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American Geophysical Union

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Phenology and its role in carbon dioxide exchange processes in northern peatlands

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Abstract Ecosystem phenology plays an important role in carbon exchange processes and can be derived from continuous records of carbon dioxide (CO2) exchange data. In this study we examined the potential use of phenological indices for characterizing cumulative annual CO2 exchange in four contrasting northern peatland ecosystems. We used the approach of Jonsson and Eklundh (2004) to derive a set of phenological indices based on the daily time series of gross primary production (GPP), ecosystem respiration (Re), and net ecosystem production (NEP) measured in the four peatland sites. The main objectives of this study were (a) to examine the variation in phenological indices across sites and (b) to determine the relationships among phenological indices, environmental conditions, and cumulative annual CO2 exchange. The phenological index used to define the “start of the growing season” showed good potential for differentiation among sites based on their average annual site GPP. Sites with earlier growing seasons had the highest average annual site GPP. The “peak CO2 exchange rate” phenological index performed best in reflecting variations among sites and for estimating annual values of GPP, Re, and NEP (Pearson correlation coefficients ranged between 0.77 and 0.99, p < 0.05 for all). The phenological indices and annual GPP, Re, and NEP were sensitive to winter (January–March) and summer (July–September) temperature and precipitation, but correlations, though significant, were weak.

1. Introduction

Northern peatlands cover between 3 and 4% of the terrestrial landscape and contain between 250 and 700 Pg carbon (C) [e.g., Tamocai et al., 2002; Yu et al., 2010]. They act as small persistent sinks for carbon dioxide (CO2) and are sources of atmospheric methane [e.g., Frolking et al., 2011]. Peatlands are potentially sensitive to climate change and variability [Moore et al., 1998] because of the tight coupling between ecosystem structure, function, and their wetness [Eppinga et al., 2009]. Since peatlands have C stores an order of magnitude greater than most other ecosystems, even relatively small changes in the net ecosystem production (NEP) could have global significance. There are few measurements of NEP for these ecosystems and few ecosystem models appropriate to simulate their C dynamics, in comparison with many other ecosystem types that store much less C. Most northern peatlands are relatively inaccessible so it is critical to improve models or to develop alternative C monitoring methods. Remote sensing approaches, for example, provide information about vegetation greenness and phenology which relate to patterns of CO2 exchange.

Recent studies have shown the importance of phenology for ecosystem CO2 exchange in forests [e.g., Churkina et al., 2005; Richardson et al., 2013; Wu et al., 2012a, 2013] and wetlands [e.g., Lund et al., 2009]. Longer growing seasons have been shown to be associated with increased gross primary production (GPP) and increased NEP [e.g., Aurela et al., 2004; Churkina et al., 2005; Richardson et al., 2010]. Yet an increase in ecosystem respiration (Re) can offset the increase in GPP, resulting in insignificant changes in NEP [e.g., Moore et al., 2006], or alternatively, increases in Re may exceed increases in GPP resulting in a net C loss to the atmosphere [e.g., Piao et al., 2008; Sacks et al., 2007]. Aurela et al. [2004] suggest that warming may increase the length of the growing season and consequently increase the C store of subarctic peatlands, but Moore et al. [2006] suggest that warmer springs will not have a strong impact on the annual C budget for temperate and boreal bogs, as earlier springs may not necessarily result in an increased use of solar radiation. Lund et al. [2009] examined patterns of NEP, GPP, and Re derived...
from eddy covariance (EC) measurements across 12 peatland and tundra sites and developed seasonal correlations with environmental variables such as climate and vegetation characteristics. They reported significant correlations between the start and length of the growing season and the summer GPP and RE across sites.

Previous phenology-C studies have mainly investigated the role of the length of the growing season or C uptake period and their transition dates (e.g., start and end of the growing season or C uptake period) on GPP. But continuous CO2 exchange data allow the extraction of a set of phenological indices that are related to the rates of plant growth (reflected by rates of photosynthesis, respiration, and net ecosystem production) in addition to the timing and duration of plant growth phases. Gu et al. (2003) proposed an approach for analyzing ecosystem phenology using the changes in GPP and CO2 exchange data from four forest sites and one grassland site, they estimated the daily maximum photosynthesis rate and developed phenological indices, such as the start, end and length of the growing season, and recovery and senescence rates of the CO2 exchange (definition of these terms are in Table 1). Jonsson and Eklundh (2004) proposed a similar method for the analysis of ecosystem phenology derived from satellite sensor vegetation index (VI) time series; they also evaluated their method with EC flux data and soil moisture data. The advantage of these approaches is that they allow for the characterization of the seasonal CO2 exchange dynamics through a variety of time-related (e.g., peak photosynthesis dates) and rate-related (e.g., peak photosynthesis rates) phenological indices. The variability of the indices across sites and years can provide information about the ecosystem plant community characteristics and its response to environmental conditions. Both studies focused mainly on the methodology of extraction of the phenological indices.

In this study, we examine the potential use of phenological indices for estimating cumulative annual CO2 exchange at northern peatlands. We used the approach of Jonsson and Eklundh (2004) to derive a set of phenological indices from the times series of GPP, RE, and NEP. We measured CO2 exchange at four northern peatlands located at different climatic settings and that reported significant correlations between the start and length of the growing season and the summer GPP and RE across 12 peatland and tundra sites and developed seasonal correlations with environmental variables such as climate and vegetation characteristics such as climate and vegetation characteristics. The variability of the indices across sites and years can provide information about the ecosystem plant community characteristics and its response to environmental conditions. Both studies focused mainly on the methodology of extraction of the phenological indices.

Table 1. Summary of the Different Phenological Indices Derived From the NEP, RE, and GPP Time Series

<table>
<thead>
<tr>
<th>Classification</th>
<th>Phenological Indices</th>
<th>Phenological Interpretation</th>
<th>NEP</th>
<th>RE</th>
<th>GPP</th>
</tr>
</thead>
<tbody>
<tr>
<td>Duration of phenological phases</td>
<td>Length of the growing season</td>
<td>Duration of photosynthetic activity</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td></td>
<td>C uptake period</td>
<td>Duration of net C uptake</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td></td>
<td>Summer lag</td>
<td>Lag between the start of the growing season and the start of the C uptake period</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Autumn lag</td>
<td>Lag between the end of the growing season and the end of the C uptake period</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Timing of phenological transitions</td>
<td>Start of the growing season</td>
<td>Start of measurable photosynthesis</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>End of the growing season</td>
<td>Start of measurable photosynthesis</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Start C uptake period</td>
<td>Start of net C uptake, switch from C source to C sink</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>End C uptake period</td>
<td>Start of net C uptake, switch from C sink to C source</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Date of annual peak CO2 exchange rate (peak date)</td>
<td>Timing of the maximum measurable CO2 exchange (center of the maturity phase)</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>CO2 exchange rates at phenological transitions and phases</td>
<td>Annual peak CO2 exchange rate (peak rate)</td>
<td>Maximum measurable level of CO2 exchange (at the center of the maturity phase)</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td></td>
<td>CO2 exchange recovery rate (recovery rate)</td>
<td>Level of CO2 exchange during the recovery (i.e., green-up) period</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td></td>
<td>CO2 exchange senescence rate (senescence rate)</td>
<td>Level of CO2 exchange during the senescence period</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
</tbody>
</table>

Phenological phases, transitions, and indices are synthesized from literature [Reed et al., 1994; Zhang et al., 2003; Gu et al., 2003; Jonsson and Eklundh, 2004]. These columns (NEP, RE, and GPP) show which indices where extracted from which data sets.
have different vegetation characteristics. The main objectives of this study were (a) to examine the variation in phenological indices across sites and (b) to examine the relationships between phenological indices, temperature and precipitation, and cumulative CO₂ exchange. The intended goal of this analysis is to improve our understanding of the role of phenology in ecosystem CO₂ exchange processes in peatlands.

2. Sites

The peatland sites used in this study include an open bog (Mer Bleue, MB), a continental moderately rich treed fen (Labiche, LB), an open, moderately rich fen (Sandhill fen, SH), and a subarctic poor fen (Kaamanen, KM). MB, LB, and SH were part of the Canadian Carbon Program (http://www.fluxnet-canada.ca) while KM was part of the CarboEurope network (http://gaia.agraria.unitus.it/newtcdc2/GHG-Europe_home/Sites.aspx). Characteristics of these four sites are provided in Table 2. All sites were equipped with an EC flux tower providing continuous measurements of net ecosystem exchange of CO₂ (NEE), which were partitioned into \( R_e \) and GPP by the site investigators (MB: Lefleur et al. [2003] and Roulet et al. [2007], LB: Flanagan and Syed [2011], SH: Sonnentag et al. [2010], and KM: Aurela et al. [2004]). In this study we used gap-filled GPP, \( R_e \), and NEP (\( \sim \) NEE), with a positive sign convention for all three measures. Positive values of NEP indicate uptake of CO₂ by the ecosystem. Both component fluxes of NEP were considered to be positive, for \( R_e \) positive values mean release of CO₂ to the atmosphere and for GPP positive values mean uptake of CO₂ from the atmosphere (i.e., \( \text{NEP} = \text{GPP} - R_e \)).

3. Methods

3.1. Phenological Indices

The methods of Jönsson and Eklundh [2004] and Gu et al. [2009] provide very similar phenological indices. Our decision to work with the method of Jönsson and Eklundh [2004] was mainly motivated by our previous experience with different phenology algorithms [Kross, 2005] and results from other studies [e.g., Studer et al., 2007; White et al., 2009] that show a more robust performance of the threshold-based methods than the local maximum or minimum (or maximum increase/decrease or maximum slope)-based methods for the estimation of ground phenological indices (using both satellite data and ground measurements). The approach used by Gu et al. [2009] is appealing because the local minimum and maximum reflect meaningful plant growth rates, but they are also sensitive to snow cover and may indicate snowmelt rather than green up in some cases [Studer et al., 2007], which is an issue with high-latitude peatlands.

We derived a set of phenological indices (Table 1 and Figure 1; see Jönsson and Eklundh [2004] for details) from daily GPP, \( R_e \), and NEP using the TIMESAT software package [Jönsson and Eklundh, 2004], including start of the growing season, end of the growing season, length of the growing season, annual peak CO₂ exchange rates, date of the peak CO₂ exchange rates, green-up or recovery rates, and senescence rates (Figure 1). Senescence rates are negative values, but for clearer comparisons and interpretation of results we used positive values throughout the text, figures, and analyses. The values of the start and end of the growing season were determined as the dates where daily GPP exceeded 5% of the seasonal amplitude (i.e., the difference between the curve minimum and maximum values). Hird and McDermid [2009] evaluated several smoothing methods for the estimation of the start of the growing season from simulated normalized difference vegetation index (NDVI) time series and reported the superior performance of the asymmetric Gaussian smoothing method of TIMESAT. This algorithm was used in our study. The 5% threshold has been used for the estimation of the start of the growing season based on climatological data and observations of the NEE in previous studies on wetlands [e.g., Aurela et al., 2004; Lund et al., 2009].

We also determined the C uptake period from the NEP time series (Table 1). The start of the C uptake period was defined as the day on which the daily smoothed NEP switched from negative to positive; the end of the C uptake period was defined as the day on which the smoothed NEP became negative again. The length of the C uptake period was calculated as the difference between the start and the end of the C uptake period. The spring lag was calculated as the difference between the start of the C uptake period and the start of the growing season; the autumn lag was calculated at the difference between the end of the growing season and the end of the C uptake period.
## Table 2. Study Site Characteristics

<table>
<thead>
<tr>
<th>Site Name</th>
<th>Lat. (°N)</th>
<th>Long. (°W)</th>
<th>Peatland Classification</th>
<th>Climate</th>
<th>pH</th>
<th>Mean Annual Temperature (°C)</th>
<th>Mean Annual Precipitation (mm)</th>
<th>Elevation Above Sea Level (m)</th>
<th>Years Used in the Analyses</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eastern peatland (Mer Bleue = MB)</td>
<td>45.41</td>
<td>75.52</td>
<td>Low-shrub ombrotrophic bog</td>
<td>TE/ER/KG</td>
<td>3.9–5.2</td>
<td>6.0 (6.7)</td>
<td>594 (942)</td>
<td>70</td>
<td>1998–2007</td>
<td>Chamaedaphne calyculata, Ledum groenlandicum, Kalmia augustifolium, Vaccinium myrtilloides, Sphagnum spp.</td>
</tr>
<tr>
<td>Western peatland (La Biche = LB)</td>
<td>54.95</td>
<td>112.47</td>
<td>Moderately rich treed fen</td>
<td>BP/SH/LB/Dfc</td>
<td>2.1 (2.5)</td>
<td>2.1 (2.5)</td>
<td>594 (378)</td>
<td>577</td>
<td>2003–2009</td>
<td>Picea mariana, Larix laricina, Betula pumila, Sphagnum spp.</td>
</tr>
<tr>
<td>Sandhill fen (SH)</td>
<td>53.80</td>
<td>104.62</td>
<td>Open moderately rich fen</td>
<td>BP/SH/M-LB/Dfc</td>
<td>0.4 (1.8)</td>
<td>0.4 (1.8)</td>
<td>467 (518)</td>
<td>486</td>
<td>2003–2006</td>
<td>Carex spp, Sphagnum spp</td>
</tr>
<tr>
<td>Kaamanen (KM)</td>
<td>69.14</td>
<td>27.30</td>
<td>Subarctic poor fen</td>
<td>BP/SH/C0</td>
<td>−1.3 (0.2)</td>
<td>−1.3 (0.2)</td>
<td>395 (398)</td>
<td>395</td>
<td>2000–2005</td>
<td>Betula nana, Ledum palustre, Sphagnum spp, forbs</td>
</tr>
</tbody>
</table>

**TE = Terrestrial ecozones Canada; ER = Ecoclimatic region Canada; KG = Koppen-Geiger.**

**a** Climate normals from the nearest Environment Canada weather station and from literature: Ottawa Macdonald-Cartier international airport, ON (MB), Athabasca, AB (LB), Waskesiu lake, SK (SH), and Aurela et al. [2004] (KM).

**b** All sites have a ground cover of Sphagnum mosses and other mosses.

**c** Tree LAI 0.39 + Sedge/Shrub LAI 1.57.
3.2. Analysis

To characterize the relationships between annual phenological indices, annual CO$_2$ exchange, and annual temperature and precipitation, we correlated all indices with annual cumulative GPP ($\text{cumGPP}$), annual cumulative $R_e$ ($\text{cumR}_e$), and annual cumulative NEP ($\text{cumNEP}$) and with monthly, seasonally, and annually averaged temperature and monthly, seasonally, and annually accumulated precipitation. We used the mean annual air temperature (MAT), annual total precipitation (TP), mean monthly temperatures (e.g., $\text{MT01}$ for mean temperature January) and total monthly precipitation (e.g., $\text{TP01}$ for January), seasonal temperature (means: e.g., $\text{MT0103}$ = January–March), and seasonal precipitation (totals: e.g., $\text{TP0406}$ = April–June). To represent seasons the year was divided into winter (January–March), spring (April–June), summer (July–September), and fall (October–December). Temperature and precipitation data were obtained from the nearest weather stations (Environment Canada stations for the Canadian sites; site station for KM). We used the Pearson correlation coefficient ($r$) to quantify the relationships between annual phenological indices, annual CO$_2$ exchange rates, and temperature and precipitation across site years. Because of the small number of site years, we used bootstrapped correlations to determine 95% confidence intervals for the correlation coefficients (confidence intervals that contained zero were not significant). To enable the evaluation of correlations across site years, we used annual anomalies of all variables calculated as the difference between the observed annual value and the observed value of the variable from a “pseudo-normal” year [e.g., Richardson et al., 2010]. The pseudo-normal year was defined as the year with the smallest difference in temperature and precipitation from long-term normal temperature and precipitation at each site. For MB, LB, SH, and KM the pseudo-normal years were respectively 2004, 2009, 2003, and 2005.

We assessed the potential of phenological indices for monitoring CO$_2$ exchange using stepwise regressions to quantify the relationships between absolute values of annual phenological indices and absolute values of $\text{cumGPP}$, $\text{cumR}_e$, and $\text{cumNEP}$ across site years. For comparison of the phenological indices across peatlands we used summary statistics of the absolute values (i.e., not anomalies) of $\text{cumGPP}$, $\text{cumR}_e$, and $\text{cumNEP}$ for each site (site $\text{cumGPP}$, site $\text{cumR}_e$, and site $\text{cumNEP}$, respectively) and summary statistics of absolute values of all phenological indices. We also used $r$ (from bootstrapped correlations) to explore the relationships between phenology and CO$_2$ exchange among sites. All analyses were conducted using PASW Statistics 18, release version 18.0 (SPSS Inc. 2009, Chicago, IL).

4. Results and Discussion

4.1. Spatial Patterns in Phenology and CO$_2$ Exchange

There was a wide range in the start, end, and length of the growing season, as well as in the start, end, and duration of the C uptake period across the sites (Figures 2 and 3c). Within sites, the range of variation among years was smaller than the range of variation among sites with exception of the end of the C uptake period at SH and the end of the growing season at KM (Figures 2 and 3c). At MB and LB, the growing season and C uptake started about 1 month earlier than at SH and KM, and the C uptake period lasted 5–6 months. At SH
and KM, the C uptake period lasted 3–4 months (Figure 3c). C uptake started, on average, between 15 days (± standard deviation (SD); ±6 days) and 23 days (±12 days) after the start of the growing season and ended between 22 days (±15 days) and 63 days (±14 days) before the end of the growing season.

In spite of the wide range in the timing of the start and end of both the growing season and C uptake periods, all the sites reached their peak NEP (mean day of year (DOY) ± SD: DOY 192 ± 5 days), peak GPP (DOY 197 ± 4), and peak $R_e$ (DOY 204 ± 7) around mid-July (Figure 3d), coinciding with the peak of the temperature (Figure 4) and 3 to 4 weeks after the annual peak of photosynthetically active radiation (data not shown). NEP was the first to peak, followed by GPP then $R_e$ (Figure 3d). Gu et al. [2003] showed similar patterns for four forest sites and one grassland site, located in Finland, Canada, and USA (between 36 and 62°N). In their study, the peak GPP rate occurred between DOY 197 (grassland) and DOY 211, with a wide range in the start and end of the growing season and latitude.

Unlike previous findings [e.g., Lund et al., 2009], we found no significant correlations between the average start and length of the growing season and the average CO$_2$ exchange among the sites. The start of the growing season correlated best with average site cumGPP ($r = -0.90$, $p < 0.1$, $n = 4$). A larger and wider distributed data set would be needed to verify these spatial relationships.

Figure 2. (a) Measured and (b) smoothed time series of NEP, $R_e$, and GPP. For Figure 2a, black dots = KM, black crosses = LB, grey dots = MB, and white dots = SH. Each dot represents the average CO$_2$ exchange for a specific day of year (across all available years per site). For Figure 2b, solid black line = KM, black dash line = LB, solid grey line = MB, and grey dash line = SH.
Across the four sites, annual site CO₂ exchange varied considerably (mean annual flux ± mean standard deviation: GPP 278 ± 31 to 875 ± 101 g C m⁻² yr⁻¹; Re: 252 ± 30 to 679 ± 102 g C m⁻² yr⁻¹; and NEP: 35 ± 19 to 198 ± 45 g C m⁻² yr⁻¹) with LB having the largest and KM the smallest exchange for GPP, Re, and NEP (Figure 3a). This pattern reflected the variations in average site leaf area index (LAI, Table 2) and is consistent with previous findings that showed the importance of vegetation characteristics, such as biomass and LAI for midsummer CO₂ exchange [Humphreys et al., 2006], and geographic location, LAI, and pH for annual NEP [Lund et al., 2009]. Comparing 12 peatland and tundra sites, Lund et al. [2009] reported highest GPP and largest annual CO₂ sink strength for two low-latitude sites with the highest LAI and pH. Leaf area determines the light absorption capacity at an ecosystem scale. Higher LAI allows for higher absorption and thus greater photosynthetic CO₂ uptake. While pH does not directly affect photosynthesis, it gives an indication of conditions (e.g., nutrient status) that can lead to high LAI and productivity [Lund et al., 2009].

Figure 3. Summary statistics of the annual CO₂ exchange and phenological indices at the four peatlands. Sites sequences on the X axes and Y axes follow mean annual temperature with the highest being left (x axis) or bottom (y axis): (a) the annual total NEP, Re, and GPP; (b) the annual peak NEP, Re, and GPP; (c) the start of the growing season (SOS); the end of the growing season (EOS); the start of the C uptake period (SCUP) and the end of the C uptake period (ECUP); (d) the date of the peak NEP, Re, and GPP; (e) the NEP, Re, and GPP recovery rates (recovery rates are negative values but are shown as positive values in this figure), and (f) the NEP, Re, and GPP senescence rates. The dots represent the annual average for each site, and the error bars represent 1 standard deviation.
CO₂ exchange recovery and senescence rates showed variable patterns among sites. At MB and LB, the GPP recovery and senescence rates at MB were almost twice that of the corresponding rates at MB, and the vegetation at LB reached a higher peak GPP than the vegetation at MB (Figures 3e and 3f). At MB and LB, the average recovery rates were similar to the average senescence rates. SH and KM had similar start of growing season dates, but they were lagged compared with LB and MB. SH had the greatest GPP recovery rate of all sites and was the first to reach its peak GPP (Figures 3e and 3f). Both KM and SH displayed a certain amount of asymmetry in GPP and NEP with senescence rates about 60–70% of their corresponding recovery rates.

The highest GPP recovery and senescence rates were observed for SH and LB, followed by KM and MB (Figure 3e), reflecting the variation in LAI and pH values of the sites (Table 2). SH and LB have near-neutral pH values, while KM and MB are more acidic. Gu et al. [2009] suggest that GPP recovery rates reflect the efficiency of the vegetation to initiate photosynthesis in response to favorable environmental conditions. GPP senescence rates reflect the efficiency of the vegetation to maintain or transfer resources before leaf fall in response to unfavorable environmental conditions. The variability of the average Rₑ recovery and senescence rates was small across all sites (Figures 3e and 3f), ranging between 0.03 and 0.04 g C m⁻² d⁻². These findings suggest that the variability of the average NEP recovery and senescence rates depended more on the corresponding GPP rates than on the corresponding Rₑ rates. We also found a strong positive correlation between GPP senescence rates and cumNEP (r = 0.98, p < 0.05, n = 4).

Future studies should evaluate the role of the GPP recovery rate in relation to LAI, pH, plant nitrogen, Rubisco, and chlorophyll content [e.g., Yasumura et al., 2006] and the role of the GPP senescence rate in relation to leaf senescence mechanisms. Leaf senescence involves a series of events related to cellular disassembly in the leaf and the mobilization of materials released during this process, including nutrient resorption, which transfers nutrients from senescing leaves to storage organs or other tissues [Aerts, 1996]. In spring, remobilization of the directly available nutrients (from storage organs versus indirect nutrients from soil) can lead to competitive early regrowth of foliage [Bausenwein et al., 2001a, 2001b]. All study sites included coverage of Sphagnum vegetation. LB and SH, the sites with the highest GPP recovery and senescence rates, had conifer trees (LB) and graminoids (SH) as dominant vegetation species. MB and KM were mainly dominated by evergreen shrubs, which have relatively lower nutrient resorption. Studies should further explore the role of nutrient resorption and dominant PFTs on GPP recovery and senescence rates.

4.2. Relationships Between Annual Phenology, CO₂ Exchange Rates, and Temperature and Precipitation

4.2.1. Relationships Between Phenology and CO₂ Exchange

C uptake is sensitive to both spring (e.g., bud burst, leaf unfolding, and start of the growing season [Hänninen, 1995; Linderholm, 2006; Richardson et al., 2010; Walther et al., 2002]) and autumn events (e.g., leaf senescence, senescence rates re...
leaf fall, end of the growing season [Piao et al., 2008; Wu et al., 2013], and to the length of the growing season and C uptake period [e.g., Aurela et al., 2004; Churkina et al., 2005; Richardson et al., 2009]). While the length of the growing season and its transitions reflect photosynthetic activity, the length of the C uptake period and its transitions reflect both respiration and photosynthetic activity. At our study sites, longer growing seasons were not associated with an earlier start of the season but with a later end of the season (data not shown). An earlier onset of the season and longer growing seasons were not associated with a longer C

Figure 5. Scatterplots of anomalies in annual phenological indices and anomalies in $\text{cum}_\text{GPP}$, $\text{cum}_\text{R_e}$, and $\text{cum}_\text{NEP}$. Scatterplots, based on all 21 site years, are for the following: (a) anomalies in $\text{cum}_\text{GPP}$ or $\text{cum}_\text{NEP}$ and LGS, (b) anomalies in $\text{cum}_\text{NEP}$ and the C uptake period (CUP), (c) anomalies in $\text{cum}_\text{NEP}$ and autumn lag, (d) anomalies in $\text{cum}_\text{GPP}$ and peak GPP rates, (e) anomalies in $\text{cum}_\text{NEP}$ and peak NEP rates, and (f) anomalies in $\text{cum}_\text{R_e}$ and peak $\text{R_e}$ rates. Black dots = MB; grey dots = KM; dark grey inverted triangles = LB; light grey triangles = SH.
upfront period nor an increased $\text{cumGPP}$ or $\text{cumNEP}$. There were strong correlations between anomalies in the start and end of C uptake, and anomalies in the C uptake period, and between anomalies in the start, end, and length of the C uptake period and the autumn lag, and anomalies in $\text{cumNEP}$ (Figure 5 and Table 3). Wu et al. [2012a, 2012b, 2013] found similar significant correlations between the timing of the start and end of both the growing season and the C uptake period, the autumn lag, and annual NEP at deciduous and evergreen forest sites and suggested the autumn lag as the most promising predictor of annual NEP. The autumn lag, the time between the end of the C uptake period and the end of the growing season, reflects the balance between photosynthesis and respiration toward the end of the growing season. Shorter days, lower radiation, and cooler temperatures contribute to the decrease of photosynthesis rates during late summer [Coursolle et al., 2006; Frolking et al., 2009]. The autumn lag thus gives an indication of the time an ecosystem takes to initiate leaf fall as a response to decreasing photosynthesis and high respiration costs [Wu et al., 2013]. Across site years, anomalies in $\text{cumNEP}$ correlated significantly with anomalies in GPP senescence rates ($r = 0.74, p < 0.01, n = 21$) and with anomalies in peak GPP rates ($r = 0.77, p < 0.01, n = 21$). Correlations were also strong and positive between anomalies in peak GPP rates and anomalies in $\text{cumGPP}$, between anomalies in peak $R_e$ rates and anomalies in $\text{cum} R_e$ and between anomalies in peak NEP rates and anomalies in $\text{cumNEP}$ across site years ($r = 0.87, 0.80$, and $0.88; p < 0.01$ for all, $n = 21$) (Figure 5 and Table 3). Stepwise regressions showed the importance of the peak anomalies in combination with anomalies in: recovery rates for explaining variations in GPP ($r = 0.86, p < 0.01, n = 21$), senescence rates for explaining variations in $R_e$ ($r = 0.72, p < 0.01, n = 21$), and the length of the growing season for explaining variations in NEP ($r^2 = 0.88, p < 0.01, n = 21$). Our findings are consistent with those of Humphreys and Lat fleur [2011] who studied interannual variations in ecosystem-scale NEP at two low arctic tundra ecosystems. They found significant correlations between the maximum photosynthetic capacity and annual accumulated NEP at the two sites. Peak GPP is affected by leaf photosynthetic capacity and LAI, which are mainly controlled by nutrient and water availability [Gu et al., 2009; Noormets et al., 2009]. Variations in the annual length of the growing season are mainly determined by meteorological conditions (e.g., temperature and photoperiod). The greater importance of peak GPP (compared to the length of the growing season) for explaining variations in $\text{cumNEP}$ suggests that ecophysiological variables could be more important than temperature and photoperiod in controlling interannual variations in both $\text{cumGPP}$ and $\text{cumNEP}$ at our sites. Although the length of the growing season represents the potential for C assimilation, it is the ecophysiological variables that affect the photosynthetic activity that will determine the actual C assimilation over the growing season.

4.2.2. Effect of Temperature and Precipitation on Phenology and CO₂ Exchange

Variations in temperature, especially in the months before seasonal life cycle events, have been shown to be highly correlated with changes in plant phenology [e.g., Penuelas and Filella, 2001; Tanja et al., 2003]. Studies have shown both significant [e.g., Richardson et al., 2010] and nonsignificant [e.g., Wu et al., 2012b] effects of spring temperatures on NEP and/or GPP in forest and nonforest (including cropland, grassland, and wetland) ecosystems. While spring warming is associated with increased annual NEP, autumn warming, on the contrary, would reduce annual NEP [e.g., Piao et al., 2008].

Our results showed significant correlations between winter and summer temperatures and precipitation and phenological indices and CO₂ exchange. Higher temperatures in February and March were associated with an earlier start of the growing season (results not shown), and higher temperatures in March were associated with an earlier C uptake (Table 4). Warmer winters were associated with a longer C uptake period, shorter autumn lags, and higher peak NEP rates. Earlier and longer C uptake periods, shorter autumn lags, and higher peak rates were all associated with higher $\text{cumNEP}$ (Table 4) which may explain the significant correlations.

### Table 3. Pearson’s Correlation Coefficients⁴ for Relationships Between Anomalies in $\text{cumGPP}$, $\text{cum} R_e$ and $\text{cumNEP}$ and Anomalies in Phenological Indices⁵

<table>
<thead>
<tr>
<th>Phenological Index</th>
<th>$\text{cumGPP}$</th>
<th>$\text{cum} R_e$</th>
<th>$\text{cumNEP}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Peak rate</td>
<td>.868d</td>
<td>.798d</td>
<td>.882d</td>
</tr>
<tr>
<td>Recovery rate</td>
<td>.472c</td>
<td>.670d</td>
<td>.578d</td>
</tr>
<tr>
<td>Senescence rate</td>
<td>.501c</td>
<td>-.547c</td>
<td>-</td>
</tr>
<tr>
<td>Start of C uptake period</td>
<td>- .604d</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>End of C uptake period</td>
<td>.756d</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Length of C uptake period</td>
<td>.849d</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Autumn Lag</td>
<td>-.826d</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Peak date</td>
<td>.714d</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

⁴Correlation analyses relate anomalies across all site years, $n = 21$.
⁵Only significant correlations are shown.
⁶Significant at the 0.05 level.
⁷Significant at the 0.01 level.
between winter temperatures and cumNEP (Table 6). Warmer winters may translate into earlier snowmelt and/or could trigger earlier onset of vascular plant activity. High-nutrient resorption capacity may also cause peatland vegetation to start the photosynthesis mechanism in early spring. These findings are consistent with Sottocornola and Kiely [2010] who found that warmer winter soil temperatures in an Atlantic blanket bog led to an earlier onset of the season, which led to higher NEP and GPP, and warmer winters led to higher GPP.

Table 5. Pearson’s Correlation Coefficients⁹ for Relationships Between Anomalies in Temperature and Precipitation, and Anomalies in cumGPP, cumRe and cumNEP

<table>
<thead>
<tr>
<th>Phenological Index</th>
<th>Temperature</th>
<th>Precipitation</th>
</tr>
</thead>
<tbody>
<tr>
<td>GPP peak rate</td>
<td>TP (.633); TP0709 (.585)</td>
<td>MT08 (--.535)</td>
</tr>
<tr>
<td>Re peak rate</td>
<td>MT07 (.50)</td>
<td></td>
</tr>
<tr>
<td>NEP peak rate</td>
<td>MT08 (--.648); MT02 (.624); MT0103 (.588); MT0709 (--.499)</td>
<td>TP (.700); TP0709 (.675); TP08 (.456)</td>
</tr>
<tr>
<td>GPP recovery rate</td>
<td>MT06 (.447); MT (.436)</td>
<td></td>
</tr>
<tr>
<td>Re recovery rate</td>
<td>MT06 (.450)</td>
<td></td>
</tr>
<tr>
<td>NEP recovery rate</td>
<td>MT08 (--.597)</td>
<td></td>
</tr>
<tr>
<td>GPP senescence rate</td>
<td>MT08 (--.678); MT02 (.610); MT05 (--.436)</td>
<td>TP (.663); TP0709 (.626)</td>
</tr>
<tr>
<td>NEP senescence rate</td>
<td>MT08 (.634); MT02 (--.604); MT0406 (.452); MT05 (.434)</td>
<td>TP (--.570); TP09 (--.545); TP0709 (--.483)</td>
</tr>
<tr>
<td>NEP Start of the C uptake period</td>
<td>MT03 (--.444)</td>
<td></td>
</tr>
<tr>
<td>NEP End of the C uptake period</td>
<td>MT08 (--.634); MT0103 (.631); MT02 (.611); MT0709 (--.594); MT03 (.531); MT05 (--.460)</td>
<td>TP09 (.584); TP (.569); TP0709 (.539); TP02 (--.513)</td>
</tr>
<tr>
<td>NEP Duration of the C uptake period</td>
<td>MT08 (--.674); MT0709 (--.646); MT0103 (.635); MT02 (.610); MT03 (.600)</td>
<td>TP09 (.624); TP0709 (.556); TP02 (--.527); TP08 (.484); TP0103 (--.473); TP08 (.683); TP0709 (.618)</td>
</tr>
<tr>
<td>NEP peak date</td>
<td>MT08 (--.861); MT06 (--.719); MT0103 (--.568); MT03 (.646); MT0406 (--.597); MT0709 (--.597)</td>
<td>TP09 (--.778); TP0709 (--.720); TP (--.564); TP08 (--.482)</td>
</tr>
<tr>
<td>Autumn lag</td>
<td>MT08 (.816); MT02 (--.669); MT0709 (.610); MT03 (--.608); MT0103 (--.528); MT05 (.446)</td>
<td></td>
</tr>
</tbody>
</table>

⁹Correlation analyses relates anomalies across all site years, n = 21. Only significant correlations are shown. MAT = mean annual air temperature; TM01 = mean temperature January; TM12 = mean temperature December; TM0103 = mean temperature from January to March; TM0102 = mean temperature from October to December; TP = total annual precipitation; TP01 = total precipitation January; TP12 = total precipitation December; TP0103 = total precipitation January–March; TP0102 = total precipitation October–December.

Anomalies in cumGPP correlated best with anomalies in the total precipitation in September (r = 0.52, p < 0.05); anomalies in cumRe correlated best with anomalies in average June and July temperatures (r = 0.52 and 0.56, p < 0.05 and p < 0.01, respectively) (Table 5). Anomalies in cumNEP were significantly correlated with anomalies in both precipitation and temperature: the average temperature in August and the total precipitation from July to September showed the highest correlations (r = −0.80 and 0.69, respectively, p < 0.01 for both) (Table 4 and Figure 6d). Peak GPP, Re, and NEP rates showed similar sensitivity to the same weather variables (Table 4 and Figure 6b).

Wetter summers were associated with a longer C uptake period (Table 4 and Figure 6a). Warmer and drier summers may lead to vegetation stress and decreased GPP, while Re may increase under warmer conditions.

A similar sensitivity to cooler and wetter summers led to shorter autumn lags (Table 4 and Figure 6c). Wu et al. [2012a] showed the importance of the autumn lag for NEP in evergreen, broad leaf, and nonforest ecosystems (crops, grassland, and wetlands), but they did not find a significant relationship between...
spring (in their study: March to May) or autumn (in their study: September to November) warming and NEP. Yet NEP may be sensitive to other seasonal intervals than the ones used by Wu et al. [2012a]. Studies have used seasons (i.e., winter, spring, summer, and autumn) that are based on a variety of different time intervals, which can make it difficult to interpret the sensitivity of GPP, $R_e$, NEP, or phenological indices to meteorological variables. Future analyses should attempt to integrate temperature and precipitation over smaller windows (e.g., days, weeks, and months) or explore the definition of seasons based on temperature thresholds or vegetation phenology [e.g., Lafleur et al., 1997].

4.3. Potential of Remote Sensing-Derived Phenology for C Monitoring in Peatlands

Our study illustrates the potential of several phenological indices for estimation of $\text{cumNEP}$, $\text{cumGPP}$, or $\text{cumR_e}$ in northern peatlands. Most of these indices can be derived from satellite images, and several studies have shown the potential of remote sensing for deriving phenological indices, such as the length of the growing season and C uptake period and their transitions [e.g., Churkina et al., 2005; Garrity et al., 2011; Richardson et al., 2009; White et al., 2009], the autumn lag [Wu et al., 2013], and peak, recovery, and senescence rates

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**Figure 6.** Variations in phenological indices, meteorological variables, and $\text{cumNEP}$. (a) Variations in the C uptake period and temperature, (b) variations in peak NEP and temperature and precipitation, (c) variations in autumn lag and temperature and precipitation, and (d) variations in $\text{cumNEP}$ and temperature and precipitation. Diamonds are negative anomalies on the z axis; triangles are positive anomalies on the z axis.
variations in $\text{cum}_\text{GPP}$, $\text{cum}_\text{NEP}$, or $\text{cum}_\text{Re}$ (Table 6). Algorithms for deriving peak values are more straightforward than algorithms for deriving the timing of the start and end of the growing season and C uptake, or recovery and senescence rates. Previous studies have shown a wide variety in estimates of the start of the growing season depending on the phenology algorithm that was used [e.g., White et al., 2009]. Defining growing season transition points from continuous data is challenging, as most of the transitions are not clear and their extraction depends on a combination of smoothing algorithms, data-compositing methods, absolute and relative thresholds, inflection points, curvature, or local minima and maxima.

The peak is a visible feature of the continuous CO$_2$ exchange data. The annual maximum NDVI can be determined as the annual maximum NDVI value from cloud-free multiday NDVI composites [e.g., Blok et al., 2011; Maxwell and Sylvester, 2012]. Daily data are often noisy; peak values may be derived as the maximum value after smoothing the data [Gu et al., 2003; Jönsson and Eklundh, 2004] or by using the 90th to 95th percentile value of the raw data (considering 10%–15% of outliers). More research is needed to assess the sensitivity of peak rates for these different methods. Satellite data can complement ground data (e.g., EC flux data and camera data) in studying visual phenology (i.e., leaf out) and “functional” phenology (i.e., start of photosynthetic activity or C uptake and peak photosynthetic rates).

### Table 6. Coefficients of Determination ($r^2$) for Relationships Between $\text{cum}_\text{GPP}$, $\text{cum}_\text{Re}$, and $\text{cum}_\text{NEP}$ and Phenological Indices

<table>
<thead>
<tr>
<th>Phenological Indices</th>
<th>Predictors</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\text{cum}_\text{GPP}$</td>
<td>Peak GPP</td>
<td>0.879$^b$</td>
</tr>
<tr>
<td></td>
<td>Peak GPP, LGS</td>
<td>0.970$^b$</td>
</tr>
<tr>
<td></td>
<td>Peak GPP, LGS, SOS</td>
<td>0.970$^b$</td>
</tr>
<tr>
<td>$\text{cum}_\text{Re}$</td>
<td>Peak $\text{Re}$</td>
<td>0.942$^b$</td>
</tr>
<tr>
<td>$\text{cum}_\text{NEP}$</td>
<td>Peak NEP</td>
<td>0.847$^b$</td>
</tr>
<tr>
<td></td>
<td>NEP Recovery rate</td>
<td>0.909$^b$</td>
</tr>
</tbody>
</table>

$^a$Stepwise regression analysis relates absolute values of variables across all site years, $n = 25$. $^b$Significant at the 0.01 level.

5. Conclusions

We studied the spatial patterns in phenological indices and CO$_2$ fluxes and the relationships between anomalies in annual phenological indices, meteorological variables, and cumulative annual CO$_2$ for four northern peatlands. Using multiyear CO$_2$ flux measurements, we showed the importance of several phenological indices derived from the CO$_2$ flux records for characterizing and/or explaining the variability in spatial and annual $\text{cum}_\text{GPP}$, $\text{cum}_\text{Re}$, and $\text{cum}_\text{NEP}$. We also showed the importance of meteorological variables for both phenology and CO$_2$ uptake. Our main findings are the following:

1. An earlier start of the growing season and longer growing seasons were not associated with an increased C uptake period, or increased GPP or NEP among sites and interannually. But the start of the growing season can play an important role for the among-site differentiation of peatlands with regard to their average $\text{cum}_\text{GPP}$. Sites with the earliest start of the growing season had the highest average $\text{cum}_\text{GPP}$. Sites with a later start of the growing season (35–49 days later) had the lowest average $\text{cum}_\text{GPP}$.

2. GPP recovery and senescence rates may provide us with important information about spring ecosystem photosynthetic capacity and leaf fall mechanisms.

3. Both spatial and annual variations in $\text{cum}_\text{GPP}$, $\text{cum}_\text{Re}$, and $\text{cum}_\text{NEP}$ were best explained by variations in peak GPP, peak $\text{Re}$, and peak NEP rates, respectively. NEP-derived phenological indices such as the C uptake period and its transitions and the autumn lag also showed some potential for explaining the variability of $\text{cum}_\text{NEP}$.

4. Peak rates, recovery rates, and senescence rates reflected variations in LAI and pH to some extent. Future studies should evaluate the role of these indices as indicators of LAI, pH, dominant PFTs, spring plant nitrogen content, Rubisco and chlorophyll content, and nutrient resorption.

5. Both phenology and CO$_2$ fluxes were more sensitive to winter (January–March) and summer (July–September) temperatures and precipitation than to spring and autumn temperatures and precipitation.

6. Understanding how phenological shifts will affect the C uptake in peatlands will improve our ability to predict future responses to changes in phenology most probably induced by climate change. All the...
studied phenological indices can be derived from satellite reflectance data, and the future use of satellite-derived phenological indices for the study of CO₂ exchange in peatlands will allow us to assess relationships between peatland production and environmental conditions across inaccessible, large areas over long time periods. Future studies should explore methods for the derivation of peak values, and data sources should be evaluated with regard to their ability in reflecting variations in annual peak GPP, Rₑ, or NEP.

**References**


KROSS ET AL.


