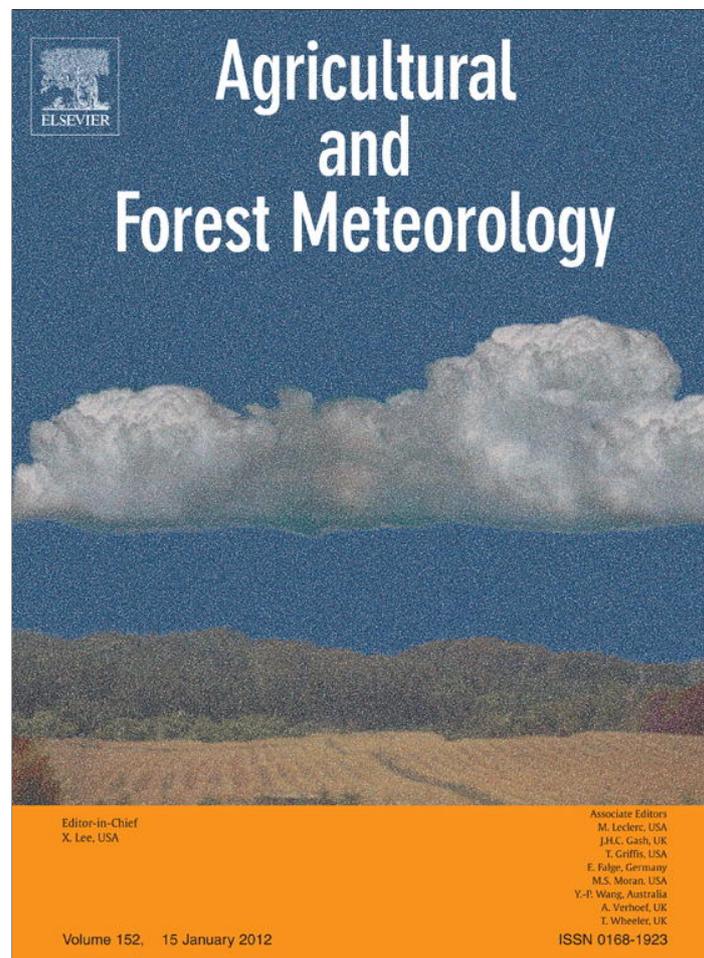


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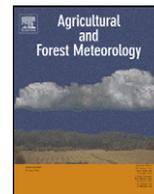
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Interannual variability of net carbon exchange is related to the lag between the end-dates of net carbon uptake and photosynthesis: Evidence from long records at two contrasting forest stands

Chaoyang Wu^{a,b,*}, Jing M. Chen^a, Alemu Gonsamo^a, David T. Price^c, T. Andrew Black^d, Werner A. Kurz^e^a Department of Geography and Program in Planning, University of Toronto, 100 St. George St., Room 5047, Toronto, ON, M5S 3G3, Canada^b The State Key Laboratory of Remote Sensing Science, Institute of Remote Sensing Applications, Chinese Academy of Sciences, Beijing 100101, China^c Natural Resources Canada, Canadian Forest Service, Edmonton, AL, T6H 3S5, Canada^d Faculty of Land and Food Systems, University of British Columbia, Vancouver, BC, Canada^e Natural Resources Canada, Canadian Forest Service-Pacific Forestry Centre, 506 West Burnside Road, Victoria, BC, V8Z 1M5, Canada

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ABSTRACT

The availability of long-term (15 years) continuous CO₂ eddy-covariance data at both deciduous and evergreen forest sites has allowed decadal analysis of the relationship between annual net ecosystem production (NEP) and the time intervals between gross primary production (GPP) and net carbon uptake (CU) transitions (e.g., start and end dates of GPP and net carbon uptake). No relationships were observed between annual NEP and the interval between the start-dates of GPP (GPP_{start}) and CU (CU_{start}) in spring (hence CU_{start} – GPP_{start} is termed the “spring interval”). Conversely, we found that interannual variability of annual NEP was strongly related to the interval between the end-dates of GPP (GPP_{end}) and CU (CU_{end}) in autumn (hence GPP_{end} – CU_{end} is termed the “autumn interval”). Extended ecosystem respiration occurring in years with late autumns could not alone explain the correlation between NEP and the autumn interval at the deciduous site, but normalization with annual GPP facilitated understanding of decreased NEP during years with longer autumn intervals at both sites. Interpretation of the autumn interval based on site-level meteorological variables showed that autumn temperature (either air temperature or soil temperature) alone cannot be used to interpret autumn interval variations for either site. Autumn global shortwave radiation caused contrasting impacts on the autumn intervals at these two sites. High autumn radiation shortened the autumn interval at the deciduous site (i.e., it increased NEP) but lengthened it at the evergreen site (i.e., it decreased NEP). To our knowledge, this is the first analysis to assess the impacts of the lag between the dates when measurable gross photosynthesis and net carbon uptake occur, and to relate these to annual NEP. Our results suggest that in contrast to previously reported emphasis on spring phenology, autumn phenology may also have a major role in regulating annual NEP, even in northern boreal forest ecosystems where temperature is considered a major limiting factor. Further, it appears that other variables, notably radiation and soil moisture, are critical for determining interannual variability in net carbon exchange.

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1. Introduction

Forest ecosystems play a significant role in the global carbon (C) cycle (Pan et al., 2011). Therefore, a better understanding of forest ecosystem responses to climate will aid in the development of ecosystem models used to assess potential impacts of future climate change on forests, including increased drought occurrence (e.g., Zhao and Running, 2010), rising CO₂ concentration (e.g., Norby

et al., 2010) and changes in precipitation regimes (e.g., Knapp et al., 2002). One important issue in climate change research is variations in plant phenology, which might be used to interpret the temporal and spatial variability of ecosystem–atmosphere fluxes (Richardson et al., 2010; Wang et al., 2011).

Recent changes in climate have been shown to affect plant phenology, which in turn have affected ecosystem processes (e.g., Richardson et al., 2010; Pan et al., 2011). Effects of recent observed changes in climate on plant phenology have been reported both at local (Dragoni et al., 2011), and continental scales (Wang et al., 2011), indicating an urgent need to evaluate phenological responses to climate variability to improve our understanding of terrestrial ecosystem sensitivity to future climate change (Morissette et al., 2009). In boreal regions, warmer spring

* Corresponding author at: Department of Geography and Program in Planning, University of Toronto, 100 St. George St., Room 5047, Toronto, ON, M5S 3G3, Canada. Tel.: +1 647 524 0310.

E-mail address: hefery@163.com (C. Wu).

temperatures tend to advance leaf out in spring, and thus contribute to increased annual carbon sequestration (Black et al., 2000; Chen et al., 2006a). However, a lack of consideration of climate change impacts on autumn temperatures may cause misinterpretation of effects on the annual carbon cycle because increased net ecosystem production (NEP) due to warmer springs can be offset by higher respiration in autumn (Piao et al., 2008). While most existing phenological analyses focus on either the growing season length (GSL) or net carbon uptake period (CUP) alone, the impacts of the lags between growing season (GS) and carbon uptake (CU) transitions (i.e., the first and last days of the GS and CU in both spring and autumn) on annual NEP are not well understood. Investigating these lags in the transitions could provide important insights into understanding the causes of interannual variability of NEP (Richardson et al., 2010).

Phenological controls of interannual variability in ecosystem productivity are an active research area among global change scientists, due largely to availability of eddy-covariance (EC) measurements of ecosystem CO₂ fluxes (Richardson et al., 2010; Pan et al., 2011; Wang et al., 2011). However, a key previous restriction to understand interannual variability in NEP has been the limited availability of long-term flux data. In general, time series longer than 10 years are desirable, because carbon cycle analysis over shorter periods is likely to have insufficient representation of interannual variability (Dragoni et al., 2011). With continuous observations occurring at some sites in North America since circa 1993, decadal-scale time-series data are now available for several sites. Here we use 15 years of continuous observations at deciduous broadleaf and evergreen needleleaf stands in the Canadian boreal region where temperatures have increased in recent decades (Black et al., 2000; Stone et al., 2002; Chen et al., 2006a). Furthermore, these data sets also provide an opportunity to evaluate the phenological controls on interannual variability in NEP in contrasting plant functional types (PFT). We present analyses of then phenological intervals (namely the time intervals in days between photosynthesis (i.e., GPP) and net carbon uptake transitions in both spring and autumn) affecting annual NEP at these two sites.

Further analyses were conducted using the autumn temperature, global shortwave radiation, and the ecosystem respiration (R_e), in comparison with the autumn interval between the end-dates of CU and GPP. These analyses tested the potential of relating the autumn interval to climate variables, and may enhance understanding of possible impacts of future climate change on forest carbon sequestration at regional to global scales. Our suggestion is that variations in the time interval between sink-source transition and the cessation of photosynthesis in autumn are a potentially important contributor to interannual variability of NEP in both deciduous and evergreen forest stands.

2. Methods

2.1. Study sites

Two mature forest sites where continuous eddy covariance measurements of CO₂ fluxes had been made for 15 years were selected for this study (Table 1). The Saskatchewan Old Aspen site (SK-OA, 53.63°N, 106.20°W) is a predominantly deciduous broadleaf stand located in Prince Albert National Park, approximately 50 km northwest of Prince Albert, Saskatchewan, Canada (Barr et al., 2007). Meteorological and EC instrumentation were installed in October 1993 for NASA's Boreal Ecosystem–Atmosphere Study (BOREAS) (1993–1996) (e.g., Black et al., 1996) and after BOREAS, measurements continued as part of the Boreal Ecosystem Research and Monitoring Sites (BERMS) program (Black et al., 2000). The stand is composed mainly of trembling aspen (*Populus tremuloides* Michx.).

Table 1
Description of the two study sites in this study.

Description	Site	
	SK-OA	MB-OBS
Vegetation type	Deciduous boreal forest	Evergreen boreal forest
Dominant species	Mature aspen with a few balsam poplar, thick hazel understory	Black spruce with occasional larch in poorly drained areas and diverse understory
Stand age (2010) ^a	89	172
Stand density (trees ha ⁻¹)	980	5450
Canopy height (m)	20.1	9.1
Leaf area index (LAI, m ² m ⁻²) ^b	2.1	4.2
Elevation (m)	601	259
Soil texture	Clay-loam	Clay-silt
Mean annual air temperature (°C)	0.4	-3.2
Mean annual precipitation	467	517

^a Stand age for these two sites were from Barr et al. (2004) and Dunn et al. (2007).

^b Data from Chen et al. (2006b).

The continuous understory reaches a mean height of 1.5–2.0 m and is composed of beaked hazelnut (*Corylus cornuta* Marsh), wild rose (*Rosa woodsii*), willows (*Salix* spp.), alder (*Alnus crispa*) and a variety of grasses and herbs.

The second site is an evergreen conifer stand, known as the Manitoba Northern Old Black Spruce site (MB-OBS, 55.88°N, 98.48°W) located in west of Thompson, Manitoba, Canada. Meteorological and EC instrumentation were also installed in 1993 as part of BOREAS (Dunn et al., 2007). The vegetation is composed predominantly of black spruce trees (*Picea Mariana* (Mill.)). The groundcover is primarily moss, with feather moss (*Pleurozium schreberi* and *Hylacomium splendens*) occupying the upland areas, and hummocky peat moss (*Sphagnum* spp.) in the bog areas.

2.2. Flux and meteorological measurements

Flux and meteorological data were obtained from Fluxnet-Canada archives (<http://www.fluxnet-canada.ca>). Data durations for SK-OA and MB-OBS were 1996–2010 and 1994–2008, respectively. Wind velocity components, air temperature, water vapor pressure, and CO₂ concentration were sampled at 20 and 4 Hz for SK-OA and MB-OBS, respectively. CO₂ fluxes were calculated as the half-hourly covariances of the vertical wind velocity component and the CO₂ mole fraction, corrected for air density effects. Net ecosystem exchange (NEE) was obtained by adding the associated rate of change of CO₂ storage in the air column beneath the EC sensors to each half-hourly CO₂ flux. Half-hourly mean values of meteorological variables were also obtained from measurements using sensors mounted on the tower and archived for later analysis (Dunn et al., 2007; Barr et al., 2007).

A standard procedure was used to obtain annual NEP from the half hourly NEE observations (i.e., NEP = -NEE). First, NEE values were removed when values of the friction velocity (u_*) were less than a threshold value (u_{*th}) (u_{*th} was 0.35 m s⁻¹ for SK-OA and 0.20 m s⁻¹ for MB-OBS). Then NEE was adjusted to account for the lack of energy balance closure (i.e., latent plus sensible heat fluxes being less than net radiation minus the energy storage fluxes) assuming that lack of closure results from EC measurements underestimating the magnitudes of the turbulent fluxes. Next, measured R_e was estimated as $R_e = NEE$ during periods when GPP was known to be zero. Finally, GPP was estimated as $-NEE + R_e$ (daytime) or as zero (nighttime and during periods when both air temperature (T_a) and soil temperature (T_s) were less than 0 °C). Empirical regressions

of nighttime NEE versus shallow soil temperature and daytime GPP versus photosynthetically active radiation (PAR) were used to estimate R_e and GPP, respectively, and gaps filled as described in Barr et al. (2004). The time-integral of NEE was partitioned into gross primary production (GPP) and ecosystem respiration (R_e) using gap-filled half-hourly values where needed.

Considering that both GPP and R_e depend on the gap-filling method and the distribution of data gaps, we used two more methods to determine these parameters. The first method was a simple approach based on empirical annual relationships to calculate both GPP and R_e :

$$R_e = f(T_s, t) = \frac{r_t(t)r_1}{[1 + \exp(r_2(r_3 - T_s))]} \quad (1)$$

where T_s is the soil temperature, $r_t(t)$ is the time-varying parameter, and r_1 , r_2 , and r_3 are empirical parameters, which are held constant over the year.

Gaps in GPP were filled using the dependence of GPP on downwelling photosynthetically active radiation (PAR) above the stand, also known as the Michaelis–Menten light-response equation,

$$GPP = f(Q, t) = \frac{p_t(t)\alpha Q A_{\max}}{\alpha Q + A_{\max}} \quad (2)$$

where $p_t(t)$ is the time-varying parameter; α is the quantum yield; and A_{\max} is the canopy-scale photosynthetic capacity. Both α and A_{\max} were held constant throughout the year.

The second approach was the daytime light response (DLR) analysis proposed by Griffis et al. (2003) which uses Eq. (2) to gap-fill the missing daytime flux data during the growing season. Light response functions have been used in several published studies and characterize the photosynthetic and respiratory characteristics of a variety of ecosystems (Landsberg and Gower, 1997). A more detailed description of these two approaches can be found in Griffis et al. (2003) and Kljun et al. (2007). The mean values of these three algorithms were used in this analysis and the standard deviations (SD) were included to show the uncertainty of carbon fluxes.

We also calculated several climatic indices to support the analysis of phenological variations and annual carbon fluxes. Spring and autumn were defined as three-month periods from March 1 to May 31 and from September 1 to November 30, respectively, considering that the temperature follows a sinusoidal pattern over a year, with coldest and warmest months generally in January and July (Fig. 1). These indices included spring (mean value from March 1 to May 31) and autumn (mean value from September 30 to November 30) T_a and T_s , soil water content (SWC, unavailable for MB-OBS), precipitation and global shortwave radiation (R_g). The first year at each site was excluded due to incomplete records, i.e., 1996 for SK-OA and 1994 for MB-OBS. These definitions of spring and autumn were also consistent with those used by Chen et al. (2000), in which impacts of spring temperature on growing season length were analyzed on several boreal forest sites (including SK-OA).

2.3. Phenological transitions

Two types of phenological transitions were calculated in this analysis, termed (1) temperature threshold (TT) method, and (2) carbon flux phenology (CFP). While we were primarily focused on the application of CFP in this analysis, the temperature threshold method was used to validate the suitability of the CFP procedure. The applications of both procedures required obtaining the transitions in the smoothed curves of daily air temperature and daily carbon fluxes (i.e., GPP and NEP). Considering these transitions may be potentially sensitive to the specific smoothing method, we used four smoothing models in our analysis, including the negative exponential, running average, running median and inverse square. The

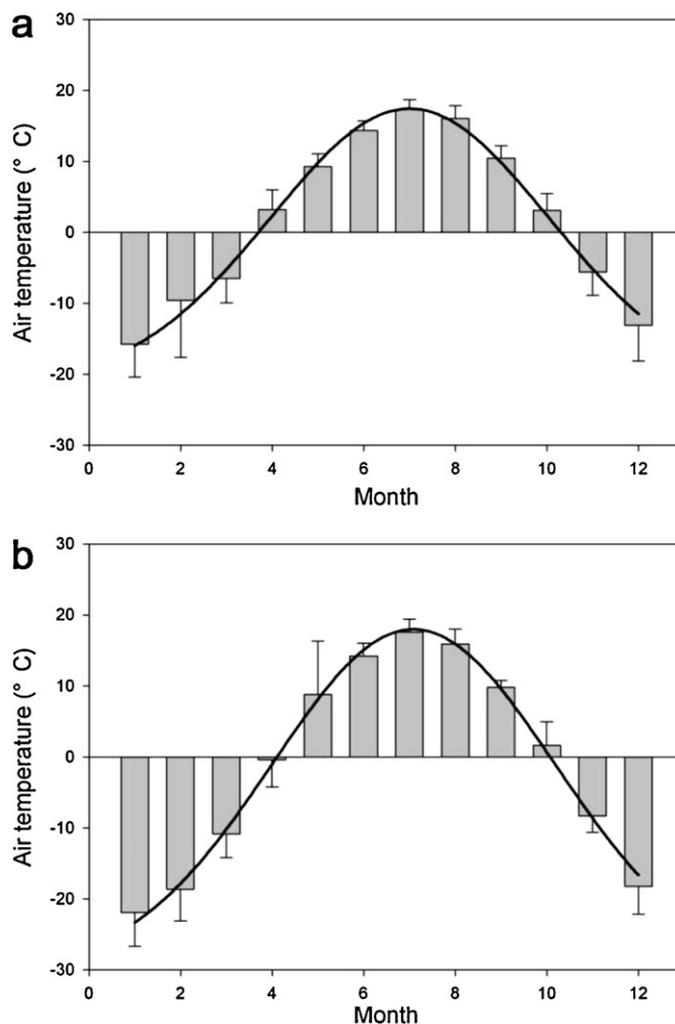


Fig. 1. Distributions of monthly air temperature for (a) SK-OA and (b) MB-OBS during the study years. Error bars indicate the standard deviations.

mean values of these calculations were used and standard deviations were also included.

2.3.1. Phenological transitions based on temperature threshold

The temperature threshold method has been commonly used to determine GSL (e.g., Chen et al., 2000) and the onset of CUP (Baldocchi et al., 2005). In this analysis, we used 5 °C as the threshold air temperature to determine the start and end of the growing season following the previous study of Chen et al. (2000), which showed good prediction ability of GSL for several boreal forest sites in Canada (including SK-OA). Furthermore, Barr et al. (2004) demonstrated that 5 °C threshold in air temperature in SK-OA site provided a good representation of the canopy duration (from spring green-up to autumn senescence) of on-site observations. We first plotted daily air temperature and each of the four smoothing methods was used to produce smoothed curves. The first and last days when the daily mean T_a curve reached 5 °C were assigned as the start and end-dates of the growing season, referred as TT_{start} and TT_{end} from hereon.

2.3.2. Phenological transitions based on daily GPP and NEP

Smoothed values of daily NEP were used to calculate the phenological transitions when net daily carbon uptake switched from negative to positive in spring and from positive to negative in autumn. Similarly, smoothed values of GPP were used to define

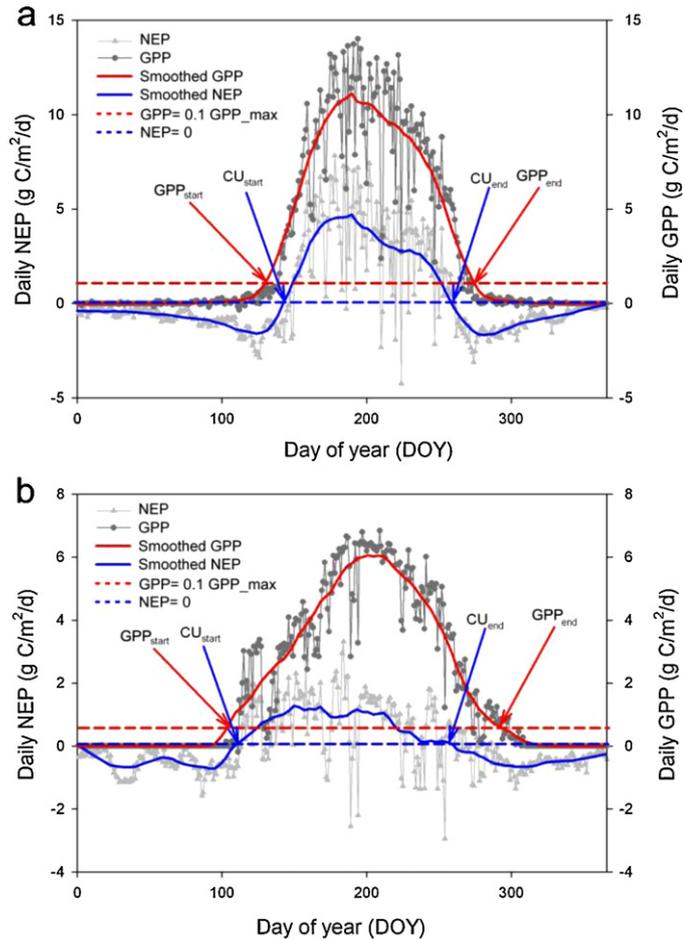


Fig. 2. Example demonstration of determination of phenological transitions using daily net ecosystem production (NEP) and gross primary production (GPP) data at (a) SK-OA in 2000 and (b) MB-OBS in 2000. The carbon uptake start (CU_{start}) and end (CU_{end}) are determined by the first and the last days of positive daily NEP, respectively. The growing season start (GPP_{start}) and end (GPP_{end}) are determined by the days when smoothed (negative exponential smooth method for example) daily GPP reaches 10% of the annual maximum smoothed daily GPP.

when photosynthesis began and ended. Using the definition of CUP proposed by White and Nemani (2003), the respective start and end-dates were then referred to as the carbon uptake start (CU_{start}) and carbon uptake end (CU_{end}), respectively (Fig. 2). We used 10% of maximum daily GPP for each year as the threshold to determine the start and end-dates of significant photosynthesis, termed GPP_{start} and GPP_{end} , respectively. Unlike constant GPP thresholds used in earlier studies (Richardson et al., 2010), our method allows variations in phenological events to be captured and compared both interannually and among different sites. The spring and autumn intervals were thus calculated as:

$$\begin{aligned} \text{Spring interval} &= CU_{start} - GPP_{start}, & \text{Autumn interval} \\ &= GPP_{end} - CU_{end} \end{aligned} \quad (3)$$

3. Results

3.1. Phenological transitions based on GPP and temperature threshold

Significant positive correlations were found between the calculated start-dates of photosynthesis (GPP_{start}) and spring

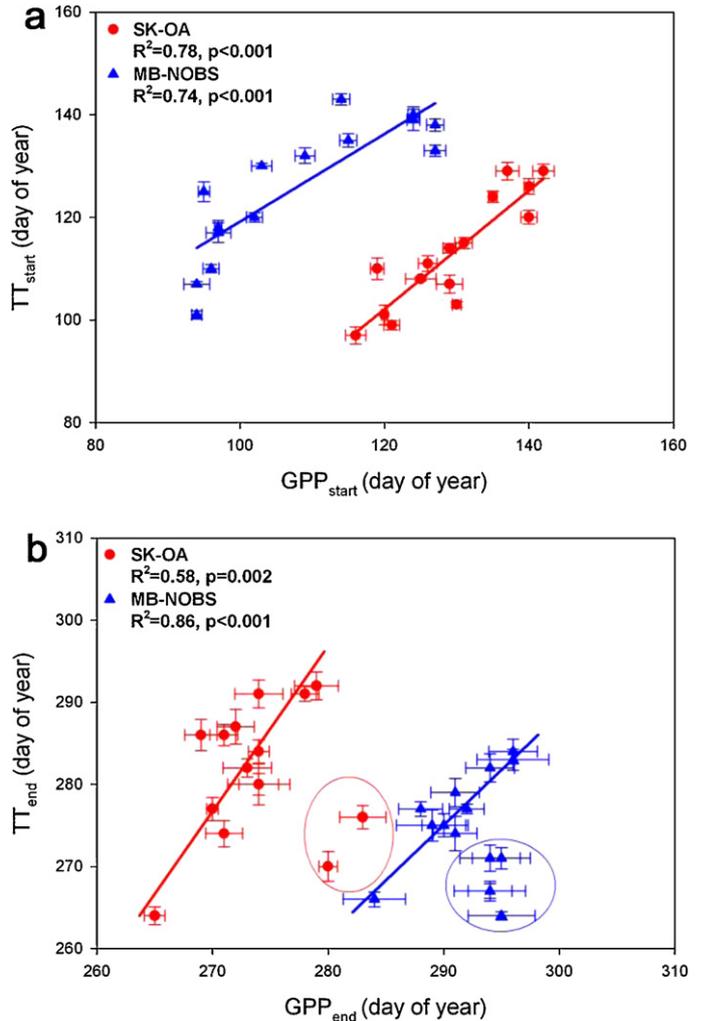


Fig. 3. Relationships between (a) starts of photosynthesis derived from daily GPP (GPP_{start}) and the start of growing season determined using the temperature threshold (TT_{start}), and relationships between (b) end of photosynthesis derived from daily GPP (GPP_{end}) and the end of growing season determined using the temperature threshold (TT_{end}). Error bars indicate standard deviations. (For interpretation of the references to color in the text, the reader is referred to the web version of the article.)

temperature threshold (TT_{start}), with coefficients of determination (R^2) of 0.78 ($p < 0.001$) and 0.74 ($p < 0.001$) at SK-OA and MB-OBS, respectively (Fig. 3). This observation indicates that determining the start of photosynthesis from daily GPP agrees well with the traditional phenological metric of spring temperature threshold. However, no correlation was found between the calculated end-date of photosynthesis (GPP_{end}) and TT_{end} for either site (Fig. 3b). Hence, it appears that the end of the growing season determined from the autumn temperature threshold does not necessarily mean the cessation of GPP. The cause of this apparent inconsistency was high daily integrals of solar radiation that could persist beyond TT_{end} . Although mean daily air temperature may have dropped below $+5^\circ\text{C}$, high incoming radiation on relatively clear days would likely keep daytime temperatures warm enough to allow significant daily GPP (exceeding the 10% of maximum GPP threshold) so long as nighttime temperatures did not drop below freezing to cause damage to photosynthetic capacity. This hypothesis is supported by the results obtained for both sites. For example, the four points circled in blue on Fig. 3b were obtained for 1995, 1996, 1998 and 2000, respectively. The average autumn radiation in these four years was $75.5 \text{ MJ m}^{-2} \text{ d}^{-1}$, almost 20% higher than the mean for the remaining years ($64.2 \text{ MJ m}^{-2} \text{ d}^{-1}$). With these years excluded,

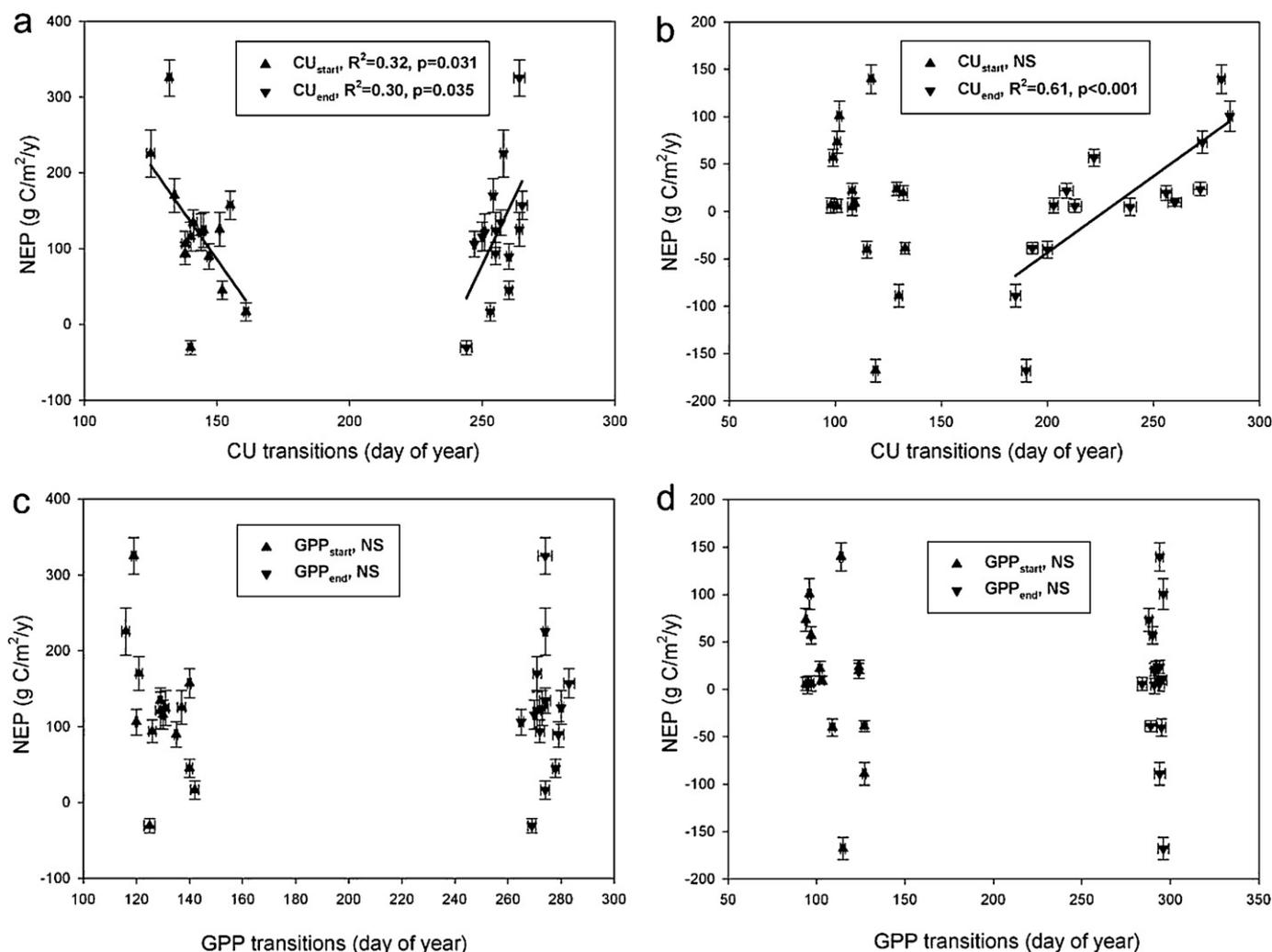


Fig. 4. Relationships between annual net ecosystem production (NEP) and carbon uptake transitions in (a) SK-OA, (b) MB-OBS, gross primary production (GPP) transitions in (c) SK-OA, and (d) MB-OBS. Error bars indicate standard deviations. NS represents not significant.

GPP_{end} for both sites was significantly correlated with TT_{end} with R^2 of 0.58 ($p=0.002$) and 0.86 ($p<0.001$) at SK-OA and MB-OBS, respectively. We suggest that such carbon flux-based metrics will have better success in predicting autumn phenology because they integrate the effects of temperature and solar radiation (and other climatic factors) better than metrics based on temperature thresholds alone (see also Richardson et al., 2010; Garrity et al., 2011; Pilegaard et al., 2011).

3.2. Comparison between spring and autumn intervals between sites

The deciduous site showed a consistently longer interval between GPP_{start} and CU_{start} in spring (mean 13.5 days, SD 2.7) than that of the evergreen site (mean 5.5 days, SD 2.8). However, in autumn, the interval between GPP_{end} and CU_{end} was much shorter at the deciduous site (mean 18 days, SD 3.1) compared with the evergreen site (mean 60 days, SD 36.2). These differences are likely associated with differences between the phenological strategies adopted by deciduous broadleaf and evergreen needleleaf forests (or functional types) (Barr et al., 2009). However, it is important to recognize that the two sites are also in distinct climate zones. The more northerly conifer-dominated site would be inherently colder and the deep organic soils would take longer to warm up, even if energy available from solar heating was the same as that

at the southern site. Conversely, the more southerly, deciduous broadleaf-dominated, the more rapidly a site might tend to cool down in autumn, even though mean temperatures could remain higher.

Deciduous forests generally take about two weeks after the start of photosynthesis for net daily carbon uptake to become positive. This is because of the time required for leaves to emerge from buds and completely expand, when photosynthesis will be depressed relative to maximum GPP, and foliar respiration rates may be exceptionally high, both contributing to low or negative carbon uptake. In autumn, deciduous forests shed their leaves, typically over a period of about two weeks and GPP_{end} must therefore occur soon after CU_{end}.

In contrast, evergreen needleleaf trees can begin to take up some carbon in spring very soon after the onset of photosynthesis, because when conditions are favorable, the existing foliage is able to contribute to GPP almost immediately. Similarly in autumn, evergreen needleleaf trees can continue to photosynthesize later in the year even after the oldest foliage (typically the most shaded in the canopy and with lowest photosynthetic capacity) has been dropped. Hence, if conditions remain clear and warm, the remaining foliage may be able to return positive daily NEP for a few more weeks. Furthermore, mild nighttime freezing may not have serious impacts on daytime photosynthesis in cold-tolerant species.

Table 2
Relationships between gross primary production (GPP) and net ecosystem production (NEP) phenological transitions (Bold type indicates difference between these two sites and NS indicates not significant).

Site	Variables	GPP _{start}	CU _{start}	CU _{end}	GPP _{end}
SK-OA	GPP _{start}				
	CU _{start}	$R^2 = 0.93, p < 0.001$			
	CU _{end}	NS	NS		
	GPP _{end}	$R^2 = \mathbf{0.42}, p = \mathbf{0.009}$	NS	$R^2 = \mathbf{0.76}, p < \mathbf{0.001}$	
MB-OBS	GPP _{start}				
	CU _{start}	$R^2 = 0.95, p < 0.001$			
	CU _{end}	NS	NS		
	GPP _{end}	NS	NS	NS	

3.3. Relationships between annual NEP and spring and autumn intervals

Both CU and GPP transitions alone were first explored for their potential in explaining interannual variability of annual NEP (Fig. 4). As might be expected, CU_{start} was negatively correlated with annual NEP at SK-OA, but somewhat surprisingly, this correlation was not observed at MB-OBS. Consistently positive relationships were also found between CU_{end} and annual NEP for both sites, with a particularly high R^2 ($R^2 = 0.61, p < 0.001$) at MB-OBS. On the other hand, the calculated GPP transitions were not significantly correlated with annual NEP at either site (Fig. 4c and d).

No correlation was observed when spring intervals (GPP_{start} – CU_{start}) were plotted against annual NEP at the two sites (Fig. 5). This appeared to be due mainly to the rapid transition of both forest types to net carbon uptake soon after the onset of the photosynthesis. However, the autumn intervals (GPP_{end} – CU_{end}) were strongly inversely correlated with annual NEP, with R^2 of 0.80 ($p < 0.001$) and 0.72 ($p < 0.001$) for SK-OA and MB-OBS, respectively. These results indicate that the duration of the autumn interval is strongly correlated to annual carbon sequestration for both plant functional types, and more significantly correlated than the durations of the GPP or CU transitions alone. To our knowledge, this is the first report of the impacts of length of autumn intervals between photosynthesis and carbon uptake transitions on annual NEP, and of the importance of using both criteria to explain interannual variability in carbon uptake. This also supports earlier work which suggests that autumn ecosystem respiration may be of greater importance than autumn photosynthesis as a determinant of determining interannual variability in NEP (e.g., Valentini et al., 2000).

To investigate this apparent negative relationship between autumn interval and annual NEP, we analyzed the impacts of autumn interval on R_e during the interval period, on annual R_e and on the ratio of annual R_e to GPP at both sites (Fig. 6). Our results showed that longer autumn intervals significantly increased R_e during the interval with R^2 of 0.90 ($p < 0.001$) and 0.95 ($p < 0.001$) for SK-OA and MB-OBS, respectively. The response of annual R_e to longer autumn intervals differed between the two PFTs, however, with only the evergreen needleleaf showing a significant increase ($R^2 = 0.72, p < 0.001$) (Fig. 6d). The regression slope indicates that a one day lengthening increases annual R_e by $2.1 \pm 0.3 \text{ g C m}^{-2}$ at the MB-OBS site. Annual R_e was not correlated with the length of the autumn interval at SK-OA site (Fig. 6c), agreeing with previous work of Barr et al. (2007) which showed that longer growing seasons had no apparent effect on R_e . The relationship between autumn interval and the ratio of annual R_e to GPP (R_e/GPP) showed significant positive impacts with R^2 of 0.83 ($p < 0.001$) and 0.68 ($p < 0.001$) for SK-OA and MB-OBS, respectively. These observations imply that longer autumns will necessarily increase the proportion of annual R_e to GPP—which is likely to be the main reason for a negative correlation with annual NEP.

3.4. Discussion

3.4.1. Relationships between GPP and NEP phenological transitions

Because intervals between GPP and NEP transitions were used in our analysis, it was of interest to explore the cross-correlations among these GPP and NEP transitions (Table 2). For the SK-OA site, we found that the start-date for GPP was positively correlated with the end-date of GPP, indicating that earlier leaf-out in spring will probably lead to earlier leaf-off in autumn. However, for the

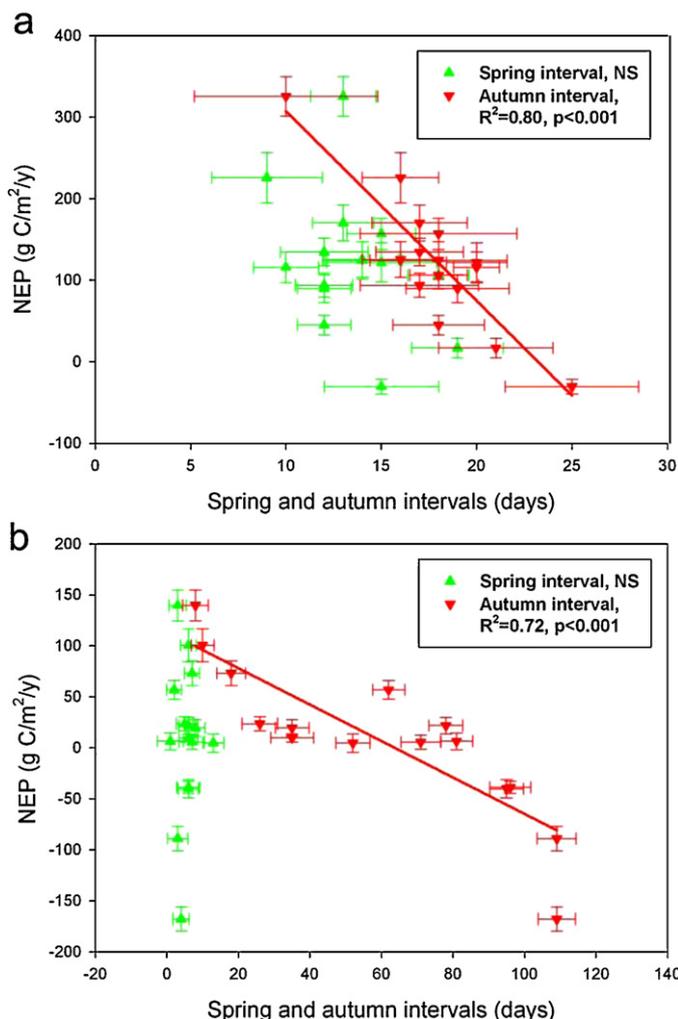


Fig. 5. Correlations between annual net ecosystem production (NEP) and spring interval (first days between GPP and net C uptake) and autumn interval (last days between net C uptake and GPP) in (a) SK-OA site and (b) MB-OBS site. Error bars indicate standard deviations. NS represents not significant.

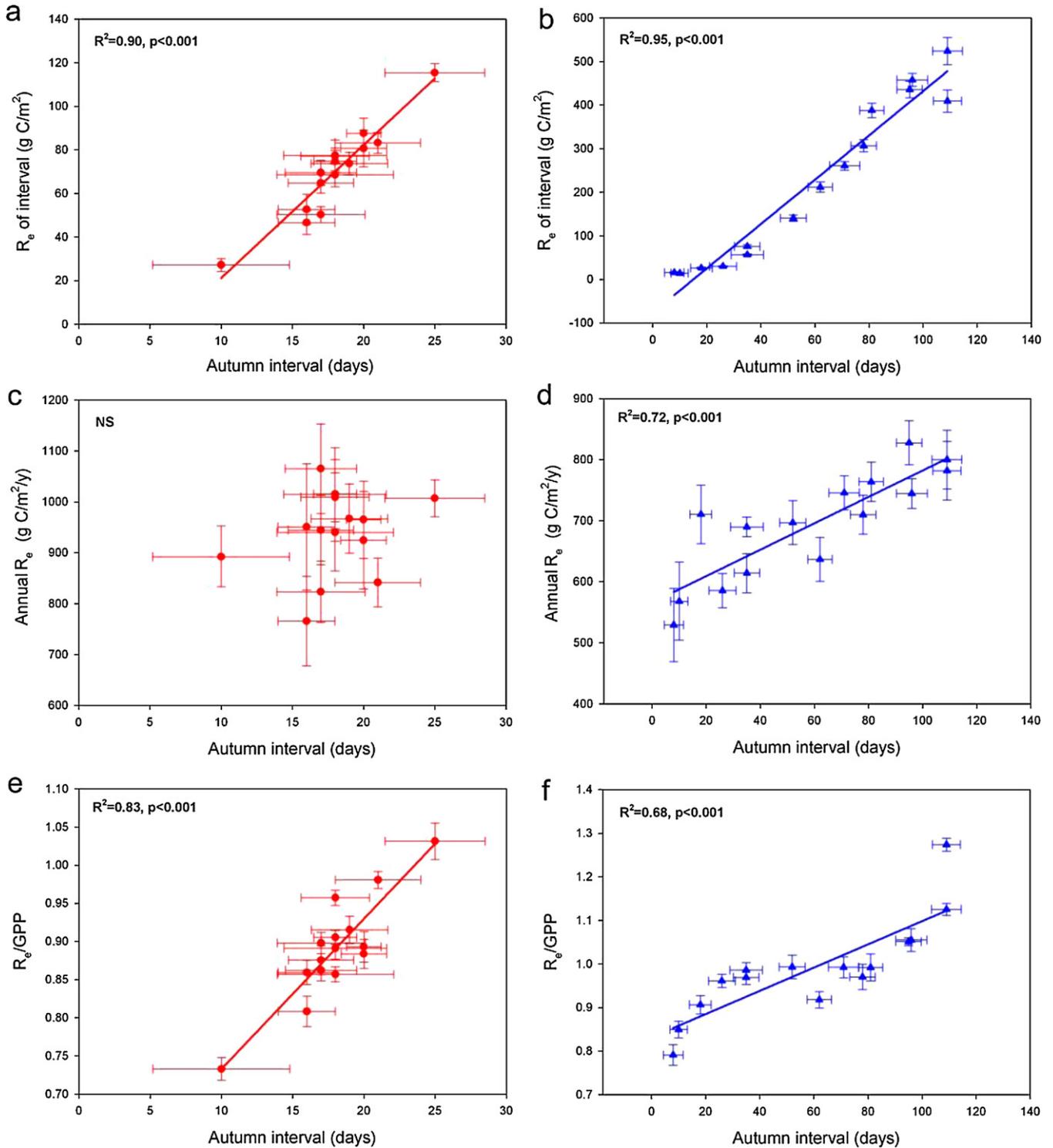


Fig. 6. Relationships between the autumn interval and interval period ecosystem respiration (R_e) for (a) SK-OA and (b) MB-OBS, annual R_e for (c) SK-OA and (d) MB-OBS, and the ratio of annual R_e to gross primary production (GPP) for (e) SK-OA and (f) MB-OBS. Error bars indicate standard deviations. NS represents not significant.

evergreen conifer site, these two events (start- and end-date for GPP) were not correlated. The other difference between these contrasting PFTs was that a positive relationship ($R^2 = 0.76, p < 0.001$) was found between GPP_{end} and CU_{end} for SK-OA, but no similar correlation was observed at MB-OBS. For both sites, earlier onset of GPP led to earlier starts of net carbon uptake as GPP_{start} and CU_{start} were positively correlated with R^2 of 0.93 ($p < 0.001$) and 0.95 ($p < 0.001$) for SK-OA and MB-OBS, respectively. This relationship would be expected because the onset of positive GPP is a necessary

precondition for positive NEP. Conversely, the other similar pattern between these two sites was that no relationship was found between the start- and end-dates of the NEP transitions.

3.4.2. Controls of spring and autumn temperatures on GPP and NEP phenological transitions

We also investigated the responses of carbon flux-based phenology to environmental controls in these boreal forest stands, particularly effects of air temperature. We therefore analyzed the

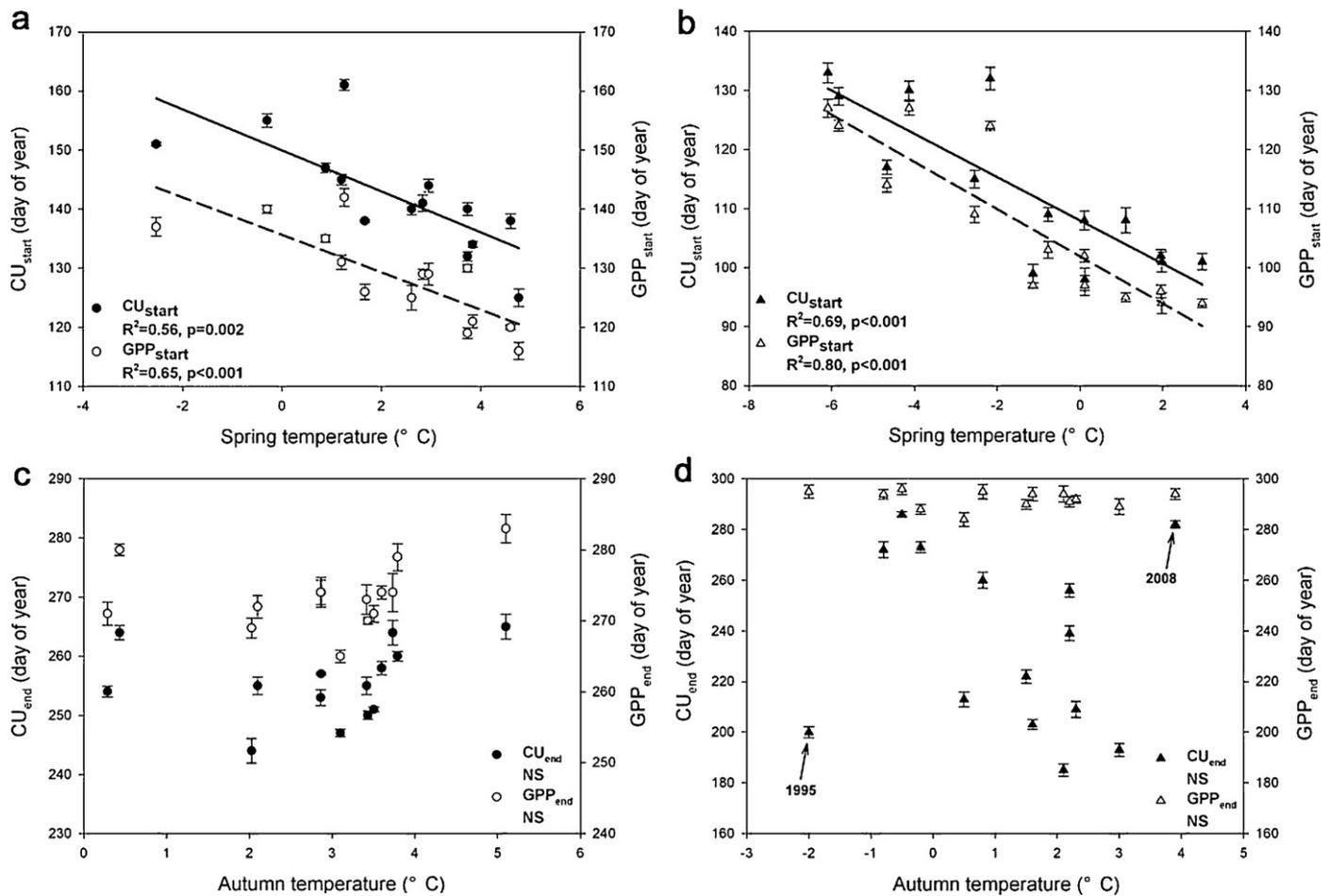


Fig. 7. Relationships between spring temperature and net carbon uptake start (CU_{start}) and gross primary production (GPP) start (GPP_{start}) in (a) SK-OA and (b) MB-OBS site. Relationships between autumn temperature and net carbon uptake end (CU_{end}) and GPP end (GPP_{end}) in (a) SK-OA and (b) MB-OBS site. Arrows indicate data of drought years for MB-OBS. Error bars indicate standard deviations and NS indicates not significant.

relationships between the timing of GPP and NEP transitions and of spring and autumn temperatures at the two sites (Fig. 7).

We found that spring temperature at both sites was negatively correlated with both GPP_{start} and CU_{start} , suggesting that high spring temperatures lead to earlier onset of both GPP and net carbon take (Fig. 7a and b). These results were consistent with the previous analyses of Black et al. (2000) and Chen et al. (2006a), both of which reported increased carbon sequestration in warmer spring years. In contrast to the generally accepted view of autumn warming effects (Piao et al., 2008), even using 15 years of observations, autumn temperatures did not correlate with either GPP_{end} or CU_{end} at either site (Fig. 7c and d). This seems to indicate that autumn temperature is only a weak determinant of the end of net carbon uptake (Fig. 5a and b).

Interestingly, for the evergreen site (MB-OBS), if two autumn drought years are excluded (1995 and 2008 with autumn precipitation of 80 and 40 mm, respectively, compared to the 15-year average of ~ 140 mm), autumn temperature then becomes significantly correlated with CU_{end} ($R^2 = 0.62, p < 0.001$). Meanwhile, a significant decrease in NEP ($R^2 = 0.55, p < 0.001$) was observed in warmer autumns, consistent with the boreal warming stimulation of fall respiration rates reported by Piao et al. (2008). Such results were not observed at the deciduous site, however, because leaf-fall was more tightly coupled to daylength and the occurrence of warmer temperatures in late autumn therefore had less impact on R_e . Hence, we suggest that responses of CU_{end} to autumn temperature could be better captured by incorporating more environmental

variables (e.g., precipitation, soil water content, etc.), but also by recognizing there are characteristic differences between evergreen and deciduous forest systems. These observations also agree with the results of Barr et al. (2007) who found that spring temperature is the primary factor controlling annual NEP at SK-OA, due to its influence on the onset of the growing season, and hence on the initiation of carbon uptake.

3.4.3. Interpreting autumn interval using autumn meteorological variables

We investigated the potential environmental controls on autumn interval, which serve as important steps for this new phenological metric to be introduced in ecosystem models (Dragoni et al., 2011; Garrity et al., 2011; Richardson et al., 2012). We found that temperature (either T_a or T_s) and precipitation were not correlated with autumn interval (Table 3). A positive relationship was found between SWC and autumn interval at SK-OA site, suggesting higher autumn soil moisture was somehow related to a lengthening of the autumn interval and hence decreased annual NEP. The most interesting aspect was that autumn global shortwave radiation (R_g) showed contrasting impacts on the autumn intervals at these two sites. For the deciduous site, increased R_g was negatively correlated with autumn interval. This could be related to increased occurrence of clear sky conditions contributing to more severe nighttime frost events, producing a more abrupt end to the growing season. Conversely, more radiation in autumn was positively correlated with autumn interval at the evergreen site, evidently because it allows

Table 3
Coefficients of determination (R^2) between autumn interval and meteorological variables.

Site	R_g ($\text{MJ m}^{-2} \text{d}^{-1}$)	T_a ($^{\circ}\text{C}$)	SWC (%)	T_s ($^{\circ}\text{C}$)	Precipitation (mm)
SK-OA	$y = -0.8x + 100$ $R^2 = 0.40, p = 0.015$	NS	$y = 1.9x - 6.9$ $R^2 = 0.43, p = 0.011$	NS	NS
MB-OBS	$y = 0.1x + 61$ $R^2 = 0.54, p = 0.002$	NS	NA	NS	NS

Note: R_g , T_a , T_s and SWC represent daily mean (from 1 September to 30 November) global shortwave radiation, air temperature, soil temperature and soil water content, respectively. NS and NA indicate not significant and not applicable.

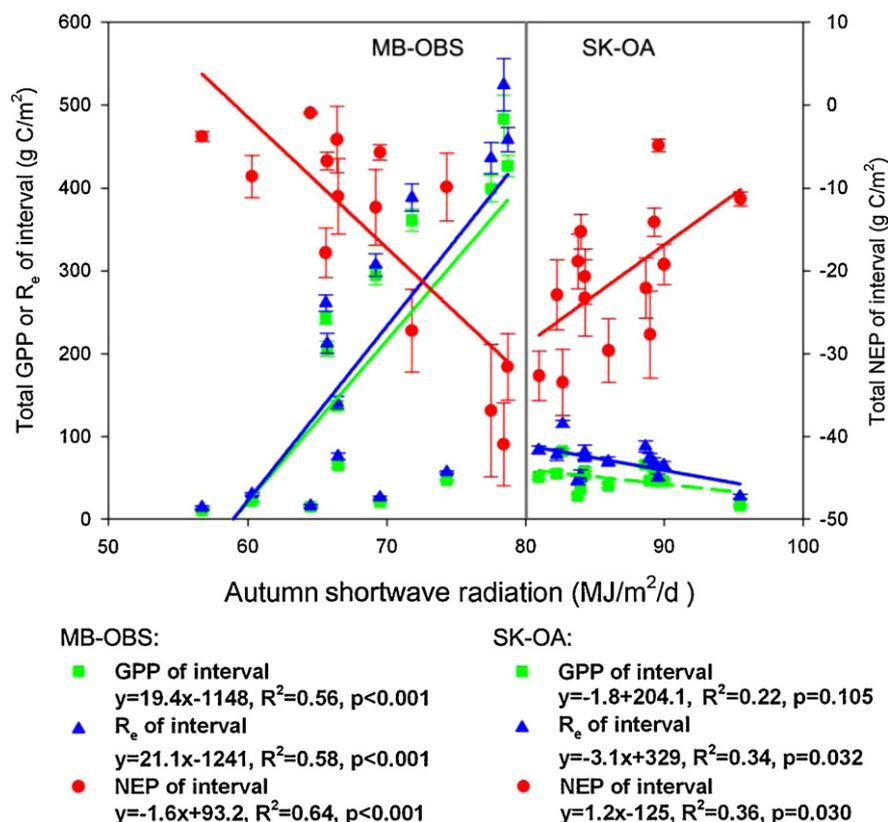


Fig. 8. Relationships between autumn radiation and gross primary production (GPP), ecosystem respiration (R_e) and net ecosystem production (NEP) during the interval period for (a) SK-OA and (b) MB-OBS site. Error bars indicate standard deviations.

additional NEP even after deciduous species would have dropped leaves, and some resilience of needleleaf photosynthetic capacity to nighttime frosts may be possible.

The autumn interval represents the period when ecosystem respiration generally exceeds photosynthesis, so we correlated autumn global shortwave radiation with NEP, GPP and R_e during this period at both sites to investigate these opposing effects of radiation on the carbon balance (Fig. 8). At SK-OA, both GPP and R_e showed clear negative correlations with autumn R_g (though the trend for GPP was barely significant ($p = 0.105$), shown by the dashed line). Conversely, at MB-OBS, both GPP and R_e showed significant positive correlations with R_g , but with generally higher values at lower radiation levels than at SK-OA (compare left and right panels of Fig. 8). At SK-OA, NEP is always negative, but the highest radiation years have the least negative values. We suggest the reason for this is that in these years, the first few days of autumn are relatively clear and both R_e and GPP during the interval are very low (compared to MB-OBS). At MB-OBS, however, the explanation for lower (more negative) NEP in high radiation years is simply that the days are clearer and warmer on average, and the response of R_e to higher temperatures is slightly greater than the response of GPP to higher radiation. Hence NEP is least negative in the years with

lowest radiation. The autumn days in such years will generally be cloudy or overcast, so daily minimum temperature would tend to be relatively warm (i.e., at night).

4. Conclusions

With extended (15-year) records of half-hourly flux observations at two sites in the Canadian boreal forest, we found that 70–80% of the observed interannual variability in annual NEP could be explained by the length of the interval between the end-dates of measured net carbon uptake and of positive GPP, which we have termed “the autumn interval”. Using this interval provided a demonstrably better estimate of annual NEP than using one or other of the same phenological transitions independently—which has been the common approach used in previous studies. To our knowledge, this is the first report on the combined effects of photosynthesis and carbon uptake end-dates on annual forest carbon sequestration. Our results show that interannual variability of NEP is affected by different responses to phenological changes, which vary among plant functional types, and may also be site-dependent. Further, our results demonstrate that autumn phenology, in particular the autumn interval, may be a strong predictor of interannual

variability in NEP, in contrast to many studies in other regions that have shown greater dependence of NEP on spring phenology. These relationships will vary in boreal forests based on functional traits. Improved ecosystem modeling for predicting responses of forest carbon budgets to climate change in boreal regions will require consideration of temperature (including occurrence of frost events), radiation, and soil moisture impacts, on autumn phenology.

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