Richardson, A.D., Andy Black, T., Ciais, P., Delbart, N., Friedl, M.A., Gobron, N., Hollinger, D.Y., Kutsch, W.L., Longdoz, B., Luyssaert, S., Migliavacca, M., Montagnani, L., William Munger, J., Moors, E., Piao, S., Rebmann, C., Reichstein, M., Saigusa, N., Tomelleri, E., Vargas, R., Varlagin, A., 2010. Influence of spring and autumn phenological transitions on forest ecosystem productivity. *Philos. T. R. Soc. B* 365 (1555), 3227–3246.
- Richardson, A.D., Hollinger, D.Y., Dail, D.B., Lee, J.T., Munger, J.W., O'keefe, J., 2009. Influence of spring phenology on seasonal and annual carbon balance in two contrasting New England forests. *Tree Physiol.* 29 (3), 321–331.
- Richardson, A.D., Keenan, T.F., Migliavacca, M., Ryu, Y., Sonnentag, O., Toomey, M., 2013. Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agric. For. Meteorol.* 169, 156–173.
- Roser, C., et al., 2002. Net CO₂ exchange rates in three different successional stages of the "Dark Taiga" of central Siberia. *Tellus B*, 54(5): 642–654.
- Ryu, Y., Berry, J.A., Baldocchi, D.D., 2019. What is global photosynthesis? History, uncertainties and opportunities. *Remote Sens. Environ.* 223, 95–114.
- Sacks, W.J., Schimel, D.S., Monson, R.K., 2007. Coupling between carbon cycling and climate in a high-elevation, subalpine forest: a model-data fusion analysis. *Oecologia* 151 (1), 54–68.
- Savitzky, A., Golay, M.J.E., 1964. Smoothing and differentiation of data by simplified least squares procedures. *Anal. Chem.* 36 (8), 1627–1639.
- Schwalm, C.R., et al., 2010. Assimilation exceeds respiration sensitivity to drought: A FLUXNET synthesis. *Global Change Biology*, 16(2): 657–670.
- Shen, M., Zhang, G., Cong, N., Wang, S., Kong, W., Piao, S., 2014. Increasing altitudinal gradient of spring vegetation phenology during the last decade on the Qinghai-Tibetan Plateau. *Agr. Forest Meteorol.* 189–190, 71–80.
- Shiga, Y.P., Michalak, A.M., Fang, Y., Schaefer, K., Andrews, A.E., Huntzinger, D.H., Schwalm, C.R., Thoning, K., Wei, Y., 2018. Forests dominate the interannual variability of the North American carbon sink. *Environ. Res. Lett.* 13 (8), 084015. <https://doi.org/10.1088/1748-9326/aad505>.
- Thomey, M.L., et al., 2011. Effect of precipitation variability on net primary production and soil respiration in a Chihuahuan Desert grassland. *Global Change Biology*, 17(4): 1505–1515.
- Tong, X., Brandt, M., Yue, Y., Ciais, P., Rudbeck Jepsen, M., Penuelas, J., Wigner, J.-P., Xiao, X., Song, X.-P., Horion, S., Rasmussen, K., Saatchi, S., Fan, L., Wang, K., Zhang, B., Chen, Z., Wang, Y., Li, X., Fensholt, R., 2020. Forest management in southern China generates short term extensive carbon sequestration. *Nat. Commun.* 11 (1) <https://doi.org/10.1038/s41467-019-13798-8>.
- Valentini, R., Matteucci, G., Dolman, A.J., Schulze, E.-D., Rebmann, C., Moors, E.J., Granier, A., Gross, P., Jensen, N.O., Pilegaard, K., Lindroth, A., Grelle, A., Bernhofer, C., Grünwald, T., Aubinet, M., Ceulemans, R., Kowalski, A.S., Vesala, T., Rannik, Ü., Berbigier, P., Loustau, D., Guðmundsson, J., Thorgeirsson, H., Ibrom, A., Morgenstern, K., Clement, R., Moncrieff, J., Montagnani, L., Minerbi, S., Jarvis, P.G., 2000. Respiration as the main determinant of carbon balance in European forests. *Nature* 404 (6780), 861–865.
- Walther et al., 2002. Ecological responses to recent climate change.
- Waring, R.H., Landsberg, J.J., Williams, M., 1998. Net primary production of forests: a constant fraction of gross primary production? *Tree Physiol.* 18 (2), 129–134.
- Wilkinson, M., Eaton, E.L., Broadmeadow, M.S.J., Morison, J.L.L., 2012. Inter-annual variation of carbon uptake by a plantation oak woodland in south-eastern England. *Biogeosciences* 9 (12), 5373–5389.
- Wohlfahrt, G., Bahn, M., Haslwanter, A., Newesely, C., Cernusca, A., 2005. Estimation of daytime ecosystem respiration to determine gross primary production of a mountain meadow. *Agric. For. Meteorol.* 130 (1–2), 13–25.
- Woodwell, G.M., et al., 1978. Biota and World Carbon Budget. *Science* 199 (4325), 141–146.
- Wu, C., Chen, J.M., 2013. Deriving a new phenological indicator of interannual net carbon exchange in contrasting boreal deciduous and evergreen forests. *Ecol. Ind.* 24, 113–119.
- Wu, C., Chen, J.M., Black, T.A., Price, D.T., Kurz, W.A., Desai, A.R., Gonsamo, A., Jassal, R.S., Gough, C.M., Bohrer, G., Dragoni, D., Herbst, M., Gielen, B., Berninger, F., Vesala, T., Mammarella, I., Pilegaard, K., Blanken, P.D., 2013. Interannual variability of net ecosystem productivity in forests is explained by carbon flux phenology in autumn. *Glob. Ecol. Biogeogr.* 22 (8), 994–1006.
- Wu, C., Chen, J.M., Gonsamo, A., Price, D.T., Black, T.A., Kurz, W.A., 2012. Interannual variability of net carbon exchange is related to the lag between the end-dates of net carbon uptake and photosynthesis: Evidence from long records at two contrasting forest stands. *Agric. For. Meteorol.* 164, 29–38.
- Xia, J.Y., et al., 2015. Joint control of terrestrial gross primary productivity by plant phenology and physiology. *Proc. Natl. Acad. Sci. U.S.A.* 112 (9), 2788–2793.
- Xu, X., Du, H., Fan, W., Hu, J., Mao, F., Dong, H., 2019. Long-term trend in vegetation gross primary production, phenology and their relationships inferred from the FLUXNET data. *J. Environ. Manage.* 246, 605–616.
- Yatskov, M.A., Harmon, M.E., Barrett, T.M., Döbelbower, K.R., 2019. Carbon pools and biomass stores in the forests of Coastal Alaska: Uncertainty of estimates and impact of disturbance. *For. Ecol. Manage.* 434, 303–317.
- Yu, G.R., et al., 2008. Environmental controls over carbon exchange of three forest ecosystems in eastern China. *Global Change Biology*, 14(11): 2555–2571.
- Zhou, S., Zhang, Y., Caylor, K.K., Luo, Y., Xiao, X., Ciais, P., Huang, Y., Wang, G., 2016. Explaining inter-annual variability of gross primary productivity from plant phenology and physiology. *Agric. For. Meteorol.* 226–227, 246–256.
- Zhou, S., et al., 2017. Dominant role of plant physiology in trend and variability of gross primary productivity in North America. *Sci Rep.* 7: 41366.
- Zhu, W.Q. et al., 2012. Extension of the growing season due to delayed autumn over mid and high latitudes in North America during 1982–2006. *Global Ecol. Biogeography*, 21(2): 260–271.
- Zohner, C.M., Benito, B.M., Svenning, J.-C., Renner, S.S., 2016. Day length unlikely to constrain climate-driven shifts in leaf-out times of northern woody plants (vol 6, pg 1120, 2016). *Nat. Clim. Change* 6 (12), 1120–1123.
- Zscheischler, J., Fatichi, S., Wolf, S., Blanken, P.D., Bohrer, G., Clark, K., Desai, A.R., Hollinger, D., Keenan, T., Novick, K.A., Seneviratne, S.I., 2016. Short-term favorable weather conditions are an important control of interannual variability in carbon and water fluxes. *J. Geophys. Res.-Biogeo.* 121 (8), 2186–2198.