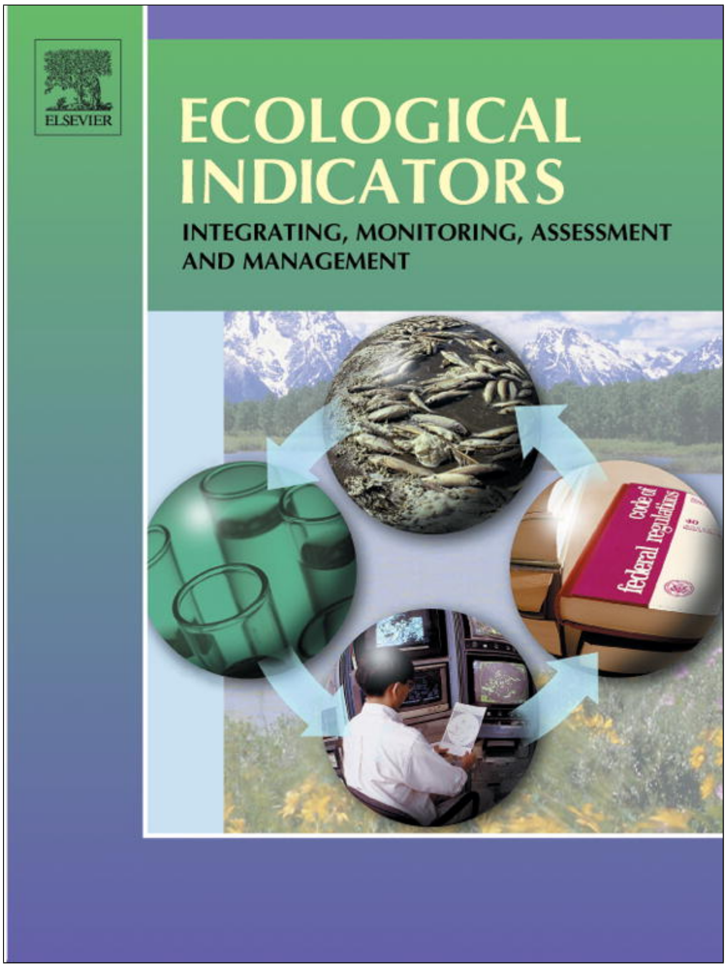

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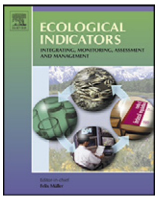

Case Study

Deriving a new phenological indicator of interannual net carbon exchange in contrasting boreal deciduous and evergreen forests

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ABSTRACT

Phenology is an important variable affecting the annual net ecosystem production (NEP) of terrestrial ecosystems. A new phenological indicator was proposed based on the ratio of respiration season length and growing season length (respiration–growth length ratio, RGR). Validation of this new phenological indicator was conducted using continuous flux measurements at contrasting boreal deciduous and evergreen forests in Canada. Analyses based on yearly anomalies of both annual NEP and phenological indicators indicated that the RGR can explain more proportion of interannual NEP variability compared to existing phenological metrics, including the carbon uptake period and the autumn lag. A multivariate regression model was used to predict the respiration–growth length ratio anomaly using anomalies of spring air temperature, autumn radiation and soil water content (SWC), which serves as a prerequisite for this indicator being scaled up for regional applications where flux data were unavailable. By normalization growing season length, interannual NEP showed comparable sensitivity to RGR variations of different plant functional types, which is a great advantage over other phenological indicators. The high potential of RGR in explaining interannual NEP variability may highlight the importance of respiration process in controlling annual NEP, which has probably been overlooked or underestimated in existing phenological studies. The comparable sensitivity of RGR to annual NEP observed at different plant functional types would favor its application in tracking interannual variability of NEP regionally and complementary to existing indices to promote our understanding of carbon sequestration with future climate change.

1. Introduction

Net ecosystem production (NEP) presents a quantitative measure of carbon fixed by the terrestrial ecosystem after the removal of ecosystem respiration (Re) with respect to gross primary production (GPP) and is therefore of significant importance to analyze the impacts of climate changes on carbon cycling (Pan et al., 2011).

Interannual variability in annual NEP is primarily driven by climate variations and increasing evidences have shown that phenological events associated with these climate variations are closely correlated with the annual NEP (Black et al., 2000; Baldocchi, 2008; White and Nemani, 2003; Churkina et al., 2005; Morisette et al., 2009; Vitasse et al., 2009; Wang et al., 2011). Therefore, phenological indicators are derived and explored for their potentials in indicating interannual NEP variability. Traditional phenological metrics are based on the transition dates of the growing season (e.g., different physiological state of the leaves) when a strong observed shift in leaf color or by the dates of bud-break in the spring and leaf senescence in the fall (White and Nemani, 2003; Churkina et al., 2005; Chen et al., 2009). Such observation in leaf status is arbitrary and thus alternative methods turn to the use of carbon flux phenology (CFP), in which phenology transitions are derived from the transient sinks or sources of CO_2 exchange measured by the continuous eddy-covariance (EC) technique (Richardson et al., 2010; Garrity et al., 2011; Wu et al., 2012a,b).

A typical phenological indicator based on CFP technology is the carbon uptake period (CUP) proposed by White and Nemani (2003) that is defined as the length of days with positive daily NEP (positive NEP indicates net carbon uptake from atmosphere). Carbon uptake period has been shown to be positively correlated with annual NEP for several ecosystems (Baldocchi, 2008; Garrity et al., 2011) and better explains interannual NEP variability than the transitions of net carbon uptake (days when net daily carbon uptake switches between negative and positive in spring and from positive to negative in autumn) (Wu et al., 2012a). This method is particularly useful considering the large database of eddy-flux measurements since later last century (Baldocchi, 2008). Combine both growing season and carbon uptake phenology, Wu et al. (2012a) found that the time lag between the end of the growing season and the cessation of net carbon uptake in autumn, i.e., autumn lag, is a better

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indicator than carbon uptake period to explain interannual NEP variability of diverse forest ecosystems.

However, a major limitation related to most existing phenological indicators is the substantial sensitivity difference in their regressions with annual NEP across deciduous and evergreen forests (Barr et al., 2009; Piao et al., 2007; Churkina et al., 2005; Richardson et al., 2010; Wu et al., 2012a). Deciduous forests are more sensitive to interannual phenological variations than evergreen species due to their larger mean fluxes (NEP, GPP). Therefore, analysis of regional NEP patterns of forests would be impossible using these phenological indicators unless plant functional types are well separated. This also implies that new phenological indicators that can overcome this problem would be a great advantage in future application. The availability of continuous flux measurements of contrasting species from the same latitude in boreal regions of Canada provides an opportunity to develop new phenological metrics in tracking interannual variability of annual NEP. Using decadal time-series flux data at three contrasting boreal deciduous and evergreen forests, we present an analysis of proposing new phenological indicators that can be used to better explain interannual net carbon exchange variations both for individual sites and across plant functional types.

2. Materials and methods

2.1. Study sites

Three Boreal Forest Research and Monitoring Sites (BERMS) were engaged in this study, including (1) a mature aspen stand (OAS, deciduous), (2) a mature black spruce stand (OBS, evergreen) and (3) a mature jack pine stand (OJP, evergreen) (Black et al., 2000; Barr et al., 2007; Dunn et al., 2007; Gaumont-Guay et al., 2009). These sites are located in the mid-boreal lowland ecoregion in the boreal plain ecozone near Prince Albert, Saskatchewan, Canada. The climate of the region is typified by short, warm, dry summers and long, cold winters. Average mean annual rainfall and air temperature at all sites are about 467.2 mm and 0.4 °C, respectively. These sites provide an opportunity to analyze the response of interannual NEP to phenological variations of contrasting species at different sites but from a similar latitude in which the regional climate differences are excluded. Detailed descriptions of site characteristics are shown in Table 1.

2.2. Flux data

Flux and meteorological data at these two sites were obtained from Fluxnet-Canada archives (http://www.fluxnet-canada.ca). Data durations for OAS, OBS and OJP were 1997–2010, 1999–2010 and 2000–2008, respectively. Velocity components, air temperature, water vapor pressure, and CO_2 concentration were sampled for each site OAS (20 Hz), OBS (4 Hz) and OJP (20 Hz). CO_2 fluxes were calculated as the half-hourly covariances of the vertical velocity component and the CO_2 mole fraction corrected for air density effects. Net ecosystem exchange (NEE) was obtained by adding to each half-hourly CO_2 flux the associated rate of change of CO_2 storage in the air column beneath the EC sensors (Barr et al., 2004).

A standard procedure was used to obtain annual NEP from the half hourly NEE observations (i.e., NEP = −NEE). NEP was also partitioned into gross primary production (GPP) and ecosystem respiration (Re) using gap-filled half-hourly values of NEE. Empirical regressions of nighttime NEE versus shallow soil temperature and daytime GPP versus photosynthetically active radiation (PAR) were used to estimate Re and GPP, respectively, and gaps filled as described in Barr et al. (2004). First, NEE values were removed when values of the friction velocity (u_*) were less than a threshold value ($u_{*\mathrm{th}}$) (around 0.35 m s^{-1} and differs slightly among sites). Then NEP 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 Re was estimated as Re = −NEP during periods when GPP was known to be zero. Finally, GPP was estimated as NEP + Re (daytime) or as zero (nighttime and during periods when both T_a and T_s were less than 0 °C).

To expand the analysis on phenological indicators, we also calculated several site level spring (mean value from March to May) and autumn (mean value from September to November) meteorological variables, including the mean daily shortwave global radiation (R_g, MJ m^{-2} d^{-1}), air temperature (T_a, °C), soil temperature (T_s, °C), precipitation (mm) and soil water content (SWC, %).

2.3. Phenological indicators

Several phenological indicators based on carbon flux phenology were used in this analysis. The daily Re, GPP and NEP were used to calculate the phenological transitions when (a) respiration season began and ended, (b) when the growing season began and ended and (c) net daily carbon uptake switched between negative and positive in spring and from positive to negative in autumn, respectively. A negative exponential model using polynomial regression and weights computed from the Gaussian density function was adopted to derive the smoothed curves for daily carbon flux (Re, GPP and NEP) observations (Fig. 1). The start and end of both respiration and growing season was determined when daily Re or GPP reached the 10% of maximum Re or GPP in the year (Wu et al., 2012a). The respective start and end days with positive NEP was identified as the start and end of net carbon uptake, following the

Table 1
Descriptions of site characteristics for the old aspen (OAS) old black spruce (OBS) and old jack pine (OJP) sites.

Sites	Old aspen	Old black spruce	Old jack pine
Lat. & Long.	53.63 N, −106.20 W	53.99 N, −105.12 W	53.92 N, −104.69 W
Vegetation type	Deciduous broad-leaf forest	Evergreen needle-leaf forest	Evergreen needle-leaf forest
Stand age (2010)	91	131	81
Dominant species	Trembling aspen, hazelnut	Black spruce, jack pine, tamarack	Jack pine, alder, lichen
Drainage[a]	Well to moderately well	Imperfect to poor	Very well
Mineral layer	Loam to clay	Sandy clay	Fine sand
Stand density (trees ha^{-1})	980	4330	1320
Tree height (m)	20.1	7.2	12.7
DBH (cm)	20.5	7.1	12.9
LAI (m^2 m^{-2})[b]	2.1	3.8	2.6

[a] Data from Gaumont-Guay et al. (2009).

[b] Data from Chen et al. (2006).

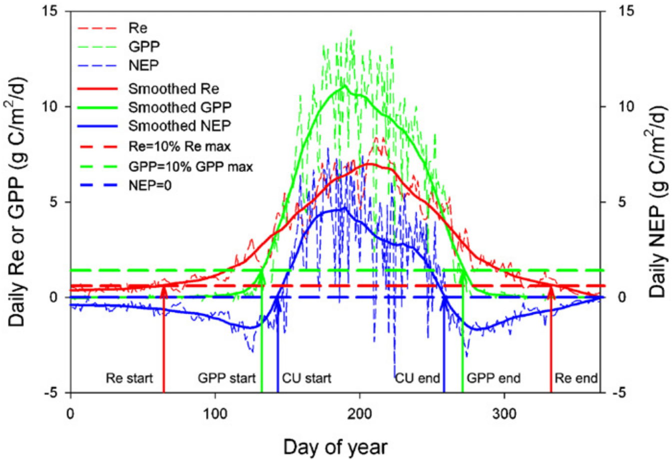

Fig. 1. Description of calculating phenological transitions using daily respiration (Re), Gross primary production (GPP) and net ecosystem production (NEP) for old aspen (OAS) in 2000. The respiration season start (Re_{start}) and end (Re_{end}) are determined by the days when smoothed daily Re reaches 10% of the annual maximum smoothed daily Re. A similar method applies to daily GPP to determine growing season start (GPP_{start}) and end (GPP_{end}). The carbon uptake start (CU_{start}) and end (CU_{end}) are determined by the first and the last days of positive daily NEP, respectively.

definition of White and Nemani (2003). With these phenological transitions from three carbon fluxes, we can determine the carbon uptake period (White and Nemani, 2003) and the autumn lag (Wu et al., 2012a):

$$\mathrm{CUP} = \mathrm{CU}_{\mathrm{end}} - \mathrm{CU}_{\mathrm{start}} \tag{1}$$

$$\text{Autumn lag} = \mathrm{GPP}_{\mathrm{end}} - \mathrm{CU}_{\mathrm{end}} \tag{2}$$

Apart from these two known indicators, we proposed a new phenological metric based on the length of respiration and growing seasons:

$$\mathrm{RGR} = \frac{Re_{\mathrm{end}} - Re_{\mathrm{start}}}{\mathrm{GPP}_{\mathrm{end}} - \mathrm{GPP}_{\mathrm{start}}} \times 100\% \tag{3}$$

where RGR represents the respiration–growth length ratio (%); ($\mathrm{Re}_{\mathrm{end}} - \mathrm{Re}_{\mathrm{start}}$) and ($\mathrm{GPP}_{\mathrm{end}} - \mathrm{GPP}_{\mathrm{start}}$) are respiration season length (RSL) and growing season length (GSL), respectively.

2.4. Statistical analyses

To analyze the relationships between interannual NEP and phenological indicators, we calculated the yearly anomalies of all variables, in which all analyses are based on transformed data to minimize temporal autocorrelation and thus allows the identification and evaluation of these correlations interannually.

$$A_i = x_i - X_{mean} \tag{4}$$

where A_i is the anomaly of one variable, x_i is the value in i year, and X_{mean} represents the mean annual value for the length of the record for each variable.

This method has been tested to be reliable in analyzing interannual variability of phenology (Richardson et al., 2010; Atkinson et al., 2011). Furthermore, our analysis made distinction between deciduous and evergreen forest sites, which reveals the effects of plant functional types on these relationships. Accordingly, the pair wise Pearson correlation coefficient (r) and p-value were used to assess these correlations.

3. Results and discussion

Before we tested the relationships between annual NEP anomaly with anomalies of various phenological indicators, temporal patterns of major carbon fluxes (NEP, GPP and Re) for each site were provided (Fig. 2). We found no significant correlation in these carbon fluxes for each site, which indicates that there was no autocorrelation in these carbon fluxes. This result also supports the assumption of independent observations of the following regression analysis.

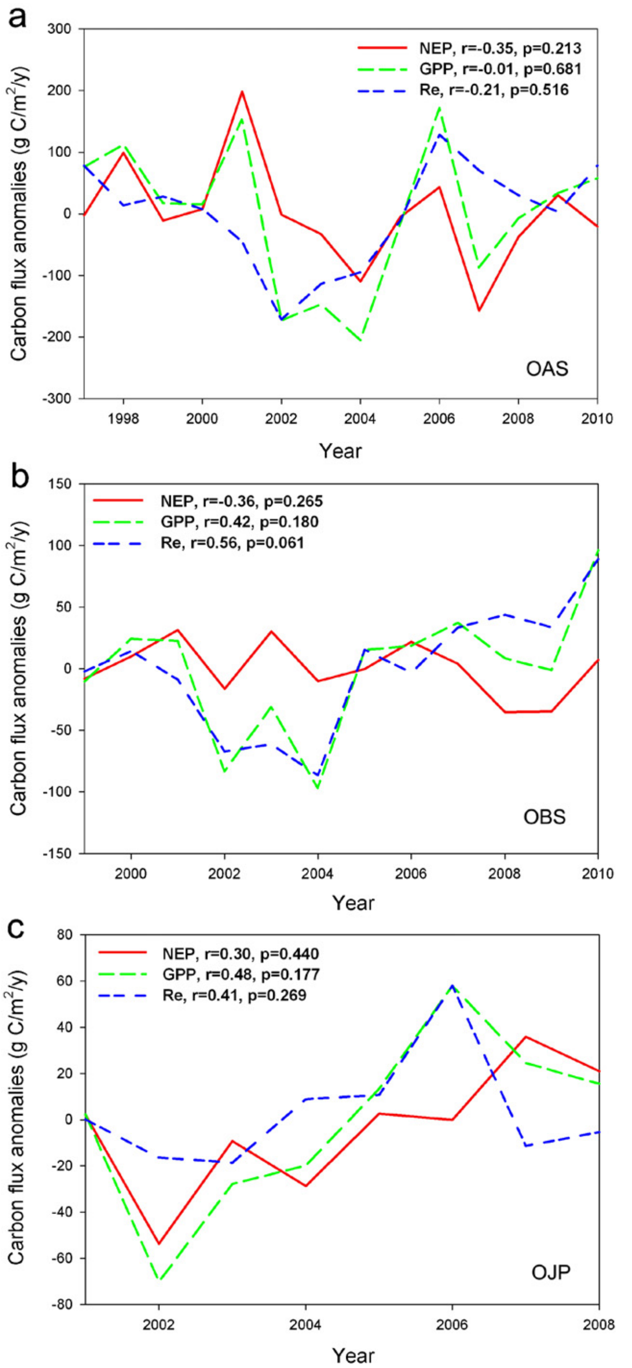

Fig. 2. Temporal patterns of carbon flux anomalies (net ecosystem production, NEP, gross primary production, GPP and ecosystem respiration, Re) at (a) old aspen (OAS), (b) old black spruce (OBS) and (c) old jack pine (OJP) sites.

We then evaluated the potential of carbon uptake period, autumn lag and RGR in explaining interannual NEP for these sites (Fig. 3). Positive relationships were found between carbon uptake period anomaly and annual NEP anomaly with Pearson correlation coefficients (r) of 0.84 ($p < 0.001$), 0.81 ($p < 0.001$) and 0.91 ($p < 0.001$) for OAS, OBS and OJP, respectively (Fig. 3a). These

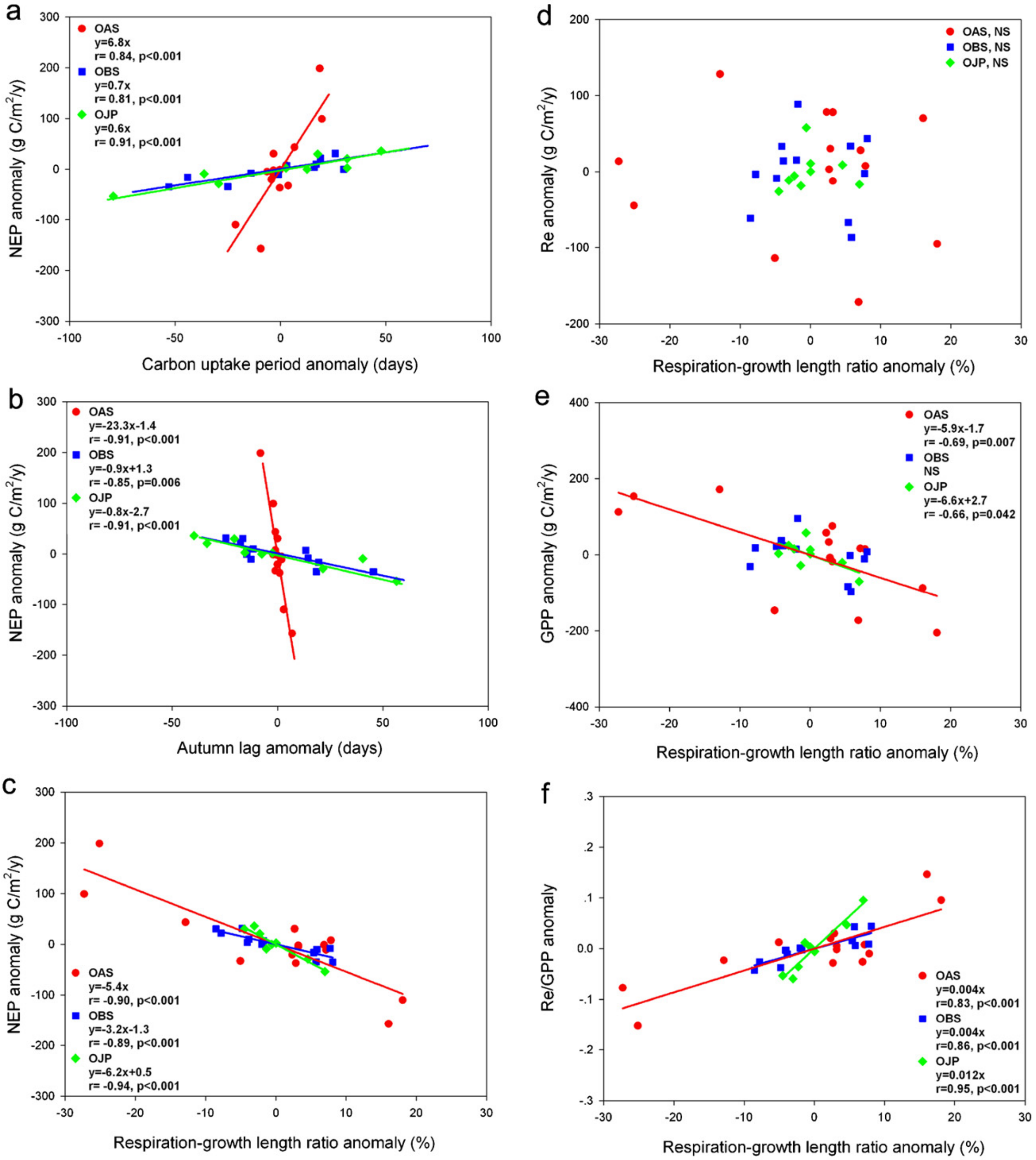

Fig. 3. Relationships between interannual net ecosystem production (NEP) anomaly and (a) carbon uptake period anomaly and (b) autumn lag anomaly and (c) respiration–growth length ratio anomaly for old aspen (OAS, ●), old black spruce (OBS, ■) and old jack pine (OJP, ◆) sites. Relationships between respiration–growth length ratio anomaly and (a) respiration anomaly (Re), (b) gross primary production (GPP) anomaly and (c) Re/GPP anomaly for old aspen (OAS, ●), old black spruce (OBS, ■) and old jack pine (OJP, ◆) sites. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

observations generally indicate that prolonged carbon uptake period would enhance annual carbon sequestration from the atmosphere of these forests sites, which agrees with previous results of both stands level (White and Nemani, 2003; Baldocchi, 2008; Dragoni et al., 2011) and regional evaluations (Wu et al., 2012a; Zhu et al., 2012). Interannual NEP anomaly was also found to be significantly correlated with autumn lag for all sites involved (Fig. 3b). Furthermore, these correlations were slightly stronger than that of the carbon uptake period as indicated by the Pearson correlation coefficients (r) of −0.91 ($p < 0.001$), −0.85 ($p = 0.006$) and −0.91 ($p < 0.001$) for OAS, OBS and OJP site, respectively.

A similar pattern of the relationships between NEP anomaly and carbon uptake period and autumn lag anomalies is that their potentials in explaining interannual NEP showed strong dependence on plant functional type. Deciduous forest (OAS) and evergreen forest (OBS and OJP) exhibited very different sensitivities in the response of annual NEP to phenological indicators. For carbon uptake period, one additional day of net carbon uptake will increase annual NEP by 6.8 g C m^{-2} for the deciduous site (OAS). In comparison, this rate decreased by almost 90% for the evergreen forests, which was illustrated by the slopes for OBS (0.7) and OJP (0.6) sites. The same pattern was also observed of autumn lag that annual NEP will decrease at a rate of 23.3 g C m^{-2} y^{-1} with the increase of autumn lag while this value was about 0.9 g C m^{-2} y^{-1} for both OBS and OJP sites. These observations imply that deciduous forests have larger interannual NEP variability than that of the evergreen sites. The reason for such difference has been discussed in previous analyses that the evergreen ecosystems may be potentially more adaptive to interannual variability in growing season with their relatively lower rates of photosynthesis continuing for longer periods. Therefore, deciduous sites may have a higher mean daily carbon fluxes (i.e. GPP, NEP) and shorter growing seasons (Churkina et al., 2005; Loustau et al., 2005; Piao et al., 2007; Richardson et al., 2010).

When using the newly developed RGR, we observed increased proportions of interannual NEP variability being explained for all sites (Fig. 3c). The Pearson correlation coefficients (r) for OAS, OBS and OJP were −0.90 ($p < 0.001$), −0.89 ($p < 0.001$) and −0.94 ($p < 0.001$), respectively, suggesting RGR is an accurate proxy of interannual NEP variability. Apart from better results observed at individual sites, the most promising point of this new phenological indicator was the comparable sensitivity to annual NEP variations. As indicated by the slopes of regressions for each site, annual NEP will decrease by 5.4 g C m^{-2}, 3.2 g C m^{-2}, and 6.2 g C m^{-2} with one percentage increase in RGR for OAS, OBS and OJP, respectively. This similar sensitivity was particularly important when RGR was used to explain interannual NEP variability for the overall dataset that a Pearson correlation coefficient (r) of 0.86 ($p < 0.001$) was acquired (slope of 5.2). However, carbon uptake period and autumn lag only presented r of 0.48 ($p = 0.003$) and 0.39 ($p = 0.024$) when they were correlated with the overall dataset. This merit of RGR suggests that it may have the high potential to be applied for carbon analysis, irrespective of differences in plant functional types that have largely constrained the applicability of traditional phenological indicators.

To understand the negative correlation between interannual anomalies between NEP and RGR, we partitioned NEP into its component fluxes, Re and GPP, to further test their responses to RGR variations. No significant correlation was found between anomalies of annual Re and RGR for individual site (Fig. 3d). On the contrary, we found annual GPP anomalies underwent significant decrease for years with higher proportions of RGR for the overall data ($r = -0.65$, $p < 0.001$). For data of single sites, both GPP anomalies decreased with increasing RGR at OAS and OJP sites, but this relationship did not exist for OBS site (Fig. 3e). If we combine both Re and GPP, very strong relationships were found between RGR and Re/GPP anomalies both for the overall dataset ($r = 0.82$, $p < 0.001$) and for data of each site (Fig. 3f), suggesting increased proportion of GPP being respired by the ecosystem for years with higher RGR and thus decreasing annual NEP. This probably is the real reason driving the negative relationship between RGR and interannual NEP variability.

Since the development of RGR was based on flux measured Re and GPP, which would be only available at flux sites and thus limiting the application of this new indicator, we then explored the correlations between anomalies of RGR and several site-level meteorological measurements, including the temperature (both air and soil temperatures), soil water content (SWC), radiation and precipitation. We only found that, for the overall dataset, RGR anomaly was significantly correlated with spring air temperature ($r = -0.42$, $p = 0.011$), autumn radiation ($r = -0.47$, $p = 0.004$) and autumn SWC ($r = 0.42$, $p = 0.010$) (data not shown for these results). Therefore, the RGR anomaly can be estimated by these variables using a multivariate regression model as,

$$\text{RGR} = -1.56 \times \text{Spring}\, T_a - 0.42 \times \text{Autumn}\, R_g + 0.41 \times \text{Autumn SWC} \quad (5)$$

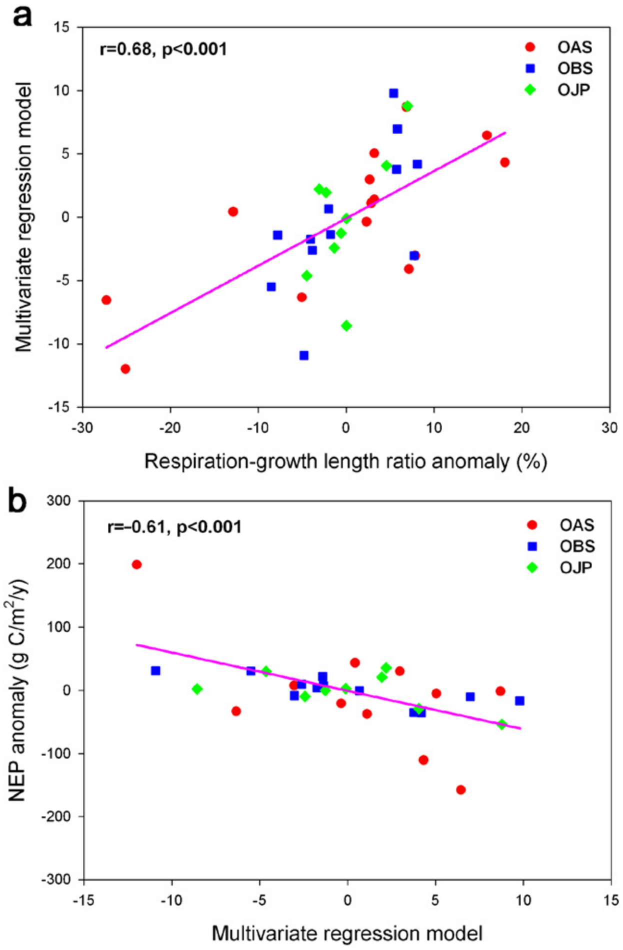

Fig. 4. Relationships between the multivariate regression model based on site-level meteorological variables and (a) respiration–growth length ratio anomaly and (b) net ecosystem production (NEP) anomaly for old aspen (OAS, ●), old black spruce (OBS, ■) and old jack pine (OJP, ◆) sites. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

This multivariate regression model was found to be significantly correlated with annual RGR anomaly with r of 0.68 ($p < 0.001$) for the overall dataset (Fig. 4a). Therefore, this simple regression algorithm using site-level meteorological variables was also shown to be useful in predicting annual NEP anomaly for the overall dataset with r of −0.61 ($p < 0.001$) (Fig. 4b).

A new phenological indicator has been developed for investigating interannual NEP variability for both deciduous and evergreen forests. Unlike previous studies that use the absolute values of phenological events, the RGR is proposed based on the proportion of respiration season length and growing season length. There are several new advantages associated with this method. First, the respiration process is incorporated in this definition, and such a procedure has not been evaluated before. Combine both respiration and growth season length, this metric has shown promising results in tracking interannual NEP variability. Therefore, our analysis may support the claim that respiration processes play important roles in controlling interannual variability in NEP (Valentini et al., 2000; Reichstein et al., 2003) and this characteristic has been overlooked in deriving phenological indicators previously. In particular, we expect that a more elegant partition of respiration into heterotrophic and autotrophic respirations would be very helpful to analyze the fundamental mechanisms that explain the importance of respiration processes since it is the basis on which NEP may change with warming (Allen et al., 2005; Yvon-Durocher et al., 2010). Second, unlike autumn lag that uses both GPP and NEP phenology, RGR turns to respiration and photosynthesis phenology, considering that NEP and GPP are unlikely to be independent because NEP = GPP − Re. Therefore, the two terms that are used to calculate autumn lag, i.e., GPP and NEP, may not be entirely independent. On the contrary, RGR would relate directly to two independent processes (i.e., Re and GPP) that combine to the dynamics of NEP. Finally, the RGR is derived through normalization of the growing season length, which is the reason for the observed comparable sensitivity between RGR and annual NEP, irrespective of differences of plant functional types. Deciduous forests have higher mean fluxes (i.e., GPP, NEP, Re) and shorter growing seasons while evergreen forests exhibit the opposite with lower amplitude in carbon fluxes and longer growing season. Therefore, any absolute measures of phenological events (e.g., carbon uptake period, autumn lag) would show very different sensitivity between deciduous and evergreen forests. However, by normalization to the growing season length, the differences associated with mean flux amplitude and growing season length can be greatly reduced, supporting the potential of RGR in explaining interannual NEP across diverse plant functional types and a useful complementary candidate to existing indices. This normalization is consistent with the suggestion that it is not always possible to derive absolute theoretical predictions, but only 'relative' theoretical prediction may be useful in operational applications (Yvon-Durocher et al., 2010). Our hypothesis is also supported by several existing literatures which suggest that the best way to understand the role of phenology in regulating carbon sequestration is through partitioning of NEP into its component fluxes, rather than investigating net carbon exchange (Richardson et al., 2010; Piao et al., 2008).

4. Conclusions

Using continuous flux measurements at three boreal deciduous and evergreen forest sites, we proposed a new phenological indicator of interannual carbon exchange. Results indicate that by combination respiration and growth phenology, the RGR was strongly correlated with annual NEP, better than traditional phenological metrics. The underling mechanism for the observed correlation is the increased proportion of Re/GPP for years with higher RGR. We also used site-level meteorological variables to explain the annual anomaly of RGR. The multivariate regression model using spring air temperature, autumn radiation and SWC indicates that the RGR anomaly can be potentially predicted from meteorological variables, which serves as an important step of RGR being scaled up for regional applications where flux data were unavailable. The potential of this phenological indicator may highlight the importance of respiration process in regulating annual NEP, which is probably overlooked. The most meaningful aspect of RGR is the comparable sensitivity to annual NEP variations across plant functional types, suggesting its potential use in regional applications and complementary to existing indices. One issue needs to be considered is that the RGR is based on calculated GPP and Re, neither of which are direct measurements from flux observations and the assumes that Re is the same during daylight and night time. Further analysis of this new indicator in different ecosystems with different climates is needed, which in turn would shed lights on the interannual carbon sequestration in the context of future climate change.

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