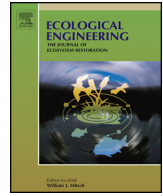




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Evidence of autumn phenology control on annual net ecosystem productivity in two temperate deciduous forests



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ABSTRACT

Phenology exercises a critical control on annual carbon uptake by terrestrial ecosystems. Autumn phenology, while less studied relative to spring phenology, may also constrain annual net ecosystem productivity (NEP). Using 17-year (1992–2008) records of C flux phenology (CFP) derived from continuous eddy covariance (EC) measurements at the Harvard Forest (HF), here we show that the autumn phenology played a more significant role than the spring phenology in controlling annual NEP. We found that the onset of carbon uptake (CU) in spring only explained 39% of annual NEP, compared to 66% of end of CU in autumn. Though neither onset nor end of gross primary productivity (GPP) was correlated with annual NEP, the autumn lag, i.e., the time lag between ends of GPP and CU, was found to have a particularly high potential in explaining annual NEP ($R^2 = 0.82$, $p < 0.001$). We further showed that the autumn lag can be modeled as a function of entirely autumn (September–November) meteorological variables, including the water vapor pressure deficit, global shortwave radiation and the surface soil temperature, indicating the autumn lag and consequently the annual NEP can be modeled in areas lacking EC measurements. The usefulness of the modeled autumn lag was evidenced in its capability to explain 70% of annual NEP at HF site. A validation of the empirical function derived from HF site using 13-year (1999–2011) independent data at the University of Michigan Biological Station (UMB) forest was promising. Estimates of autumn lag using the exactly same meteorological variables proposed at HF site but different regression coefficients were highly correlated with the observed autumn lag ($R^2 = 0.87$, $p < 0.001$) at UMB site. The correlation decreased slightly ($R^2 = 0.83$, $p < 0.001$) if the regression coefficients found at HF site was also used, which subsequently explained 46% of annual NEP ($p = 0.011$) for UMB site. These results advocate for the inclusion of autumn phenology in terrestrial ecosystem models in order to predict the interannual variability of C sequestration more accurately, but also indicate challenges in deriving appropriate models even for the same plant functional types.

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1. Introduction

Phenology is one of the most important factors affecting the annual carbon (C) sequestration, i.e., the net ecosystem productivity (NEP), in terrestrial ecosystems (Richardson et al., 2012, 2013), and is thus important for ecosystem restoration of forests (Stokes et al., 2012; Wu et al., 2013a,b; Baldocchi et al., 2005). Interannual variability in NEP is primarily driven by year-to-year variability in climate (Desai, 2010; Tang et al., 2011), and, therefore, phenological indicators that detect the dates of first occurrence of biological events (e.g., leaf-out) have been shown to be effective predictors of changes in growing season duration and, consequently,

annual growth patterns and magnitude (Sun et al., 2003; White and Nemani, 2003; Richardson et al., 2010; Wu et al., 2012; Wu and Chen, 2013).

Traditional phenological indicators, including the start and end of the growing season in spring and in autumn, respectively, have been described by the dates when a strong change in leaf color is observed from remote sensing or ground measurements, or by the dates of bud-break in the spring and leaf senescence in the fall (White and Nemani, 2003; Zhang et al., 2004; Garrity et al., 2011; Gonsamo et al., 2012a). The main focus of these methods is detecting the dates when important changes were observed in vegetation color (particularly greenness) (Zhang et al., 2004). The limitation associated with such methods, however, is the empirically determined phenological indicators (e.g., spectral indices) and/or limited samples (e.g., bud-break and first flowering date) of trees that are not well representations of the whole ecosystem. With continuous

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measurements of C exchange using the eddy-covariance (EC) technique, an alternative method makes use of C flux phenology (CFP), which quantifies the starts and ends of growing season and C uptake by directly observed net ecosystem exchange (NEE) and modeled gross primary productivity (GPP) (Richardson et al., 2010; Garrity et al., 2011; Gonsamo et al., 2012b). For example, start of growing season could be determined when daily GPP exceeds certain thresholds, e.g., $1 \text{ g C/m}^2/\text{d}$ in Richardson et al. (2010), while C uptake phenology is modeled when the daily NEP curve crosses zero value (Wu et al., 2013a).

Spring phenology has been previously identified as an effective indicator of annual carbon uptake (e.g., Richardson et al., 2009), and considerable efforts have been made to quantify how spring canopy phenology relates to the timing of C cycling processes central to NEP. For example, warmer springs tended to increase annual NEP by causing earlier leaf-on in a boreal deciduous forest in Canada (Black et al., 2000). Later analysis by Barr et al. (2009) additionally demonstrated that spring temperature was a primary variable regulating annual NEP in boreal forests. However, a temperature-driven increase in NEP in the spring could be offset by higher ecosystem respiration (R_e) in autumn, indicating a possible net carbon loss in boreal ecosystems if warming occurs throughout the year (Piao et al., 2008). Such observations suggest a possible role for autumn phenology in controlling interannual variability of NEP. Recent stand and regional scale studies further indicate that a warmer climate may modify North America's terrestrial C sink by delaying the start to autumn (Dragoni et al., 2011; Zhu et al., 2012; Wu et al., 2012, 2013a). Therefore, more work should be focused on phenological events at the end of the growing season, considering that the initial growth of temperate forests may be less dependent on temperature than boreal ecosystems (Dragoni and Rahman, 2012; Richardson et al., 2013; Wu et al., 2013b).

To investigate the role of autumn phenology on interannual variability of NEP, long-term flux data and associated meteorological measurements at both Harvard Forest (HF) (1992–2008) and University of Michigan Biological Station (UMB) forest (1999–2011) were used in this study. The specific objectives were to (1) analyze how spring and autumn phenology control annual NEP, (2) develop appropriate algorithms for modeling seasonal phenology variation and thus annual NEP, and (3) test the broad applicability of an empirically derived phenological algorithm for annual C estimation using independent data acquired at a different site.

2. Materials and methods

2.1. Study sites

Two temperate deciduous broadleaf forest sites were used in this study: the Harvard Forest (HF) and the University of Michigan Biological Station (UMB) forest. Data from the HF site were mainly selected for algorithm development as a longer duration of observations was available (1992–2008) while data from the UMB site (1999–2011) were used for independent validation of a general phenology model.

The HF tower site ($42^\circ 32' 16'' \text{ N}$, $72^\circ 10' 17'' \text{ W}$, 340 m elevation) is located within the upland plateau between the Boston Basin to the east and the Connecticut Valley to the west. The vegetation is dominated by deciduous species, including red oak (*Quercus rubra*), red maple (*Acer rubrum*), black birch (*Betula lenta*) and white pine (*Pinus strobus*) (Urbanski et al., 2007). Maximum canopy height is approximately 20–24 m and soils are composed of mainly sandy loam glacial till with alluvial and colluvial deposits. The climate is cool, moist temperate with July mean temperature 20°C and annual mean precipitation of about 1100 mm.

The UMB site is located on a level to gently sloping high outwash plain in northern lower Michigan ($45^\circ 33' 35'' \text{ N}$ $84^\circ 43' 01'' \text{ W}$, 234 m elevation). The forest is a secondary mixed northern hardwood ecosystem mainly composed of bigtooth aspen (*Populus grandidentata Michx.*) and trembling aspen (*Populus tremuloides Michx.*) with lesser representation by paper birch (*Betula papyrifera Marsh.*), red oak, red maple, and white pine. Canopy height is 22 m and soils are excessively drained, sandy, mixed frigid Entic Haplothsods consisting of 92% sand, 7% silt and 1% clay (Gough et al., 2009). Mean annual temperature is 55°C and mean annual precipitation is about 817 mm.

2.2. Flux and meteorological data

Level-4 products of C fluxes and meteorological variables for these two sites were downloaded from the AmeriFlux network (<http://publiccornlgov/ameriflux/dataproductshtml>), which contain gap-filled and friction velocity (u_*) filtered records at varying time intervals with flags regarding the quality of the original and gap-filled data Annual GPP, NEP (i.e., -NEE), and R_e values for each year were extracted. The half-hourly measurements of NEE were gap-filled using the Artificial Neural Network (ANN) method (Papale and Valentini, 2003) and/or the Marginal Distribution Sampling (MDS) method (Reichstein et al., 2005). The ANN method is an empirical non-linear regression model consisting of nodes connected by weights which are effectively the regression parameters. Certain input variables, such as air temperature, daytime vapor pressure deficit (VPD), and global shortwave radiation, are needed in the training process to produce modeled NEP (Papale and Valentini, 2003). If the required variables for ANN method are not available, the MDS method is selected to gap-fill NEP and a short-term temperature sensitivity of ecosystem respiration is then used to partition NEP into GPP and R_e (Reichstein et al., 2005).

2.3. Phenological indicators

In this analysis, we used phenological metrics derived from both daily GPP and NEE, including the GPP onset (day of year), GPP end (day of year), CU onset (day of year), CU end (day of year) and the autumn lag (days).

A negative exponential model, using polynomial regression and weights computed from the Gaussian density function, was adopted to derive smoothed curves for daily NEE and GPP observations (Fig. 1). The respective start and end days with negative daily NEE can then be determined, hereafter referred to as the CU onset and CU end, respectively (White and Nemani, 2003). The GPP onset and GPP end were determined as the days when the smoothed daily GPP reached 10% of the seasonal maximum smoothed daily GPP (Wu et al., 2012). Unlike a fixed GPP threshold in previous analyses, the 10% of seasonal maximum GPP would allow the capture of spatial and temporal variations in growth rhythms. The autumn lag was calculated as the time lag between the ends of GPP and CU (Wu et al., 2012, 2013a).

3. Results

3.1. Interannual variations of phenological indicators at HF site

Interannual variations of CU onset for HF showed a significantly decreasing pattern ($R^2 = 0.39$, $p = 0.008$) from 1992 to 2008, implying that C uptake has advanced by 0.9 days/year during the study time period (Fig. 2a). The CU end, however, was delayed by 11 days/year ($R^2 = 0.56$, $p < 0.001$). GPP onset and GPP end also showed substantial interannual variations at HF site (Fig. 2b). While GPP onset did not show a significant pattern, we found that the GPP

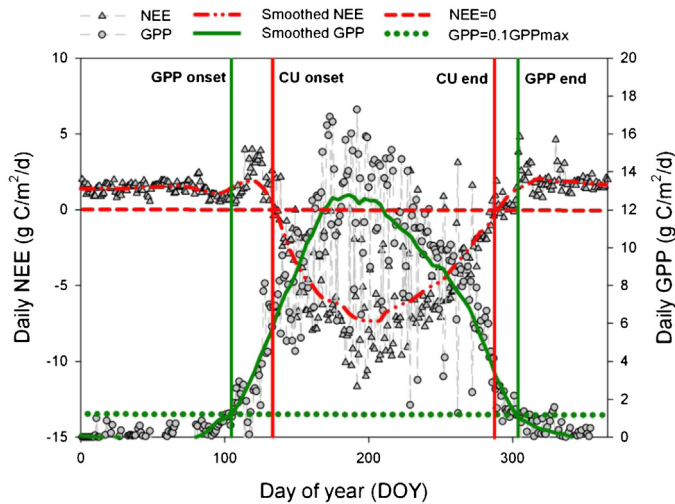


Fig. 1. Description of calculating phenological indicators in this study using data of Harvard Forest site in 2004. The onset and end of gross primary productivity (GPP) is defined when smoothed daily GPP curve reached the 10% of seasonal maximum. The onset and end of carbon uptake (CU) is defined when smoothed daily net ecosystem exchange (NEE) curve switched from positive to negative in spring and from negative to positive in autumn.

end was significantly delayed by 0.3 days/year ($R^2 = 0.30$, $p = 0.026$) over 17 years. Since autumn lag was calculated as the duration between GPP end and CU end, a significant decreasing pattern ($R^2 = 0.39$, $p = 0.007$) was observed for the autumn lag with a rate of 0.8 days/year (Fig. 2c). A possible reason for the decrease of autumn lag is the delay of CU end (Wu et al., 2013a) and consequently the increase of C uptake period (CUP).

3.2. Impacts of phenological indicators on annual NEP at HF site

Impacts of the phenological variations on annual NEP were also investigated (Fig. 3). The CU onset was found to be negatively correlated with annual NEP ($R^2 = 0.39$, $p = 0.007$), indicating that a one day advance of CU onset in the spring increased annual NEP by 133 g C/m². The CU end showed a positive correlation with annual NEP ($R^2 = 0.66$, $p < 0.001$) and a one day delay in CU end during autumn increased annual NEP by 161 g C/m². Combine both CU onset and end, we also found that one day increase in the carbon uptake period (CUP), i.e., time duration between CU onset and end, would enhance annual NEP by 99 g C/m² ($R^2 = 0.70$, $p < 0.001$). Phenological transitions in GPP (i.e., GPP onset and end) and the length of growing season (GSL, i.e., time duration between GPP onset and end), were demonstrated to have limited impacts on annual NEP, with no significant relationship detected between annual NEP and the three GPP-based phenological metrics. Our results imply that the autumn CU phenology exerts greater control than spring phenology over annual NEP, with CU end explaining 66% of annual NEP variation and CU onset explaining 39%. The importance of autumn phenology was further confirmed from the result presented in Fig. 3c that 82% of interannual NEP variability can be explained by the autumn lag, the number of days between ends of GPP and CU.

3.3. Deriving an empirical function to estimate autumn lag and annual NEP at HF site from meteorological variables

While these phenological metrics derived from C flux data provided a distinct perspective into analyzing the autumn phenology control on annual NEP, it is not applicable for regions where flux data are unavailable as they require daily NEE and GPP time series.

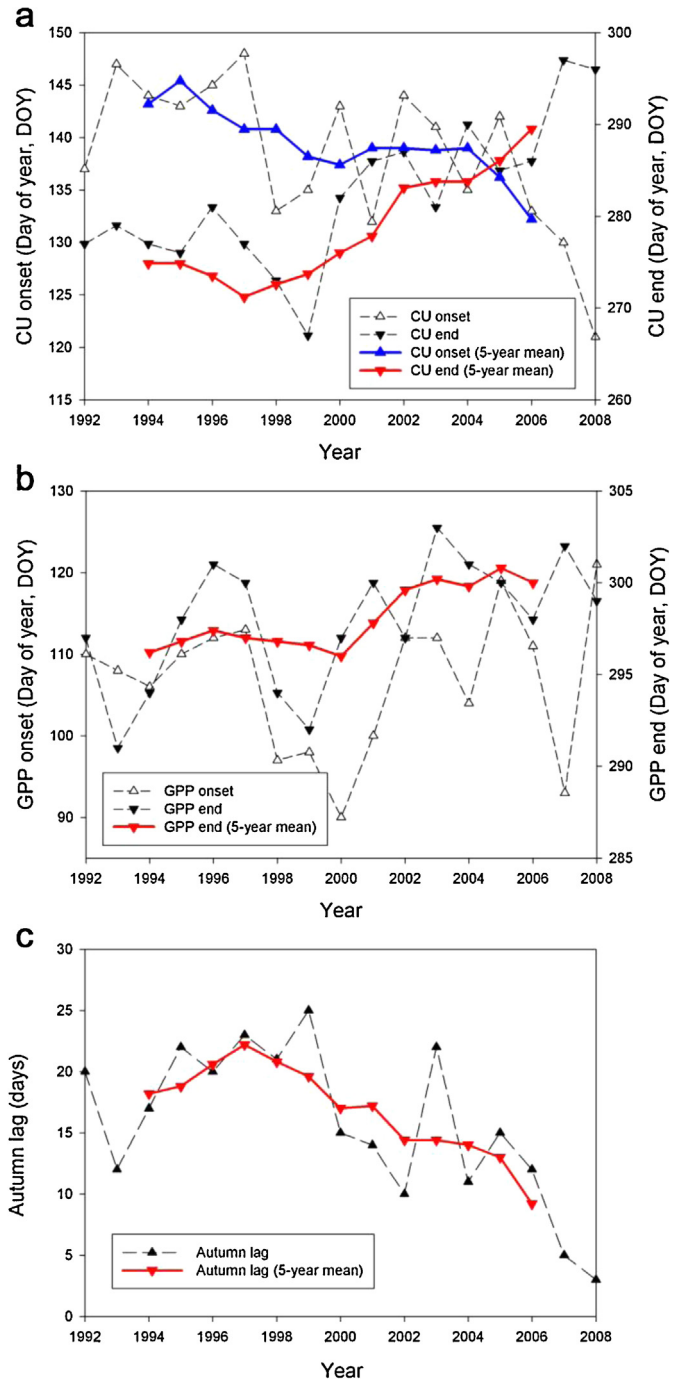


Fig. 2. Interannual variations of (a) carbon uptake (CU) onset and end, (b) gross primary productivity (GPP) onset and end, and (c) the autumn lag at Harvard Forest. Blue and red lines in (a) represent 5-year moving averages of CU onset and end, respectively. The red line in (b) is the 5-year moving average of GPP end. The red line in (c) is the 5-year moving average of autumn lag. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

To circumvent this problem, we explored the potential of explaining the phenological transition days using spring (March–May) and autumn (September–November) site-level meteorological variables, including the sensible heat, latent heat, water vapor pressure deficit (VPD), global shortwave radiation (R_g), air temperature (T_a), soil temperature (T_s) and the precipitation (Table 1).

Table 1
Relationships between phenological indicators and spring (March–May) and autumn (September–Nov) meteorological variables at Harvard Forest site.

Phenological variables	Sensible heat (W/m ²)	Latent heat (W/m ²)	Vapor pressure deficit (VPD, hPa)	Global shortwave radiation (R_g , W/m ²)	Air temperature (T_a , °C)	Soil temperature (T_s , °C)	Precipitation (mm)
CU onset	NS	NS	$R^2 = 0.51, p = 0.001$	$R^2 = 0.55, p < 0.001$	NS	NS	NS
CU end	NS	NS	NS	$R^2 = 0.54, p < 0.001$	NS	$R^2 = 0.57, p < 0.001$	NS
GPP onset	NS	NS	NS	NS	$R^2 = 0.39, p = 0.007$	NS	NS
GPP end	NS	$R^2 = 0.43, p = 0.008$	NS	NS	NS	$R^2 = 0.28, p = 0.028$	NS
Autumn lag	NS	NS	$R^2 = 0.33, p = 0.015$	$R^2 = 0.51, p = 0.001$	NS	$R^2 = 0.41, p = 0.005$	NS

Note: GPP onset, CU onset, CU end, GPP end and autumn lag represent the gross primary productivity onset, carbon uptake onset, carbon uptake end, gross primary productivity end and autumn lag (i.e., the time lag between the ends of GPP and CU), respectively. Sensible heat and latent heat are not included for 2007–2008 subject to data availability NS represents no significant correlation is observed.

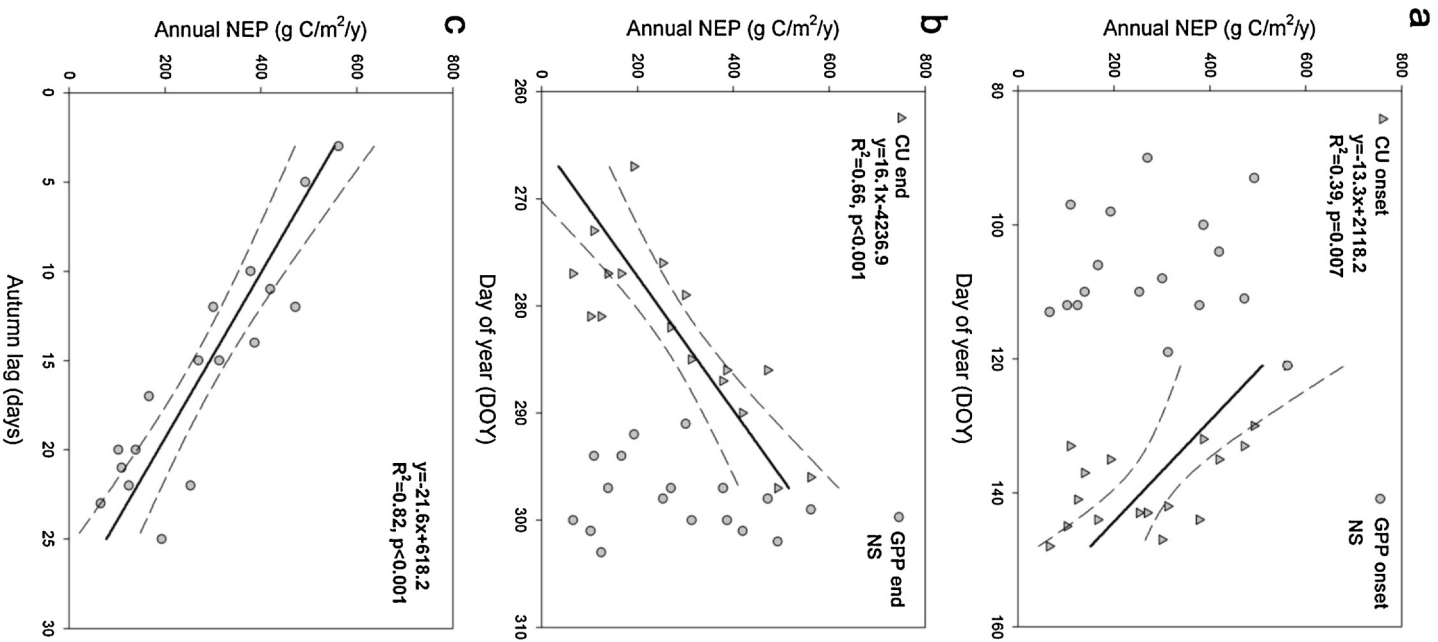


Fig. 3. Relationship between annual net ecosystem productivity (NEP) and (a) onsets of carbon uptake (CU) and gross primary productivity (GPP), (b) ends of CU and GPP, and (c) autumn lag, i.e., the time lag between ends of GPP and CU at Harvard Forest site.

As shown in Table 1, the CU onset was found to be significantly and positively influenced by spring VPD ($R^2 = 0.51, p = 0.001$) and R_g ($R^2 = 0.55, p < 0.001$). The CU end was positively correlated with autumn R_g ($R^2 = 0.54, p < 0.001$) but negatively correlated with autumn T_s ($R^2 = 0.57, p < 0.001$). Considering the positive correlation between CU end and annual NEP, we can infer that higher autumn R_g may enhance annual NEP by extending canopy duration and increasing light interception but higher T_s

would lead to decreased annual NEP because of higher R_e (Vesala et al., 2010). This is consistent with the results of Piao et al. (2008) showing a net carbon loss from boreal ecosystems during warmer autumns.

The GPP onset was only correlated with spring T_a ($R^2 = 0.39$, $p = 0.007$), indicating that warmer T_a will accelerate the start of canopy photosynthesis. This result agrees with reports that initiation of spring photosynthesis is mainly triggered by rising air temperature or accumulated degree days (note that the start of growth of deciduous trees may also controlled by light) in temperate and boreal ecosystems (Sun et al., 2003; Barr et al., 2009). Recent results of Piao et al. (2012) further show that the spring green-up date, as indicated by satellite data, is dependent on spring temperature as well as regional altitude. The GPP end was negatively correlated with both latent heat ($R^2 = 0.43$, $p = 0.008$) and T_s ($R^2 = 0.28$, $p = 0.028$), demonstrating warmer autumn T_s would lead to an earlier end of photosynthesis. One thing should be addressed that higher T_s does not necessarily mean higher T_a (e.g., no correlation was found between T_s and T_a for this site).

We found that interannual variation in autumn lag can be explained by several meteorological variables, including the autumn VPD ($R^2 = 0.33$, $p = 0.015$), R_g ($R^2 = 0.51$, $p = 0.001$) and T_s ($R^2 = 0.41$, $p = 0.005$). Since autumn lag showed the highest potential in explaining annual NEP, we focused on modeling autumn lag using these meteorological variables. Therefore, an empirical multivariate linear regression function (referred as HF.f hereafter) was developed to model autumn lag as,

$$\text{Modeled Autumn Lag} = -5.7\text{VPD} - 2.1R_g + 3.5T_s + 14.6 \quad (1)$$

Correlation analysis showed that the modeled autumn lag using HF autumn VPD, R_g and T_s explains 82% ($p < 0.001$) of observed variation in autumn lag (Fig. 4a). Using an autumn lag model, we can predict annual NEP from meteorological variables (i.e., VPD, R_g and T_s) with high confidence at the site level ($R^2 = 0.70$, $p < 0.001$) (Fig. 4b).

3.4. Independent validation at the UMB site

To examine whether our empirical function estimating annual NEP from modeled autumn lag can be applied to other sites, we tested it using independent data at the UMB site (Fig. 5). Since autumn lag at UMB site might be modeled with different meteorological variables from HF site, we first tested variables that are potentially useful in explaining autumn lag. Results showed a similar conclusion at the HF site that autumn lag of UMB site was significantly correlated with autumn VPD ($R^2 = 0.33$, $p = 0.031$), R_g ($R^2 = 0.28$, $p = 0.043$) and T_s ($R^2 = 0.30$, $p = 0.039$) while T_a and precipitation were demonstrated to have very limited potential in explaining autumn lag. Therefore, VPD, R_g and T_s were also selected to estimate autumn lag in this extension. Fig. 5a shows that autumn lag at UMB site can also be modeled as Modeled Autumn Lag = $-4.8\text{VPD} - 0.72R_g + 1.9T_s + 20.8$ (referred as UMB.f hereafter) (\blacktriangle points, $R^2 = 0.87$, $p < 0.001$). Estimates of autumn lag using the HF.f, i.e., coefficients for autumn VPD, R_g and T_s shown in Eq. (1), also significantly correlated with UMB observations (\bullet points, $R^2 = 0.83$, $p < 0.001$), only differing in a larger bias of 57 days compared with 0.5 days using UMB.f. These modeled autumn lag using both HF.f and UMB.f were then applied to the estimation of annual NEP at UMB site (Fig. 5b). Annual NEP showed significant correlations with both modeled autumn lags, and it was reasonable that autumn lag using HF.f provided slightly lower R^2 of 0.46 ($p = 0.011$) compared with R^2 of 0.56 ($p = 0.003$) for autumn lag with UMB.f. These results imply that modeling autumn phenology would be very useful to improve estimates of annual NEP but the

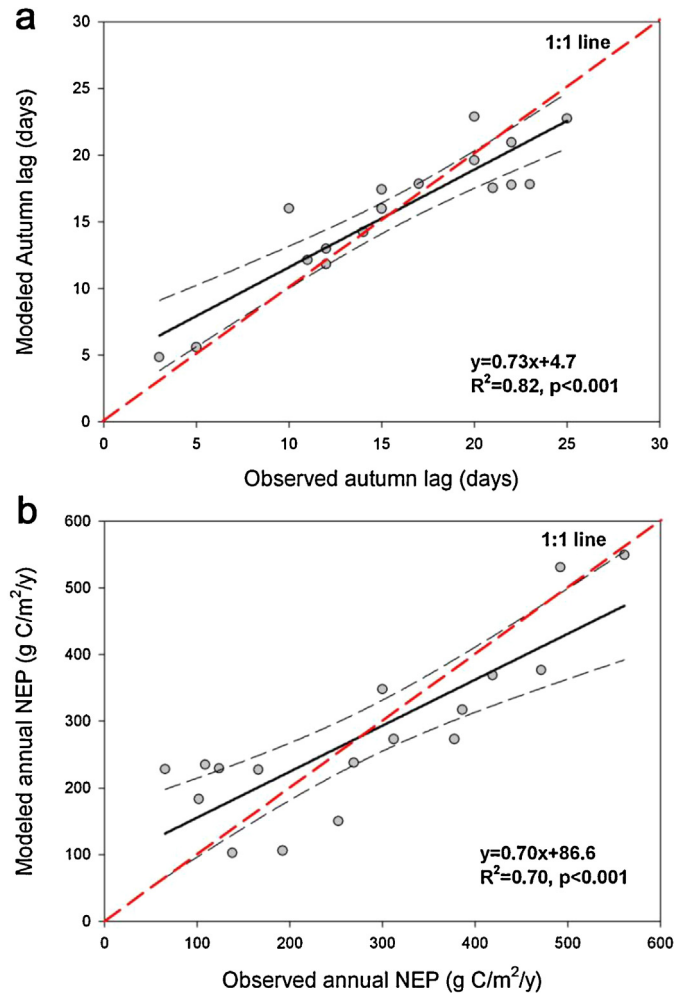


Fig. 4. Relationship between observed autumn lag and modeled autumn lag using autumn (September–November) vapor pressure deficit (VPD), global shortwave radiation (R_g) and soil temperature, and between observed annual net ecosystem productivity (NEP) and modeled NEP at Harvard Forest site.

parameterization across sites is still challenging even for the same plant functional type.

3.5. Physiological explanation of the empirical model of autumn lag

To support the selection of these meteorological variables (i.e., autumn VPD, R_g and T_s) in modeling autumn lag, we provided a physiological explanation of C fluxes in responding to autumn climate conditions. To achieve this, we calculated the total GPP and R_e during the autumn lag time and explored their responses to several autumn (September–November) meteorological variables, including VPD, R_g , T_s , T_a and precipitation (Table 2). For HF site, we found that both GPP and R_e were significantly correlated with T_s with R^2 of 0.71 ($p < 0.001$) and 0.56 ($p = 0.003$), respectively. Moderate R^2 around 0.30 were obtained when VPD and R_g were used to correlate with GPP or R_e , though these relationships were not statistically significant (p values ranged from 0.058 to 0.11), indicating neither VPD nor R_g alone can explain GPP or R_e variations. For UMB site, VPD, R_g and T_s can be used to interpret GPP (R^2 ranged from 0.33 to 0.45) and R_e (R^2 ranged from 0.24 to 0.48) during the lag time.

These correlations may first justify the use of VPD, R_g and T_s in empirically modeling autumn lag and thus annual NEP. A possible

Table 2

Interpreting total gross primary productivity (GPP) and ecosystem respiration (R_e) during the autumn lag time using autumn (September–November) meteorological variables at both sites.

Site		Vapor pressure deficit (VPD, hPa)	Global shortwave radiation (R_g , W/m ²)	Soil temperature(T_s , °C)	Air temperature(T_a , °C)	Precipitation (mm)
HF	GPP	NS	NS	$R^2 = 0.71, p < 0.001$	NS	NS
	Re	NS	NS	$R^2 = 0.56, p = 0.003$	NS	NS
UMB	GPP	$R^2 = 0.33, p = 0.015$	$R^2 = 0.45, p = 0.003$	$R^2 = 0.37, p = 0.010$	NS	NS
	Re	$R^2 = 0.41, p = 0.005$	$R^2 = 0.48, p = 0.001$	$R^2 = 0.24, p = 0.047$	NS	NS

Note: NS represents no significant correlation is observed.

explanation at HF site could be that though either VPD or R_g alone cannot explain GPP and R_e , a combination of both with T_s could improve the predictive ability of NEP estimation. More importantly, we suggest that the respiration process might be potential underestimated in phenological analyses, which also implies the importance of considering biogeochemical controls of ecosystem respiration because high GPP is not necessarily mean high NEP (Maynard et al., 2012; Dean et al., 2012).

4. Discussions

Compared to previously observed roles of spring phenology on annual NEP, we found that the autumn phenology may be equally or, perhaps, more important to predict annual NEP using long-term records of flux data at two deciduous forest sites. Several analyses have reported the impact of CU end on annual NEP (Richardson et al., 2010; Dragoni et al., 2011; Pilegaard et al., 2011; Wu et al., 2012), but very few have examined the role of autumn phenology. For HF, both CU end and autumn lag were stronger proxies of annual NEP than was CU onset. We observed similar results at the UMB site, with autumn lag explaining 62% ($p = 0.001$, data not shown here) of annual variability in NEP; no significant relationship was found between annual NEP and the CU onset at UMB, implying a stronger effect of autumn phenology on annual NEP.

Since our analysis emphasized the carbon flux phenology, challenges persist in applying our results to ecosystems for which flux data are limited. This issue is of particular importance because appropriate representation of phenology would greatly enhance the capability of ecosystem models in predicting carbon sequestration (Richardson et al., 2012). Better representation of spring phenology has been shown to improve model simulations of ecosystem functioning in response to climate change (Gonsamo et al., 2012a; Melaas et al., 2013). In our analysis, we also used the site-level meteorological variables to model the autumn phenological indicators (i.e., the autumn lag) and the usefulness of such an attempt was shown by the explained 70% of annual NEP variations solely by autumn meteorological variables for the HF site. The independent validation using data at the UMB site suggests the importance of autumn phenology in controlling annual NEP in temperate deciduous forests. In particular, it suggests that the autumn phenology (i.e., autumn lag) can be modeled using the same meteorological variables identified from the HF site, a finding that is useful for the upscaling of autumn phenology and its inclusion in ecosystem models. HF-derived model coefficients were effective in predicting the relative response of NEP at UMB to changes in autumn lag, as evidenced by comparable regression slopes for site-specific UMB and off-site HF models. However, we should also be careful that simple extension of the empirical algorithm may also lead to biased estimates of annual NEP and further investigations to other sites or species are especially needed because of diverse regional climates and different adaptive strategies among plant functional types.

A limitation of our analysis is the lack of physiological interpretation of autumn phenology using meteorological variables so that we only provided a multivariate linear regression algorithm to model autumn lag. This can be attributed to limited understandings on factors controlling senescence and dormancy in autumn (Richardson et al., 2013). For example, the ends of both GPP and CU may be controlled by multiple factors. Therefore, impacts of any changes associated with one variable could be potentially enhanced or mitigated by another. This may explain the spatial patterns of modeled annual NEP in Fig. 4b that the modeled annual

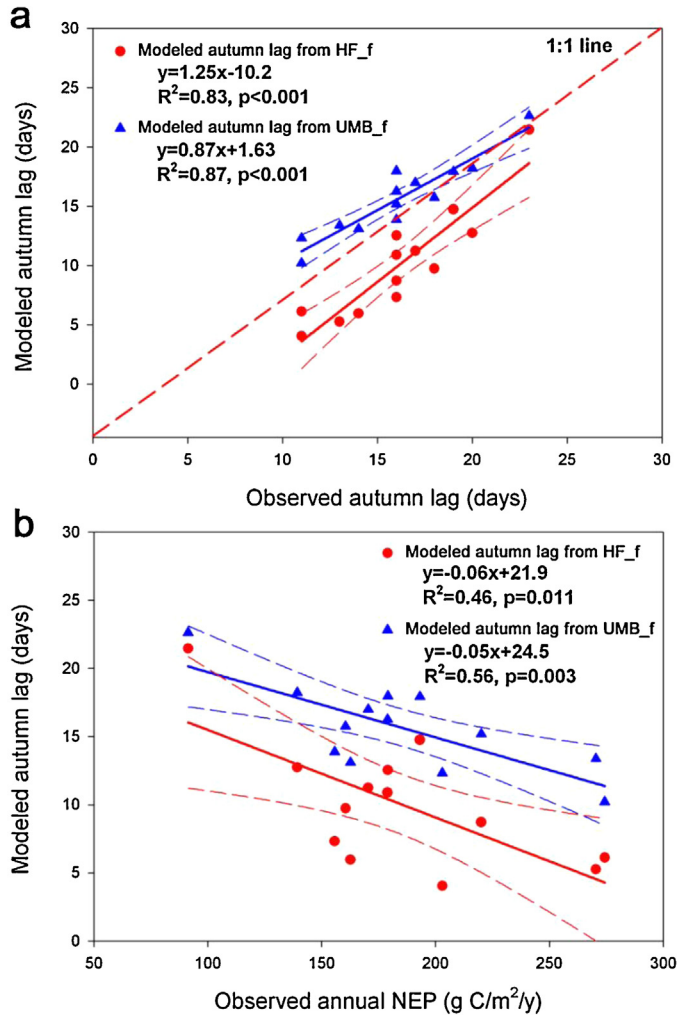


Fig. 5. Relationships between (a) observed autumn lag and modeled autumn lag using both empirical functions derived from Harvard Forest (HF.f) and University of Michigan Biological Station (UMB.f) for UMB site. (b) Relationships between observed annual net ecosystem productivity (NEP) and modeled autumn lag using both empirical functions derived from Harvard Forest (HF.f) and University of Michigan Biological Station (UMB.f) for UMB site.

NEP tends to overestimate NEP at the low range while underestimating at the high range. This issue could be potentially resolved by selecting the appropriate variables for a specific time and it may also indicate the shifts between variables that are controlling vegetation phenology.

5. Conclusions

Using long-term (17 years) flux data at Harvard Forest, we showed that the autumn phenology was a stronger predictor than spring phenology of interannual variability in NEP. The autumn lag, derived from autumn transitions of GPP and NEE, was demonstrated to have particularly high potential ($R^2 = 0.82$, $p < 0.001$) in explaining annual NEP, compared to the 39% of annual NEP variation explained by a spring phenological indicator (CU onset). We further found that the autumn water vapor pressure deficit, global shortwave radiation and soil temperature can be parameterized to model interannual variation in autumn lag ($R^2 = 0.82$, $p < 0.001$), with 70% of annual NEP at HF site explained by autumn meteorological variables. The usefulness of our finding was demonstrated by the correlation between annual NEP and the same autumn meteorological variables at the UMB site. In particular, our analyses contribute to a growing body of evidence demonstrating that autumn phenology places an important control on annual NEP in temperate forests and, thus, incorporating autumn phenological controls on C cycling processes in ecosystem models may improve predictions of NEP. Modeling annual C uptake will also be useful for forest restoration study and provide decisions on ecosystem conservation and biodiversity in the context of future climate change. Further investigation should center on determining how generalizable autumn phenology models are to other forested ecosystems and provide validation for additional sites encompassing various plant functional types.

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