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Interannual variability of net ecosystem productivity in forests is explained by carbon flux phenology in autumn

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ABSTRACT

Aim To investigate the importance of autumn phenology in controlling interannual variability of forest net ecosystem productivity (NEP) and to derive new phenological metrics to explain the interannual variability of NEP.

Location North America and Europe.

Method Flux data from nine deciduous broadleaf forests (DBF) and 13 evergreen needleleaf forests (ENF) across North America and Europe (212 site-years) were used to explore the relationships between the yearly anomalies of annual NEP and several carbon flux based phenological indicators, including the onset/end of the growing season, onset/end of the carbon uptake period, the spring lag (time interval between the onset of growing season and carbon uptake period) and the autumn lag (time interval between the end of the carbon uptake period and the growing season). Meteorological variables, including global shortwave radiation, air temperature, soil temperature, soil water content and precipitation, were also used to explain the phenological variations.

Results We found that interannual variability of NEP can be largely explained by autumn phenology, i.e. the autumn lag. While variation in neither annual gross primary productivity (GPP) nor in annual ecosystem respiration (R_e) alone could explain this variability, the negative relationship between annual NEP and autumn lag was due to a larger R_e /GPP ratio in years with a prolonged autumn lag. For DBF sites, a longer autumn lag coincided with a significant decrease in annual GPP but showed no correlation with annual R_e . However, annual GPP was insensitive to a longer autumn lag in ENF sites but annual R_e increased significantly.

Main conclusions These results demonstrate that autumn phenology plays a more direct role than spring phenology in regulating interannual variability of annual NEP. In particular, the importance of respiration may be potentially underestimated in deriving phenological indicators.

Keywords

Carbon cycle, ecosystem respiration, forest, gross primary productivity, net carbon exchange, phenology.

INTRODUCTION

Phenology is an important control on carbon (C) sequestration in terrestrial ecosystems (e.g. Richardson *et al.*, 2010). Net ecosystem productivity (NEP), which represents the difference between gross primary production (GPP) and ecosystem respiration (R_e), is primarily driven by interannual variability in climate, and, therefore, several phenological indicators have been proposed to track changes in annual growth patterns (Sun *et al.*, 2003a; White & Nemani, 2003; Baldocchi, 2008; Morissette *et al.*, 2009).

Most phenological metrics quantify the duration of the growing season or of the period of net C uptake. Growing season transitions have been described by the dates when a strong change in leaf colour (particularly greenness) is observed from remote sensing or ground measurements, or by the dates of bud-break in the spring and leaf senescence in the autumn (White & Nemani, 2003; Garrity *et al.*, 2011). Significant uncertainty exists in this method due to variations in thresholds arising from site-specific factors (Chen *et al.*, 2000) and thus it may not be robust for global applications (Gea-Izquierdo *et al.*, 2010). With continuous measurements of C exchange using the eddy-covariance (EC) technique, an alternative method makes use of C flux phenology (Richardson *et al.*, 2010; Garrity *et al.*, 2011). In the C flux phenology approach, growing season phenology is quantified by the dates when daily GPP reaches an empirical threshold (e.g. $1 \text{ g C m}^{-2} \text{ day}^{-1}$) in spring or becomes lower than this value in autumn (Garrity *et al.*, 2011), and net C uptake phenology is described by the dates when daily NEP switches from negative to positive in spring and from positive to negative in autumn (White & Nemani, 2003; Richardson *et al.*, 2010). After the determination of these transitions of growing season and net C uptake, we can derive growing season length (GSL) and net C uptake period (CUP), respectively.

Spring phenology has been previously identified as a potential indicator of annual C uptake (e.g. Black *et al.*, 2000). The main reason for such enhancement in C sequestration was found to be the prolonged growing season (Chen *et al.*, 2000). In boreal ecosystems, this is driven by the warmer spring air temperature that triggers the recovery of photosynthesis (Sun *et al.*, 2003b; Barr *et al.*, 2009). However, in temperate ecosystems, where the growth of plants is not limited solely by cold temperatures, the potential of spring phenology to explain interannual NEP is uncertain. Furthermore, the increase in NEP due to a warmer spring could be offset by higher respiration rates due to higher temperatures in autumn (Piao *et al.*, 2008; Richardson *et al.*, 2010). Recent stand- and regional-level studies have indicated that the greatest effect of a warmer climate in increasing C sequestration in North America could be through a delayed start to autumn (Dragoni *et al.*, 2011; Garrity *et al.*, 2011; Zhu *et al.*, 2012).

Although both growing season and net C uptake phenologies have been shown to have impacts on annual NEP, the capability of a single indicator to explain interannual variability in NEP is still limited, and this may affect the application of phenology in ecosystem models (Richardson *et al.*, 2012). Therefore, to analyse

the effect of phenology on interannual variability of NEP, a possible alternative approach may be to consider both growing season (i.e. GPP) and net C uptake (i.e. NEP) phenologies jointly, given the close coupling between photosynthesis and respiration. Using 212 site-years of flux data obtained at 22 forest sites across North America and Europe (with a median time duration of 9 years), this paper attempts to explain interannual variability of NEP using both growing season and net C uptake phenologies, and to investigate the mechanisms and feedbacks involved in the interactions between phenological variations and ecosystem C uptake. Our hypotheses are: (1) that phenological metrics incorporating both GPP and NEP are able to better predict interannual variability in NEP than either alone, and (2) that the value of the respiration process in deriving phenological indicators may be greater than previously assumed.

METHODS

Study sites

In this analysis, we identified 22 forest ecosystems in the global flux network that complied with the following criteria: at least 5 years of continuously and complete data records, with less than 20% gap-filled in each year; availability of site-level meteorological data; and no recent disturbances, i.e. fire, harvest. The complete dataset covered a variety of forest ecosystems in North America and Europe (Fig. 1). The vegetation at these sites could be classified broadly into two plant functional types (PFT), with nine deciduous broadleaf forests (DBF) and 13 evergreen needleleaf forests (ENF). The inset in Fig. 1 presents the ranges of mean annual temperature, precipitation and NEP for these sites (where positive NEP denotes a gain of carbon by the ecosystem). Further details description of these sites are given in Table 1.

Flux and site meteorological measurements

Half-hourly ecosystem CO_2 flux data were continuously measured at each site using the EC technique (Baldocchi *et al.*, 2001). Several procedures derived by respective regional flux networks were applied to partition net ecosystem exchange (NEE) into GPP and R_e to facilitate the evaluation of the relationship between NEP and phenological changes.

For Canadian sites, estimation of GPP and R_e was achieved by using two empirical relationships: (1) between nighttime NEE and nighttime temperature, and (2) between daytime GPP and photosynthetically active radiation. The procedure for gap-filling is described in Barr *et al.* (2004) and was adopted as the standard method for all FLUXNET-Canada sites. For the AmeriFlux and European sites, level-4 products were used which contain gap-filled and friction velocity (u^*) filtered records of C fluxes at varying time intervals with flags regarding the quality of the original and gap-filled data. Annual GPP, NEP and R_e values for each site were extracted. The half-hourly measurements of NEE were gap-filled using the artificial neural network

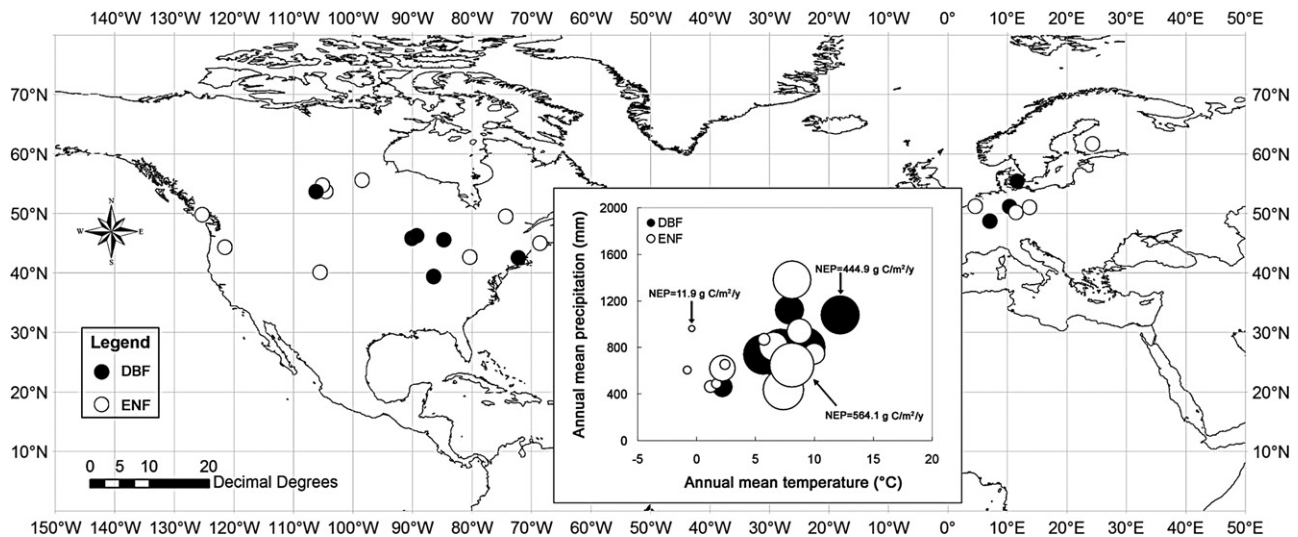


Figure 1 Spatial distribution of the 22 sites in this study: DBF (●) and ENF (○) represent deciduous broadleaf forests and evergreen needleleaf forests, respectively. The inset shows the dynamical ranges of mean annual temperature (x -axis), precipitation (y -axis) and net ecosystem productivity (NEP; the value of annual NEP is indicated by the area covered by each circle) of these sites.

(ANN) method (Papale & Valentini, 2003) and/or the marginal distribution sampling (MDS) method (Reichstein *et al.*, 2005).

One typical uncertainty of conventional flux-derived GPP is its estimation using nighttime data. A recent analysis of Lasslop *et al.* (2010) provided an alternative method to calculate GPP from daytime data using a hyperbolic light-response curve-fit to daytime NEE. Their results demonstrate that despite site-specific differences between the methods, statistical studies of multiple sites based on the FLUXNET database remain robust and support our analysis across multiple sites. Moreover, we are primarily interested in anomalies of GPP and NEP over time, which are strongly constrained by the data, regardless of the partitioning algorithm.

We also calculated seasonal means for several meteorological variables, including the daily shortwave global radiation (R_g , $\text{MJ m}^{-2} \text{ day}^{-1}$), mean air temperature (T_a , $^{\circ}\text{C}$), mean soil temperature (T_s , $^{\circ}\text{C}$), total precipitation (mm) and mean soil water content (SWC, %). The spring means were computed for the months of March, April and May and the autumn means for September, October and November. Some sites did not provide all these measurements, limiting some of the analyses to a subset of sites.

Phenological indicators

We used three growing season phenological metrics derived from GPP, including start of the growing season (GS_{start} , day of year), end of the growing season (GS_{end} , day of year) and GSL (days). Similar to growing season phenology, net C uptake phenological indicators, derived from NEP, were the start of C uptake (CU_{start} , day of year), the end of C uptake (CU_{end} , day of year) and the CUP (days) (White & Nemani, 2003).

In addition to the above-mentioned phenological metrics, two new phenological metrics were also derived. These were the

'spring lag' between CU_{start} and GS_{start} and the 'autumn lag' between GS_{end} and CU_{end} , both measured in days (equation 1):

$$\text{spring lag} = \text{CU}_{\text{start}} - \text{GS}_{\text{start}} \quad (1)$$

$$\text{autumn lag} = \text{GS}_{\text{end}} - \text{CU}_{\text{end}}$$

Introduction of these two metrics was based on the concept of quantifying the length of critical spring and autumn periods when photosynthesis is active, but ecosystem respiration is still higher than photosynthesis.

The following procedures were used to calculate these phenological metrics for each year. A negative exponential model, using polynomial regression and weights computed from the Gaussian density function, was adopted to derive smoothed curves for daily NEP and GPP observations (Fig. 2). The respective start and end days with positive NEP can then be determined, hereafter referred to as the CU_{start} and CU_{end} , respectively. The GS_{start} and GS_{end} were determined as the days when the smoothed daily GPP reached 10% of the annual maximum smoothed daily GPP. This 10% of GPP threshold was determined based on a comparison of other methods, including the degree-day indicator (Chen *et al.*, 2000), cumulative temperature sum (Thum *et al.*, 2009) and a fixed minimum daily GPP (e.g. $1 \text{ g C m}^{-2} \text{ day}^{-1}$; Richardson *et al.*, 2010). Unlike the constant GPP thresholds used in earlier studies, our method, with a threshold GPP in the range of $0.5\text{--}1.5 \text{ g C m}^{-2} \text{ day}^{-1}$ (differing among sites and year) allows for variations in phenological events to be captured and compared both interannually and spatially (Wu *et al.*, 2012).

Statistical analysis strategy

We calculated the yearly anomalies of all variables for each site, which allowed the identification and evaluation of these corre-

Table 1 Detailed description of study sites in this study.

Site_ID	Site_name	Latitude (degrees)	Longitude (degrees)	Altitude (m)	Time range	Land cover	Climate
CA-OAS	Old Aspen	53.63	-106.20	530	1997–2010	DBF	Boreal
US-HAI	Harvard Forest EMS Tower	42.54	-72.17	340	1992–2006	DBF	Temperate–continental with hot or warm summers
US-UMB	Michigan Biological Station	45.56	-84.71	234	1999–2009	DBF	Temperate–continental with hot or warm summers
US-MMS	Morgan Monroe State Forest	39.32	-86.41	275	1999–2008	DBF	Subtropical–mediterranean
US-SYV	Sylvania Wilderness Area	46.24	-89.35	540	2002–06	DBF	Temperate–continental with hot or warm summers
US-WCR	Willow Creek	45.80	-90.08	520	1999–2006	DBF	Temperate–continental with hot or warm summers
DE-HAI	Hainich	51.08	10.45	430	2000–07	DBF	Temperate
DK-SOR	Soroe–LilleBogskov	55.49	11.64	40	2000–09	DBF	Temperate
FR-HES	Hesse Forest–Sarrebouurg	48.67	7.06	300	2001–08	DBF	Temperate
CA-OBS	Old Black Spruce	53.99	-105.12	629	1999–2010	ENF	Boreal
CA-TP4	Turkey Point Mature White Pine	42.71	-80.36	184	2003–10	ENF	Temperate–continental with hot or warm summers
CA-OJP	SSA Old Jack Pine	53.92	-104.69	579	2000–08	ENF	Boreal
CA-MAN	Old Black Spruce	55.88	-98.48	259	1995–2008	ENF	Boreal
CA-QFO	Quebec Mature Boreal Forest	49.69	-74.34	382	2004–09	ENF	Boreal
CA-CAI	British Columbia–Mature Forest Site	49.87	-125.33	300	1999–2010	ENF	Temperate
US-HO1*	Howland Forest (main tower)	45.20	-68.74	60	1996–2008	ENF	Temperate–continental with hot or warm summers
US-ME2	Metolius – intermediate aged ponderosa pine	44.45	-121.56	1253	2002–10	ENF	Subtropical–mediterranean
US-NR1	Niwot Ridge Forest	40.03	-105.55	3050	1999–2007	ENF	Boreal
BE-BRA	Brasschaat (De Inslag Forest)	51.31	4.52	16	2004–09	ENF	Temperate
DE-THA	Anchor Station Tharandt – old spruce	50.96	13.57	380	2000–06	ENF	Temperate
DE-WET	Wetzstein	50.45	11.46	785	2002–08	ENF	Temperate
FI-HYY	Hyytiälä	61.51	24.17	181	1997–2007	ENF	Boreal

*Data for 2005 were replaced by the US-HO2 site, 800 m away of a identical forest, due to a damaged instrument for several months in the spring of 2005. DBF and ENF represent deciduous broadleaf forest and evergreen needleleaf forest, respectively.

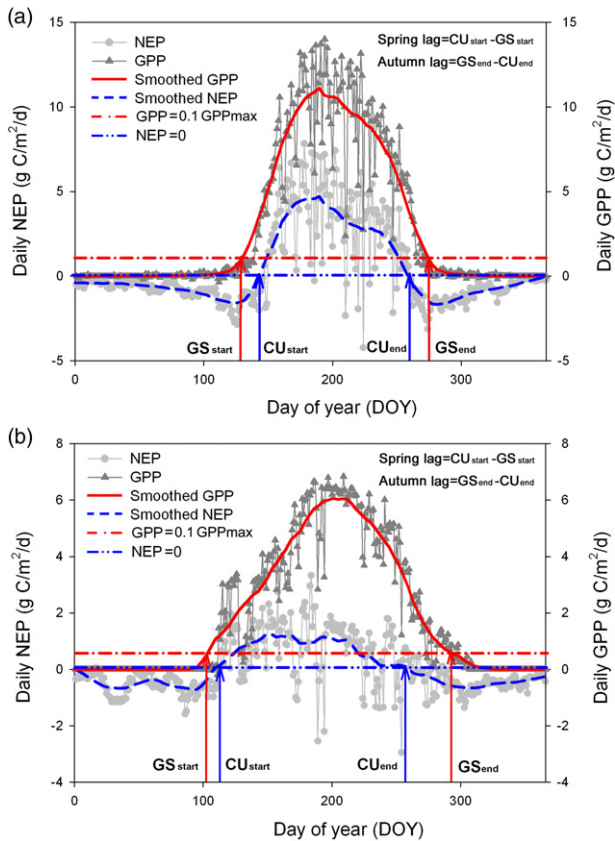


Figure 2 Examples of the determination of phenological transitions using daily net ecosystem productivity (NEP) and gross primary productivity (GPP) data at (a) CA-OAS (deciduous broadleaf forest) in 2000 and (b) CA-MAN (evergreen needleleaf forest) in 2000. The C uptake start (CU_{start}) and end (CU_{end}) are determined by the first and the last days of positive daily NEP, respectively. The growing season start (GS_{start}) and end (GS_{end}) are determined by the days when smoothed daily GPP reaches 10% of the annual maximum smoothed daily GPP. The C uptake period (CUP) is calculated as the time period between CU_{start} and CU_{end} . For interpretation of the references to color in the text, the reader is referred to the online version of the article.

lations interannually across sites (Richardson *et al.*, 2010). Yearly anomalies of these variables, i.e., annual C fluxes, phenological indicators and meteorological variables, were calculated using the following approach. The yearly anomaly of a variable with a significant trend over the length of the record was defined as the difference between an observed value and its predicted value using a regression function fitted to annual values,

$$A_i = x_i - f_{(year,i)} \quad (2)$$

For variables without trends (correlation test was set at 0.05 significant level), the yearly anomalies were calculated as the difference between an observed value and the mean of annual value,

$$A_i = x_i - X_{mean} \quad (3)$$

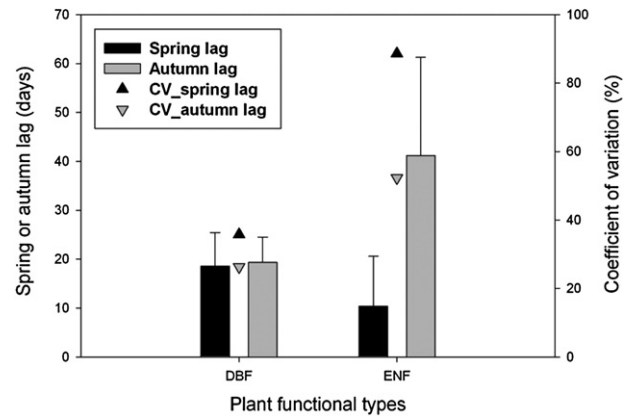


Figure 3 Comparison of the mean spring lag and autumn lag and their coefficients of variation (CV, %) for deciduous broadleaf (DBF) and evergreen needleleaf forests (ENF). Statistical tests indicate that these four variables are significantly different ($P < 0.05$) between these two type of forests. Error bars indicate the standard deviations of the means.

where A_i is the anomaly of a variable, x_i is the observation value in year i , $f_{(year,i)}$ is the predicted value from the regression function, and X_{mean} represents the mean annual value for the length of the record for the variable.

RESULTS

Comparison of spring and autumn lags between PFTs

Spring and autumn lags clearly exhibit differences in variability among DBF and ENF sites (Fig. 3). DBF sites generally had a longer spring lag (18.6 ± 6.8 days) than ENF sites (10.4 ± 10.2 days). In contrast, the DBF sites had a shorter autumn lag (19.4 ± 5.1 days) compared with 41.2 ± 20.1 days for the ENF sites.

The ENF sites consistently exhibited greater variation in the time lags than the DBF sites, irrespective of the dynamical ranges in either the spring or autumn lags. This result indicates that although ENF sites may sometimes be able to begin uptake of C very early in spring, they are also subject to greater inter-annual variability. This is because the foliage of evergreen conifer species is typically more tolerant of low temperatures than are deciduous broadleaf species.

Relationships between spring and autumn lags

We also identified potential relationships between the spring and autumn lags. For DBF sites, an increase of 1 day in the spring lag was associated with a 0.18-day lengthening of the autumn lag (Fig. 4a; $r = 0.31$, $P = 0.003$). By comparison, this effect of spring lag on autumn lag was not observed for ENF sites. We also found a significant relationship at DBF sites

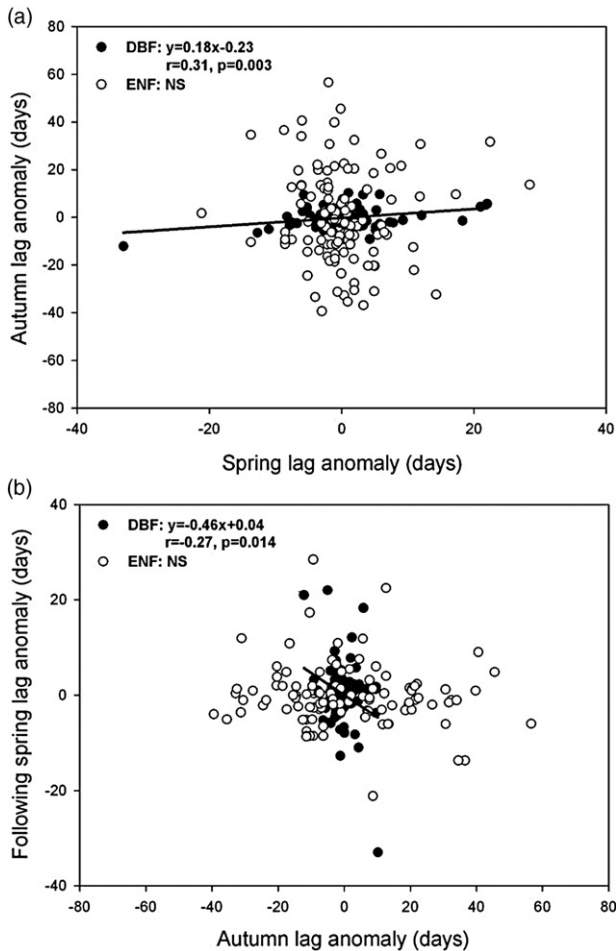


Figure 4 Relationships between the autumn lag and (a) spring lag of the same year, and (b) spring lag of the following year. Units of slopes of regressions are days while the intercept is unitless.

between the autumn lag and the spring lag of the following year, but no comparable effect at ENF sites. At the DBF sites, a lengthening of the autumn lag by 1 day was related to a shortening of the spring lag in the following year of about 0.46 days (Fig. 4b; $r = -0.27$, $P = 0.014$).

Relating interannual variability of NEP to growing season and net C uptake phenology

We explored the relationships between the anomalies of annual NEP and the anomalies of each phenological indicator for the growing season and C uptake period (Fig. 5). All three growing season phenological indicators, derived from GPP, were found to have limited power to explain the interannual variability of NEP consistently at all sites; no significant correlation was obtained for either DBF or ENF sites (Fig. 5a–c).

Weak negative relationships were found between the annual NEP anomaly and CU_{start} with Pearson correlation coefficients (r) of -0.25 ($P = 0.019$) and -0.34 ($P < 0.001$) for DBF and ENF

sites, respectively, suggesting that earlier onset of net C uptake generally increased annual C sequestration. CU_{end} , i.e. the end date of the C uptake period, conversely, showed a positive effect on the annual NEP, and its effect was stronger than CU_{start} with r of 0.29 ($P = 0.006$) and 0.48 ($P < 0.001$) for DBF and ENF sites, respectively. Combining these results for CU_{start} and CU_{end} , it is expected that a positive relationship would be observed between CUP and annual NEP ($r = 0.34$, $P = 0.001$ and $r = 0.52$, $P < 0.001$ for DBF and ENF sites, respectively).

Using combined growing season and net C uptake phenology to explain interannual variability in NEP

We did not observe significant correlations between the spring lag and annual NEP for either DBF or ENF sites (Fig. 6a). By comparison, we obtained stronger relationships between annual NEP and autumn lag with r of -0.71 ($P < 0.001$) and -0.68 ($P < 0.001$) for DBF and ENF sites, respectively (Fig. 6b). Longer autumn lags are expected to decrease annual NEP because after GPP has declined to near zero, any further delay will only promote higher R_e . This analysis with the combined phenology suggests that while the spring lag has no effect on annual NEP, the time lag between the end of net C uptake and the end of the growing season (i.e. termination GPP) explains a significant proportion of interannual NEP variability, irrespective of differences in plant functional types and other ecoregional characteristics.

We also explored the relationships between the spring and autumn lags and annual NEP for each site (Table 2). Spring lag still showed limited potential in indicating annual NEP and we only found two sites where the correlations between spring lag and NEP were significant (CA-MAN and US-ME2). By comparison, the autumn lag was significantly correlated with annual NEP at 11 sites out of 13 (not significant at only DE-HAI and US-NR1 sites). The relative large P -value (0.069) for CA-QFO was probably due to the short duration of measurements at this site (hence relatively few samples). For the remaining sites, autumn lag was highly correlated with annual NEP with r ranging from 0.71 ($P = 0.006$) at US-HO1 up to 0.97 ($P = 0.006$) at US-SYV. The slope of the autumn lag and annual NEP regression showed the sensitivity of decrease in NEP in response to longer autumn lag. DBF sites had steeper slopes than did the ENF sites. For example, the slope at CA-OAS indicates that a 1-day increase in autumn lag was associated with an average decrease of 23.3 g C m^{-2} in annual NEP, corresponding to approximately 18% of mean annual NEP during the period of measurements. However, for the ENF sites, e.g. CA-OBS, a 1-day increase in autumn lag reduced mean annual NEP by as little as 1.7%.

We also partitioned annual NEP into annual GPP and R_e , to evaluate their responses to variations in autumn lag. As shown in Fig. 7(a, b), there was a distinct difference between DBF and ENF sites with respect to responses of annual GPP and R_e to autumn lag. An increase in autumn lag corresponded to a decrease in annual GPP at the DBF sites ($r = -0.26$, $P = 0.014$), while it had no significant effect on GPP at ENF sites. By com-

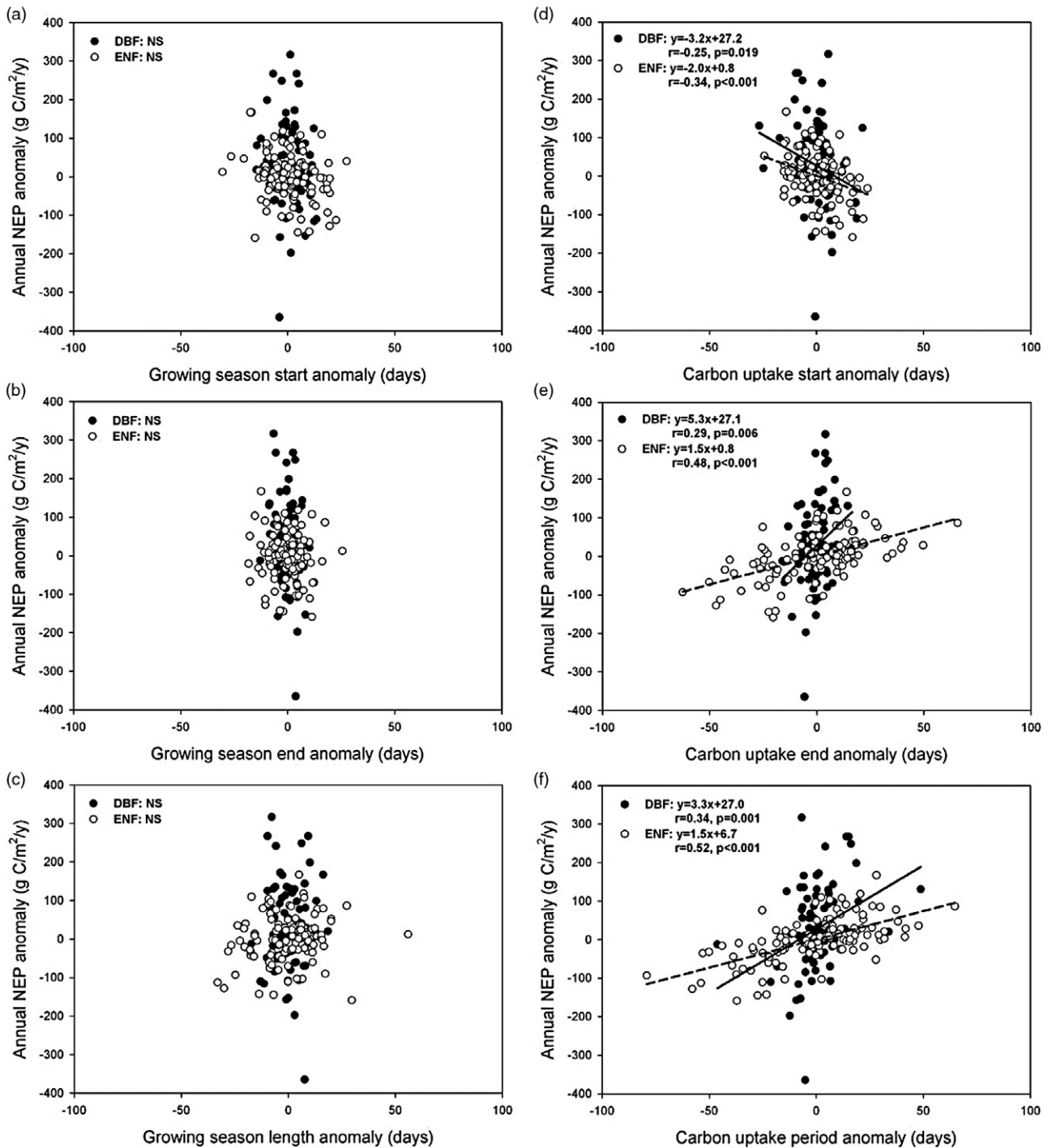


Figure 5 Relationships between annual net ecosystem productivity (NEP) anomalies and anomalies of phenological metrics: (a) growing season start, (b) growing season end, (c) growing season length, (d) C uptake start, (e) C uptake end, and (f) C uptake period for deciduous broadleaf (DBF, ●) and evergreen needleleaf (ENF, ○) forests. NS represents no significant correlation and a positive anomaly in start and end metrics means occurrence later than the mean, i.e. a delay. Units of regression slopes and intercepts are g C m⁻² day⁻¹ and g C m⁻² year⁻¹, respectively.

parison, annual R_e significantly increased with autumn lag at ENF sites ($r = 0.36$, $P < 0.001$), while a longer autumn lag had no apparent influence on R_e at DBF sites. To further understand this difference, we examined the relationship between the ratio of

annual R_e to GPP (R_e/GPP) and autumn lag. Significant positive correlations between annual R_e/GPP anomaly and autumn lag anomaly were obtained with r of 0.70 ($P < 0.001$) and 0.48 ($P < 0.001$) for DBF and ENF sites, respectively. Therefore, an

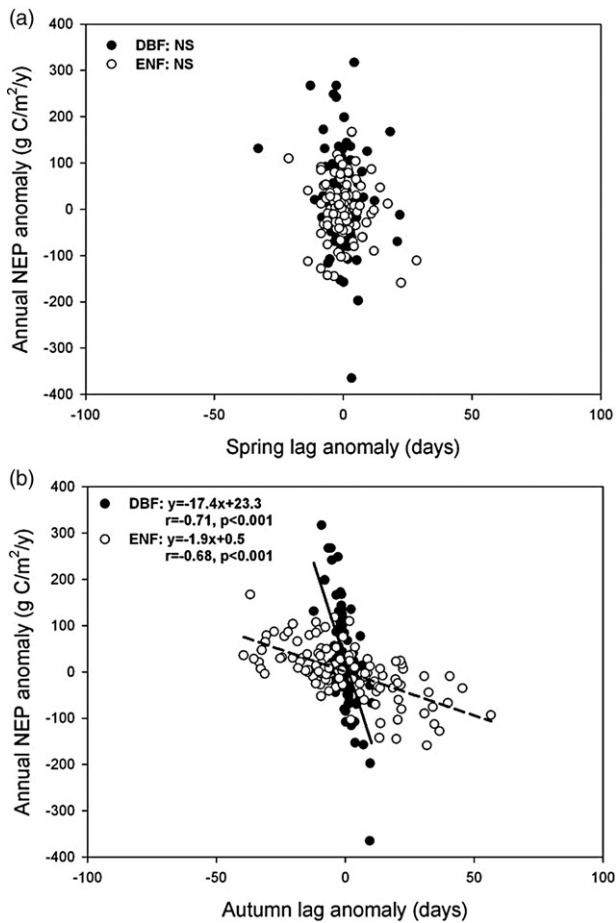


Figure 6 Relationships between annual net ecosystem productivity (NEP) anomalies and anomalies of (a) spring lag (i.e. start of C uptake behind the start of the growing season, CU_{start} minus GS_{start}), and (b) autumn lag (i.e. end of the growing season behind the end of C uptake, GS_{end} minus CU_{end}) for deciduous broadleaf (DBF, ●) and evergreen needleleaf (ENF, ○) forests. NS represents no significant correlation. Units of regression slopes and intercepts are $g\ C\ m^{-2}\ day^{-1}$ and $g\ C\ m^{-2}\ year^{-1}$, respectively.

increase in autumn lag leads to a greater proportion of R_c compared to GPP and thus a reduction in annual NEP, but the mechanisms involved differ between deciduous and evergreen dominant stands.

We observed that for DBF ecosystems, a longer autumn lag reduced annual GPP so that less GPP was available to contribute to annual NEP. The reason for this observed decrease in annual GPP is the decreased ratio of GPP to GSL with increasing autumn lag ($r = -0.28$, $P = 0.007$, data not shown), instead of variations in either GSL or GS_{end} .

Controls on autumn lag

Impacts of several site-level meteorological variables on autumn lag were considered, including global shortwave radiation (R_g), precipitation, SWC and air and soil temperatures in autumn (Table 3). Of these, average SWC was positively correlated with

autumn lag at DBF sites ($r = 0.28$, $P = 0.041$), implying that high SWC in autumn will increase autumn lag and thereby decrease annual NEP. For ENF sites, autumn lag was positively correlated with T_s ($r = 0.30$, $P = 0.001$).

Further investigation shows that the autumn lag is inversely dependent upon the CU_{end} phenological transitions (Fig. 8), i.e. as CU_{end} is increasingly delayed, the autumn lag becomes shorter on average. For DBF sites, a 1-day delay in CU_{end} resulted in autumn lag being 0.4 day shorter ($r = -0.62$, $P < 0.001$). In the case of ENF sites, this sensitivity increased to 0.8 day ($r = -0.90$, $P < 0.001$). The strong negative relationships between autumn lag and CU_{end} for both DBF and ENF sites also indicates that values of GS_{end} for both plant functional types should be relatively stable, which is confirmed by average coefficients of variation of GS_{end} for DBF and ENF sites of 1.7% and 2.3% compared with 2.7% and 7.5% for CU_{end} s respectively.

DISCUSSION

Biophysical interpretation of spring and autumn lags

Spring lag is a measure of the time required for photosynthesis to be initiated and to catch up with ecosystem respiration, though it may also be related to recovery from a more or less severe winter. At the beginning of a growing season, temperatures are generally cool and both GPP and R_c are small (Chen *et al.*, 2000). However, as the leaves become fully expanded following bud-break, GPP increases faster than R_c as stored carbon reserves are depleted and photosynthesis takes over as the primary source of carbon for plant growth. This drives the transition from net carbon loss to net carbon gain for the ecosystem (Wu *et al.*, 2012).

The autumn lag is caused largely by the effects of leaf senescence, but is evidently moderated by extended periods of warm temperatures. Photosynthesis rates decrease during late summer for physiological reasons while days become shorter and average light levels and mean temperatures decrease (Coursolle *et al.*, 2006). In both DBF and ENF ecosystems, leaves probably reach a critical C balance, where leaf-level NEP becomes negative and respiration becomes a net cost to the plant. However, an important difference is that in DBF systems this transition to negative NEP is a signal to initiate leaf-fall as the decrease in photosynthesis cannot support enough chlorophyll in foliage (Doi & Takahashi, 2008). After this occurs, a late period of warm weather is of little benefit. For ENF systems, however, only the oldest and least efficient foliage is discarded, and the remaining leaves are designed to tolerate winter freezing; hence there is the potential for further low rates of photosynthesis while temperatures remain favourable during autumn (or even throughout the winter in mild temperate climates).

Growing season and net C uptake phenology

Unlike previous evaluations, we considered both growing season (GPP) based and net C uptake (NEP) based metrics. Our results indicate that growing season based phenology does not alone

Table 2 Relationship between the autumn lag and annual net ecosystem production (NEP) for each site.

Site_ID	Spring lag		Autumn lag		Average annual NEP (\pm SD) (g C m ⁻² year ⁻¹)
	<i>r</i> (<i>P</i> -value)	Slope (g C m ⁻² day ⁻¹)	<i>r</i> (<i>P</i> -value)	Slope (g C m ⁻² day ⁻¹)	
CA-OAS	NS		-0.91 (< 0.001)	-23.3	126 \pm 22
US-HA1	NS		-0.80 (< 0.001)	-14.9	245 \pm 33
US-UMB	NS		-0.74 (0.009)	-11.5	185 \pm 15
US-MMS	NS		-0.90 (< 0.001)	-30.6	445 \pm 33
US-SYV	NS		-0.97 (0.006)	-8.8	28 \pm 57
US-WCR	NS		-0.93 (< 0.001)	-36.2	393 \pm 58
DE-HAI	NS		NS		504 \pm 67
DK-SOR	NS		-0.61 (0.041)	-10.1	182 \pm 27
FR-HES	NS		-0.72 (0.045)	-17.9	469 \pm 42
CA-OBS	NS		-0.82 (0.001)	-0.8	46 \pm 22
CA-TP4	NS		-0.93 (< 0.001)	-5.3	180 \pm 83
CA-OJP	NS		-0.91 (< 0.001)	-0.8	33 \pm 28
CA-MAN	-0.63 (0.015)	-5.9	-0.81 (< 0.001)	-1.3	21 \pm 59
CA-QFO	NS		-0.73 (0.069)	-0.4	12 \pm 10
CA-CA1	NS		-0.86 (< 0.001)	-2.9	419 \pm 109
US-HO1	NS		-0.71 (0.006)	-1.9	239 \pm 53
US-ME2	-0.74 (0.022)	-4.7	-0.92 (< 0.001)	-6.6	473 \pm 111
US-NR1	NS		NS		32 \pm 21
BE-BRA	NS		-0.86 (0.029)	-2.9	130 \pm 91
DE-THA	NS		-0.85 (0.016)	-13.5	564 \pm 86
DE-WET	NS		-0.86 (0.012)	-3.1	47 \pm 101
FI-HYY	NS		-0.75 (0.008)	-2.8	203 \pm 53

NS, no significant correlation.

provide sufficient predictive power to account for the interannual variability in NEP, which is not surprising because NEP is determined by net differences in ecosystem photosynthesis and respiration. An earlier start or later end to seasonal GPP may not ensure a large enough increase in gross C uptake to offset increased C losses from R_e , which is affected by several variables (Reichstein *et al.*, 2003).

Net C uptake phenology, which accounts for respiration, shows some potential in explaining interannual NEP variability. The relationship between annual NEP and CU_{end} indicates that a late autumn would increase annual C sequestration, which agrees with previous analyses by Richardson *et al.* (2010) and Dragoni *et al.* (2011). We also found that CU_{end} has a greater ability than CU_{start} to explain interannual NEP variability for both DBF and ENF sites, indicating that autumn phenology indicators are more robust than spring phenology in controlling annual NEP, and this has not been revealed in previous studies with fewer sites and shorter time series (Black *et al.*, 2000; Chen *et al.*, 2000; Barr *et al.*, 2009). A possible reason for the underestimation of the importance of autumn phenology in these earlier studies is that these analyses focused mainly on boreal forests. The better performance of CU_{end} in explaining annual NEP is also supported by recent findings (Dragoni *et al.*, 2011; Pilegaard *et al.*, 2011; Zhu *et al.*, 2012), all of which suggest that it is a delayed onset of dormancy, rather than an advanced leaf emergence date, that contributes mainly to a prolonged growing season and hence increased annual NEP.

Although annual NEP did not correlate well with phenological indicators based on the growing season alone, this does not necessarily mean that growing season phenology is not useful. The outstanding issue is how to use the information and to derive integrated indicators of annual NEP. By incorporating this into the calculation of autumn lag, we obtained a quantitative indicator of the critical time period at the end of the growing season when ecosystem respiration can exceed gross photosynthesis. These results indicate that the timing and magnitude of decline of GPP in the autumn are important for predicting NEP. Further, it highlights the important role that ecosystem respiration may play in regulating annual NEP (Valentini *et al.*, 2000). This hypothesis is also supported by existing studies that suggest that the best way to understand the role of phenology in regulating C sequestration is through partitioning of NEP into its component fluxes, rather than investigating solely net C exchange (e.g. Piao *et al.*, 2008).

Impacts of plant functional types

The reason for lagged effects of spring and autumn lags between DBF and ENF sites lies in the correlation between spring lag and CU_{start} . For DBF sites, spring lag was positively correlated with CU_{start} ($r = 0.61$, $P < 0.001$), which conversely was not significant at ENF sites ($r = 0.15$, $P = 0.098$). Considering that both CU_{start} and autumn lag decreased annual NEP, it is reasonable that spring lag was only significantly correlated with autumn lag at

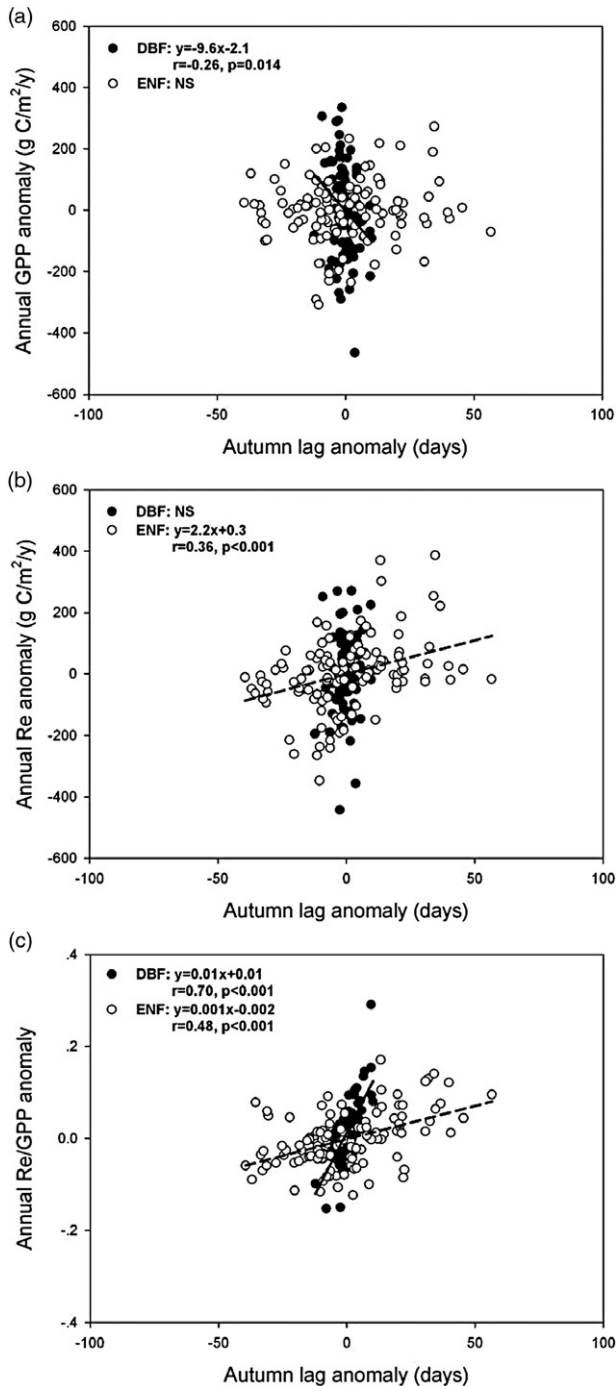


Figure 7 Relationships between autumn lag anomaly and (a) annual gross primary productivity (GPP) anomaly, (b) annual ecosystem respiration (R_e) anomaly, and (c) the annual R_e /GPP anomaly for deciduous broadleaf (DBF, ●) and evergreen needleleaf (ENF, ○) forests. NS represents no significant correlation. Note in the units of the slope and intercepts of the regression equations in (a) and (b) are $\text{g C m}^{-2} \text{ day}^{-1}$ and $\text{g C m}^{-2} \text{ year}^{-1}$ and the slope of the regression equation in (c) is 0.01 day^{-1} and 0.001 day^{-1} for DBF and ENF, respectively, while the intercepts are unitless.

DBF sites. Lagged effects of autumn lag on the following spring lag between DBF and ENF are more complicated. Longer autumn lag indicates lower annual NEP for both PFTs and therefore further affects carbohydrate storage, which is an important source of carbon for new leaves in DBF sites. Thus, we may observe an influence of autumn lag on the following spring lag at DBF sites. For ENF sites, this lagged effect may be not evident, especially considering the large variations of spring lag at ENF sites.

PFT also plays an important role in determining the relationships between annual NEP and phenological indicators, these differences could be important when assessing the sensitivities of DBF and ENF ecosystems to future climate change. It is apparent that DBF sites are more sensitive to interannual phenological variations than ENF sites, as indicated by the larger regression slopes between annual NEP and phenological indicators. The ENF ecosystems may be better adapted to interannual variability in growing season length given their ability to sustain low rates of photosynthesis beyond the deciduous forest growing seasons, but DBF sites have higher mean daily GPP and NEP and shorter growing seasons than ENF sites (Fig. 2; see also: Churkina *et al.*, 2005; Richardson *et al.*, 2010). One particular issue related to DBF sites is that there are two potential hypotheses for the decrease of annual GPP in years with longer autumn lag. One is that the annual curves of both daily GPP and NEP shift backward in time (i.e. both ends occur earlier) with the NEP curve approaching zero much earlier. The other hypothesis is that GSL is relatively stable, but daily GPP is lower during the growing season. It is clear that the latter happens for those years with longer autumn lag and this is particularly useful for ecosystem modelling.

The most interesting distinction between DBF and ENF sites is in the relationship between autumn lag and annual NEP. Richardson *et al.* (2010) suggested that autumn GPP and R_e are close to unity with variations in the end of net C uptake. Our analysis, on the other hand, shows an increased ratio of annual R_e to GPP as GS_{end} approaches. The reason is that we are not focusing on the transition but on the time duration from the CU_{end} to GS_{end} . The definition of CU_{end} implies the time at which daily GPP equals daily R_e ($R_e/\text{GPP} = 1.0$), after which both GPP and R_e decrease but R_e/GPP increases. This is consistent with other studies which report that autumn temperature tends to increase R_e more than GPP in autumn (Piao *et al.*, 2008; Vesala *et al.*, 2010). The transition continues until GS_{end} which is the point when daily GPP has declined to 10% of the seasonal maximum.

Implications of responses of autumn lag to environmental forcing

Most of the meteorological variables were of limited value in estimating autumn lag, indicating that challenges remain in using only climate data to predict annual NEP. Specifically, for DBF sites, higher SWC was positively correlated with autumn lag while T_s was found to be significantly correlated with autumn lag at ENF sites. For both situations, a longer autumn

Table 3 Relationships between autumn lags and meteorological variables.

Meteorological variables		R_g (MJ m ⁻² day ⁻¹)	T_a (°C)	T_s (°C)	Precipitation (mm)	SWC (%)
Deciduous broadleaf forest	r	-0.08	0.10	0.17	0.02	0.28
	P -value	0.475	0.339	0.117	0.494	0.041
Evergreen needleleaf forest	r	-0.09	0.12	0.30	0.04	0.10
	P -value	0.656	0.183	0.001	0.697	0.383

R_g , T_a , T_s and SWC are daily mean (from September to November) global shortwave radiation, air temperature, soil temperature and soil water content, respectively. Bold font indicates significant correlations were found.

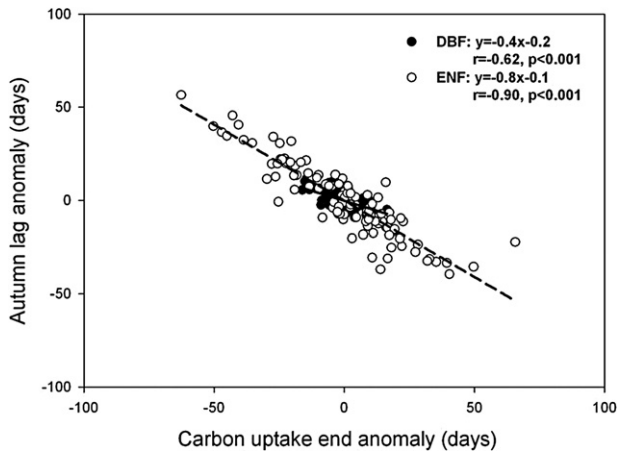


Figure 8 Relationships between the C uptake end anomaly and the autumn lag for deciduous broadleaf forests (DBF, ●) and evergreen needleleaf forests (ENF, ○). Units of regressions are days and the slopes are unitless.

lag indicates decreased annual NEP. It should be noted that for both DBF and ENF sites, high SWC and T_s would both favour increased soil respiration, which accounts for 50–95% of total R_e (Valentini *et al.*, 2000; Reichstein *et al.*, 2003). Our analysis confirmed this with positive correlations of annual R_e and SWC anomalies ($r = 0.27$, $P = 0.041$) at DBF sites, and of annual R_e and the T_s anomalies ($r = 0.21$, $P = 0.040$) at ENF sites. These responses indicate that the rate of net C loss from northern ecosystems in response to autumn warming may be species (or ecosystem) dependent. These findings also agree with those of Richardson *et al.* (2010) that statistically significant effects of autumn temperature on net or gross productivity are not assured.

Uncertainties in the variations of net C uptake with phenology may explain the existence of specific sites where autumn lag may not be a good indicator of annual NEP. For example, at the US-NR1 site the spring season is considered the most important determinant of annual NEP (Monson *et al.*, 2005). The unmanaged, old-growth forest at the DE-HAI site, however, consists of various tree species whose specific phenology in both spring and autumn is suggested to be dominated by factors other than soil temperature or moisture (Knohl *et al.*, 2003). This may explain why the general correlation between autumn lag and annual NEP is low.

CONCLUSIONS

Our analysis investigates the variability of autumn phenology and its role in the annual C budget, in contrast with many previous studies of phenology and C balance which have focused mainly on spring phenology. Although it has often been assumed that autumn phenological transitions may play an important role in determining annual net C uptake in forests, there has been limited evaluation of this idea using field studies. Using multiyear flux measurements from both North America and Europe, we have shown that a significant amount of the interannual variability in annual NEP can be explained by a newly developed phenological metric, termed the ‘autumn lag’, which emphasizes the importance of autumn phenology. To the best of our knowledge, this is the first analysis that shows the importance of autumn phenology in controlling interannual variability in NEP and respiration based on the time lag between growing season and C uptake transitions is particularly meaningful for C sequestration. These results are potentially important in understanding interannual variability in NEP, and the role of future climate change in determining this interannual variability. Considering the further applications of this autumn lag temporally and spatially, it is of great interest to develop new algorithms that can estimate autumn lag using a combination of ground data and/or satellite observations.

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