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Variability in exchange of CO_2 across 12 northern peatland and tundra sites

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Abstract

Many wetland ecosystems such as peatlands and wet tundra hold large amounts of organic carbon (C) in their soils, and are thus important in the terrestrial C cycle. We have synthesized data on the carbon dioxide (CO_2) exchange obtained from eddy covariance measurements from 12 wetland sites, covering 1–7 years at each site, across Europe and North America, ranging from ombrotrophic and minerotrophic peatlands to wet tundra ecosystems, spanning temperate to arctic climate zones. The average summertime net ecosystem exchange of CO_2 (NEE) was highly variable between sites. However, all sites with complete annual datasets, seven in total, acted as annual net sinks for atmospheric CO_2. To evaluate the influence of gross primary production (GPP) and ecosystem respiration (R_{eco}) on NEE, we first removed the artificial correlation emanating from the method of partitioning NEE into GPP and R_{eco}. After this correction neither R_{eco} ($P = 0.162$) nor GPP ($P = 0.110$) correlated significantly with NEE on an annual basis. Spatial variation in annual and summertime R_{eco} was associated with growing season period, air temperature, growing degree days, normalized difference vegetation index and vapour pressure deficit. GPP showed weaker correlations with environmental variables as compared with R_{eco}, the exception being leaf area index (LAI), which correlated with both GPP and NEE, but not with R_{eco}. Length of growing season period was found to be the most important variable describing the spatial variation in summertime GPP and R_{eco}; global warming will thus cause these components to increase. Annual GPP and NEE correlated significantly with LAI and pH, thus, in order to predict wetland C exchange, differences in ecosystem structure such as leaf area and biomass as well as nutritional status must be taken into account.

Keywords: carbon, carbon dioxide, eddy covariance, mire, net ecosystem exchange, peatland, photosynthesis, respiration, tundra, wetland

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Introduction

Wetlands are characterized by having their water table permanently or periodically close to the soil surface. One consequence of the poorly aerated soil conditions is that decomposition rates in wetlands are reduced. Peatlands are wetland ecosystems with long-term (millennial) transformation of atmospheric carbon dioxide (CO_2) into organic material, i.e. peat, making these ecosystems important in the terrestrial carbon (C) cycle. The average rate of C accumulation in northern peatlands during the

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Holocene has been estimated to be 15–30 g C m^{-2} yr^{-1}, which has resulted in a soil C pool of 200–450 Pg (Gorham, 1991; Tolonen & Turunen, 1996; Turunen *et al.*, 2002).

CO_2 uptake through gross primary production (GPP) and subsequent loss through autotrophic and heterotrophic respiration, collectively referred to as ecosystem respiration (R_{eco}), constitute the two major C fluxes in undisturbed peatland ecosystems (Roulet *et al.*, 2007; Nilsson *et al.*, 2008). The difference between these two fluxes represents the net ecosystem exchange (NEE). Although they are not dealt with in this analysis, other C fluxes such as the methane (CH_4) exchange and dissolved C exported with water are also important components of the total annual net C balance. Depending on wetland type the importance of these non-CO_2 flux components varies, and either or both may significantly influence the annual net C balance and may also turn the system from sink to source (Christensen *et al.*, 2007; Roulet *et al.*, 2007; Limpens *et al.*, 2008; Nilsson *et al.*, 2008).

The NEE and its components (GPP, R_{eco}) in peatlands are known to vary considerably both between different sites (Bubier *et al.*, 1998; Frolking *et al.*, 1998; Moore *et al.*, 2002; Lindroth *et al.*, 2007) as well as inter-annually within sites (Aurela *et al.*, 2004; Roulet *et al.*, 2007; Sagerfors *et al.*, 2008). Various controlling factors for this variation have been suggested. Based on chamber measurements in a diverse peatland complex, Bubier *et al.* (1998) found that summertime rates of NEE and respiration followed the trophic sequence of bog < poor fen < intermediate fen < rich fen, illustrating the importance of nutrient availability. Differences in NEE rates are generally found among various plant communities (Bubier *et al.*, 2003; Riutta *et al.*, 2007) and differences in vegetation composition between sites may also result in different responses to inter-annual variation in environmental conditions (Glenn *et al.*, 2006). Thus, also within sites, NEE and its flux components can vary greatly (Bubier *et al.*, 1998, 2003; Riutta *et al.*, 2007). However, Humphreys *et al.* (2006) studied seven Canadian peatlands and found that daily average summertime NEE rates measured by the eddy covariance (EC) method were similar across sites, despite differences in water table depth (WTD), trophic status and plant communities. Between-site differences in GPP and R_{eco} were found to correlate with vegetation indices such as leaf area index (LAI) and aboveground biomass (Humphreys *et al.*, 2006). Within four Nordic peatlands, Lindroth *et al.* (2007) found that after detrending for the seasonal variation the average air temperature was the main driver for half-monthly averages of GPP and R_{eco}. Soil wetness has been shown to be an important factor for the inter-annual variability of wetland NEE. Several studies have reported net CO_2 losses during dry years, while the same sites are CO_2 sinks in less dry years (e.g. Shurpali *et al.*, 1995; Lafleur *et al.*, 1997; Alm *et al.*, 1999). Summertime drought may affect both R_{eco} and GPP (Aurela *et al.*, 2007; Lund *et al.*, 2007; Lafleur, 2009).

Beyond the pressure of land-use change, climatic change together with nitrogen (N) deposition are the most important factors altering peatland ecosystem functioning (Limpens *et al.*, 2008). In sub-arctic wetlands with permafrost, small increases in temperature can affect the physical stability of these ecosystems leading to permafrost degradation with implications for the biological dynamics and potentially severe consequences for the storage of organic C (Johansson *et al.*, 2006; Tarnocai, 2006). Peatlands in temperate and boreal regions are expected to experience drought conditions as a result of increased temperatures and evapotranspiration rates, which may cause decreased C sink strength (Tarnocai, 2006). High N deposition in nutrient-poor peatlands, together with increased N mineralization rates due to global warming (Rustad *et al.*, 2001), can impose changes in plant composition and ecosystem structure with important effects on the C retention (Berendse *et al.*, 2001; Malmer & Wallén, 2005).

During the past two decades, the EC technique (Aubinet *et al.*, 2000) has become a key tool for measuring CO_2 exchange at the landscape level. One advantage with this type of measurement compared with leaf cuvettes and soil chambers is that it allows large scale monitoring of whole ecosystem CO_2 exchange, which makes it especially appropriate for studying ecosystem physiology (Baldocchi, 2003). Wetlands have been an underrepresented ecosystem type in EC flux networks. However, recently several research groups have initiated EC measurements in these ecosystem types. These data are now available through Fluxnet, a global network of micrometeorological flux measurement sites (Baldocchi *et al.*, 2001). The Fluxnet database, from which 12 northern peatland and wet tundra sites are used in this study, has the advantage that data have been treated and gap filled in a consistent manner, thus eliminating potential biases. The purpose of this study was to synthesize EC NEE and its components (R_{eco} and GPP) across an unprecedented range of northern peatland and wet tundra ecosystems from the Fluxnet database and to investigate whether possible differences can be explained by climatic and environmental variables such as temperature, precipitation, solar radiation, WTD, vegetation indices and nutritional status.

Materials and methods

Sites and data availability

We have used EC data of the CO_2 exchange from 12 northern peatland and wet tundra sites (Table 1) from

Table 1 Main site and measurement setup characteristics of the 12 northern peatland and wet tundra sites in this study

Site	CA-Mer	CA-WP1	CA-WP2	CA-WP3	FI-Kaa	FI-Sii	PL-WET	SE-Deg	SE-Faj	US-Atq	US-Brw	US-Ivo
Latitude	45.41	54.95	55.54	54.47	69.14	61.83	52.76	64.18	56.27	70.47	71.32	68.49
Longitude	−75.52	−112.47	−112.33	−113.32	27.30	24.19	16.31	19.55	13.55	−157.41	−156.63	−155.75
Elevation (m)	70	540	730	670	155	162	54	270	140	N/A	1	N/A
Climate	Temperate	Boreal	Boreal	Boreal	Sub-arctic	Boreal	Temperate	Boreal	Temperate	Arctic	Arctic	Arctic
Wetland type	Open bog	Treed poor fen	Poor fen	Rich fen	Poor fen	Poor fen	Rich fen	Poor fen	Treed bog	Wet tundra	Wet tundra	Wet tundra
Dominant vegetation	*Chamaedaphne calyculata*, *Vaccinium myrtilloides*, *Sphagnum* spp.	*Picea mariana*, *Larix laricina*, *Betula pumila*, *Sphagnum* spp.	*Andromeda polifolia*, *Carex limosa*, *Sphagnum* spp.	*Carex lasiocarpa*, *Salix pedicellaris*, *Drepanocladus aduncus*	*Ledum palustre*, *Empeterum nigrum*, *Sphagnum* spp.	*Eriophorum vaginatum*, *Carex rostrata*, *Sphagnum* spp.	*Carex* spp., *Typha latifolia*, *Sphagnum* spp.	*E. vaginatum*, *Vaccinium oxycoccus*, *Sphagnum* spp.	*Calluna vulgaris*, *Erica tetralix*, *Sphagnum* spp.	*E. vaginatum*	*Carex aquatilis*, *Dupontia fischeri*, *Arctophila fulva*	*E. vaginatum*, *Betula nana*, *Sphagnum* spp.
LAI ($m^2 m^{-2}$)	1.3	2.6	1.5	1.1	0.7	0.4	2.3	N/A	N/A	1.1	1.5	N/A
pH	3.9	6.2	4	6.5	4.4	3.6	6.3	4	3.9	4.4	5.4	N/A
T_{air} (°C)*	6.0 (5.8)	2.0 (2.1)	N/A (2.1)	N/A (2.1)	0.2 (−1.1)	4.2 (3)	8.5 (8.5)	2.1 (1.2)	7.8 (6.2)	−10.7 (−12.3)	N/A (−12.5)	−9.3 (N/A)
Precipitation sum (mm)*	815 (910)	440 (504)	N/A (504)	N/A (504)	471 (474)	N/A (713)	509 (526)	453 (523)	N/A (700)	157 (93)	N/A (86)	252 (N/A)
Gas analyzer	LI-6262, LI-7000	LI-7000	LI-7500	LI-7500	LI-6262	LI-7000	LI-7500	LI-6262	LI-6262	ATDD/ NOAA	ATDD/ NOAA	ATDD/ NOAA
Anemometer	Gill R3	Gill Solent	Campbell CSAT3	Campbell CSAT3	SWS-211	Metek USA-1	Gill R3	Gill R2	Gill R3	Gill R3	Gill R3	Gill R3
Data period (YY.MM)	98.05–05.12	03.07–05.12	04.04–04.10	04.04–04.11	00.01–06.12	04.05–05.12	04.01–05.12	01.01–05.12	05.07–06.08	99.05–06.12	98.06–02.10	03.10–06.12
No. of data years†	7	2	0	0	7	1	2	4	1	4	0	2
Citation	Roulet *et al.* (2007)	Syed *et al.* (2006)	Glenn *et al.* (2006)	Glenn *et al.* (2006)	Aurela *et al.* (2004)	Aurela *et al.* (2007)	Chojnicki *et al.* (2007)	Sagerfors *et al.* (2008)	Lund *et al.* (2007)	Oechel *et al.* (2000)	Oechel *et al.* (2000)	Oechel *et al.* (2000)

*First value indicates average during data period, while value within parentheses indicates long-term average.
†Number of data years is sometimes lower than what the data period indicates. This is because not all sites have year-round measurements.

the Fluxnet database (http://www.fluxdata.org). These sites represent wetland types ranging from ombrotrophic and minerotrophic peatlands, in both temperate and boreal climates, to wet tundra ecosystems. To avoid confusion with other wetland ecosystems we denote them here in the more specific terms, northern peatlands and wet tundra. EC measurements as well as ancillary data from each site have been submitted to Fluxnet. Within this network, NEE data have been processed, gap filled, and partitioned into GPP and R_{eco} according to standardized processing procedures. In short, the CO_2 fluxes were corrected for storage and screened for insufficient turbulence (u^* filtered), spikes and outliers (Reichstein *et al*., 2005; Papale *et al*., 2006). Gap-filling was done using marginal distribution sampling (Moffat *et al*., 2007) and artificial neural network (Papale & Valentini, 2003) techniques, while NEE partitioning was based on modelling R_{eco} using the Lloyd & Taylor (1994) temperature regression model according to Reichstein *et al*. (2005). GPP was subsequently calculated as the difference between modelled R_{eco} and measured (and gap filled) NEE. These gap filling and flux partitioning procedures may provide results that deviate from what have been reported earlier for the individual sites based on other methods (see site references in Table 1). However, in an inter-site comparison study the usage of standardized procedures is important to avoid differences stemming from data processing.

Data analyses

For the calculations of annually averaged NEE, GPP and R_{eco}, only sites with at least 1 full year of data were included. No gap filling beyond the Fluxnet calculation procedures has been performed in the present study. We have adopted the micrometeorological sign convention where positive fluxes and balances depict CO_2 emissions from the ecosystem and negative fluxes and balances represent CO_2 uptake by the ecosystem. Ecosystem respiration has a positive sign, whereas GPP has a negative sign. NEE is thus negative when GPP exceeds R_{eco}, which constitutes a CO_2 sink. In addition, we have chosen to omit wintertime measurements using open-path gas analyzers for the CO_2 concentration measurements in cold climates (boreal and arctic). Open-path sensors have recently been found to measure apparent CO_2 uptake during cold off-season periods when it is not physiologically reasonable (Burba *et al*., 2008). This can lead to underestimation of the cold period CO_2 release, and hence overestimation of the annual CO_2 sink.

To investigate the drivers of the CO_2 exchange across the peatland and tundra sites, seasonally and annually averaged NEE, R_{eco} and GPP were analysed for correlation with the following seasonally and annually averaged/summed variables: average air temperature (T_{air}), sum of incoming photosynthetic photon flux density during growing season, precipitation sum (Prec), water balance sum (WB: difference between precipitation and evapotranspiration), average WTD and vapour pressure deficit (VPD), growing degree days (GDD: threshold temperature 5 °C), maximum of 16-day averages of normalized difference vegetation index (NDVI) and enhanced vegetation index (EVI) from the MODIS Land Product Subsets (http://daac.ornl.gov/MODIS/), length of growing season (GS_{length}: growing season starts when average daily air temperature rises above 5 °C for 7 consecutive days and consequently ends when temperature falls below 5 °C), start day of growing season (GS_{start}), end day of growing season (GS_{end}), LAI and pH. Variations in summertime (June–August) averages of NEE, R_{eco} and GPP were further analysed by stepwise regression using the environmental variables listed above. Explaining variables were added to the model if their significance (of F value) was <0.05, and if there was no or low multicollinearity among them (variance inflation factor, $VIF<2$). All variables were tested for normality using the Kolmogorov–Smirnov test before using parametric tests (SPSS 12.0.1, SPSS Inc.).

In the flux partitioning method (Reichstein *et al*., 2005), GPP is calculated from the difference between NEE and R_{eco}. Therefore, a correlation analysis of GPP vs. R_{eco} or GPP vs. NEE may lead to artificial or spurious correlation of the type Y vs. $Y+X$ (Brett, 2004), since the variables being considered are nonindependent. To be able to investigate whether a correlation exists independent of the flux partitioning method, the spurious correlation obtained from the calculation procedure must be estimated. To achieve this, we have used a bootstrap simulation methodology (Brett, 2004) where the considered NEE and R_{eco} data sets were copied 1000 times, columns of data randomly sorted independent of each other, and a random GPP data set calculated from the difference between NEE and R_{eco}. An array of 1000 random correlation coefficients (r) was used to estimate the influence of the flux partitioning method (Brett, 2004). The procedure was repeated 10 times for each evaluation to estimate the significance and standard deviation (SD).

Results

Seasonal and annual CO_2 exchange

Wintertime NEE fluxes were fairly similar across sites with January fluxes being on average 0.13 ± 0.13 (mean SD) $g\,C\,m^{-2}\,day^{-1}$ ($n=7$, Fig. 1a). Most sites had no or very low photosynthetic activity during wintertime (Fig. 1c), the exception being PL-WET where wintertime

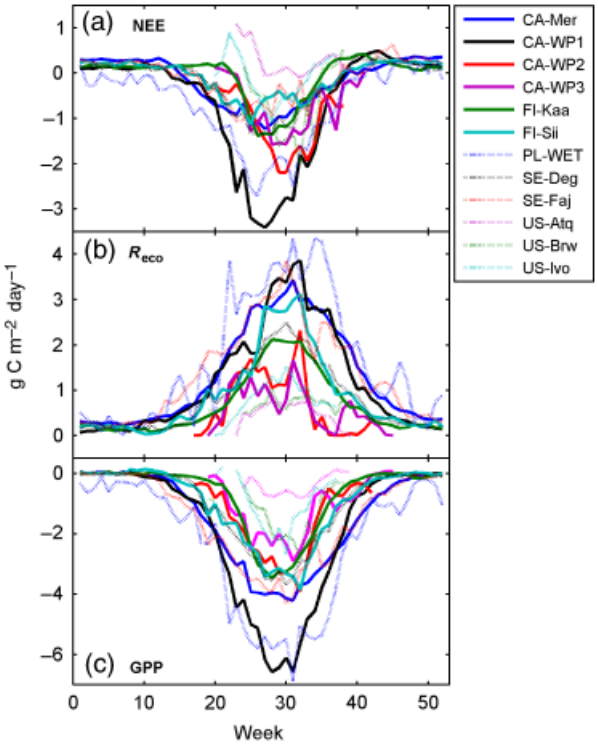

Fig. 1 Average weekly net ecosystem exchange (NEE) and its components [gross primary production (GPP), ecosystem respiration (R_{eco})] in the study sites. (a) NEE is directly measured in the sites and gap filled according to Fluxnet procedures; (b) R_{eco} is modelled according to Fluxnet procedures; (c) GPP is the difference between R_{eco} and NEE. For sites with several years of data, averages in NEE, R_{eco} and GPP are shown. Error bars have been excluded to increase readability of the graphs.

air temperatures were relatively mild compared with other sites (average $T_{air} = 0.2\,^{\circ}C$ between December and February). The time of the year when the ecosystems switched from being a net CO_2 source to a sink was largely a reflection of latitudinal differences, with early springtime switches in temperate sites (PL-WET, SE-Faj, CA-Mer and also the boreal site CA-WP1), while boreal and arctic sites switched to sinks later in the year. There were large between-site differences in summertime NEE, with CA-WP1 and PL-WET having high net uptake rates, while the Alaskan sites US-Atq and US-Ivo showed early-summer net CO_2 emissions to the atmosphere. In these sites photosynthetic activity was low during early summer and NEE was dominated by respiratory emissions during this period. Average NEE rate in July for all sites was $-1.2 \pm 0.88\,g\,C\,m^{-2}\,day^{-1}$ ($n = 12$); but rates varied considerably between < -3 and $0\,g\,C\,m^{-2}\,day^{-1}$.

The between-site differences in summer GPP were similar in pattern but more pronounced than those seen for NEE (Fig. 1c). CA-WP1 and PL-WET had high GPP rates (c. $-6\,g\,C\,m^{-2}\,day^{-1}$) compared with the other sites between weeks 20 and 37; while US-Atq had relatively low summertime GPP rates ($> -1\,g\,C\,m^{-2}\,day^{-1}$). The other sites ranged between -4 and $-2\,g\,C\,m^{-2}\,day^{-1}$ during midseason. Less pronounced differences between sites were seen for summertime R_{eco} fluxes (Fig. 1b). The highest R_{eco} rates were generally found in PL-WET, but during midseason CA-WP1, SE-Faj, CA-Mer and FI-Sii had similar R_{eco} rates as PL-WET, slightly above $3\,g\,C\,m^{-2}\,day^{-1}$. The northernmost sites generally had the lowest R_{eco} rates.

Averaging the exchange rates for all sites with complete annual NEE data sets yielded an average annual net CO_2 uptake of $-103 \pm 103\,g\,C\,m^{-2}\,yr^{-1}$($n = 7$), with annual averages of GPP and R_{eco} being -514 ± 206 and $411 \pm 128\,g\,C\,m^{-2}\,yr^{-1}$, respectively (Fig. 2). The sub-data set with complete annual NEE measurements in this study comprised seven peatland sites and 24 site years all of which were net CO_2 sinks. The CO_2 sink strength was weakest at the sub-arctic site Fi-Kaa, and based on the growing season NEE data the Alaskan tundra sites also seemed to be weak sinks or even possibly sources of CO_2 (Fig. 1a). The two sites with highest annual net CO_2 uptake were low latitude sites with high LAI and pH (Table 1); CA-WP1 being a treed fen and PL-WET, a rich fen with a dense vascular plant community.

Environmental controls on NEE, R_{eco}, and GPP

Summertime NEE across all 12 sites correlated with GPP (Table 2), also after accounting for spurious corre-

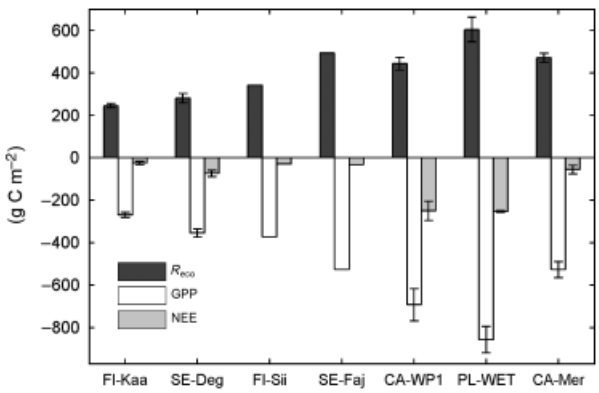

Fig. 2 Annual averages of net ecosystem exchange (NEE) and its components [gross primary production (GPP), ecosystem respiration (R_{eco})], for sites with at least one complete year of data. Sites are organized for latitude, in such way that the leftmost site (FI-Kaa) is the most northerly situated, and the rightmost site (CA-Mer) is the most southerly situated. Error bars depict standard error for sites with >1 year of data.

lation stemming from the flux partitioning procedure ($P = 0.033 \pm 0.005$), indicating that sites with high photosynthesis rates were also strong CO_2 sinks. There were also significant relationships between NEE and R_{eco} ($P = 0.039$) and NEE and LAI ($P = 0.006$, Fig. 3a), i.e. sites with high LAI constituted strong summertime CO_2 sinks. Summertime R_{eco} showed positive correlations with GS_{length}, GS_{stop}, T_{air}, VPD and NDVI, as well as a negative correlation with GS_{start} ($P < 0.05$). Sites with long growing seasons, high temperatures, VPD and NDVI also have high R_{eco} rates. GPP generally correlated with the same variables as R_{eco} but not as strongly (note opposite sign due to the sign convention), the exception being the significant relationship between GPP and LAI ($P = 0.036$). This behaviour can be explained by the strong relationship between GPP and R_{eco} ($P < 0.001$). However, according to the bootstrap simulation the significant correlation between GPP and R_{eco} was affected by the flux partitioning procedure as the nonspurious correlation had an associated P value of 0.128 ± 0.009 (Table 2), i.e., after accounting for the methodologically derived relationship no significant correlation between GPP and R_{eco} occurred. For both R_{eco} and GPP, the most significant variable describing summertime flux components was GS_{length} (Fig. 3b and c), where a prolonged growing season would increase both R_{eco} and GPP. Using stepwise regression analysis, LAI and precipitation were found to explain 89% of the spatial variation in summertime NEE (Table 3). Adding precipitation to the model increased the r^2 value from 0.68 to 0.89. For GPP, GS_{length} and LAI explained 86% of the spatial variation. The product of GS_{length} and LAI, which can be interpreted as leaf area duration, explained 80% of the variation in GPP. For R_{eco}, only GS_{length} was found to be significant, explaining 75% of the variation.

There was a significant relationship between annual NEE and GPP using a standard Pearson's correlation analysis (Table 4), but after accounting for spurious correlation the relationship was no longer significant ($P = 0.110 \pm 0.009$). There was no significant correlation between annual NEE and R_{eco} ($P = 0.162$). Annual R_{eco} showed similar correlations with environmental variables as the summertime averages, while annual GPP correlated with LAI ($P = 0.037$) and pH ($P = 0.029$). As was the case for the summertime averages, there was a significant correlation between annual NEE and LAI ($P = 0.009$). In addition, annual NEE also correlated with pH ($P < 0.001$). Sites with high LAI and pH also have high annual net CO_2 uptake.

Based on the seven sites with complete annual data sets the relationship between GPP and R_{eco} was exam-

Table 2 Matrix with correlation coefficients for average summer-time (June–August) NEE and its components (R_{eco} and GPP) and ancillary data

	NEE	R_{eco}	GPP	T_{air}	PPFD	Prec	WB	WTD	VPD	EVI	NDVI	GS_{length}	GS_{start}	GS_{stop}	LAI	pH
NEE	1	−0.60*	0.86***[a]	−0.35	−0.43	−0.35	0.07	0.47	−0.51	−0.06	−0.48	−0.42	0.42	−0.41	−0.83**	−0.59
R_{eco}		1	−0.92***[b]	0.80**	0.57	0.48	−0.09	−0.21	0.70*	0.12	0.70*	0.88***	−0.87***	0.85***	0.48	0.06
GPP			1	−0.68*	−0.57	−0.46	0.09	0.43	−0.67*	−0.10	−0.67*	−0.76**	0.75**	−0.74**	−0.70*	−0.33
T_{air}				1	0.60*	0.78**	0.18	−0.13	0.96**	0.57	0.94***	0.95***	−0.95***	0.90***	0.15	−0.12
PPFD					1	0.58	0.19	−0.38	0.60	0.43	0.64*	0.47	−0.52	0.39	0.32	−0.31
Prec						1	0.70*	0.56	0.76**	0.51	0.77**	0.69*	−0.68*	0.64*	−0.15	−0.18
WB							1	0.90**	0.20	0.19	0.17	0.08	−0.06	0.08	−0.46	−0.23
WTD								1	−0.42	−0.48	−0.32	0.07	0.01	0.10	−0.64	−0.22
VPD									1	0.62*	0.98***	0.88***	−0.92***	0.79**	0.30	0.05
EVI										1	0.69*	0.39	−0.38	0.39	−0.04	−0.09
NDVI											1	0.88***	−0.89***	0.82**	0.31	0.00
GS_{length}												1	−0.98***	0.97***	0.24	0.04
GS_{start}													1	−0.90***	−0.25	0.02
GS_{stop}														1	0.25	0.13
LAI															1	0.66
pH																1

*Correlation is significant at the $\alpha = 0.05$ level; **$\alpha = 0.01$ level; ***$\alpha = 0.001$ level (two-tailed significance test).
[a]$P = 0.033 \pm 0.005$ (SD); [b]$P = 0.128 \pm 0.009$ according to 10 bootstrap simulations, respectively, accounting for the spurious correlation emanating from the derivation of GPP from the difference between NEE and R_{eco} (see 'Materials and methods').
NEE, net ecosystem exchange; R_{eco}, ecosystem respiration; GPP, gross primary production; T_{air}, average air temperature; PPFD, photosynthetic photon flux density; Prec, precipitation sum; WB, water balance sum; WTD, water table depth; VPD, vapour pressure deficit; EVI, enhanced vegetation index; NDVI, normalized difference vegetation index; GS_{start}, start day of growing season; GS_{length}, length of growing season; GS_{stop}, end day of growing season; LAI, leaf area index.

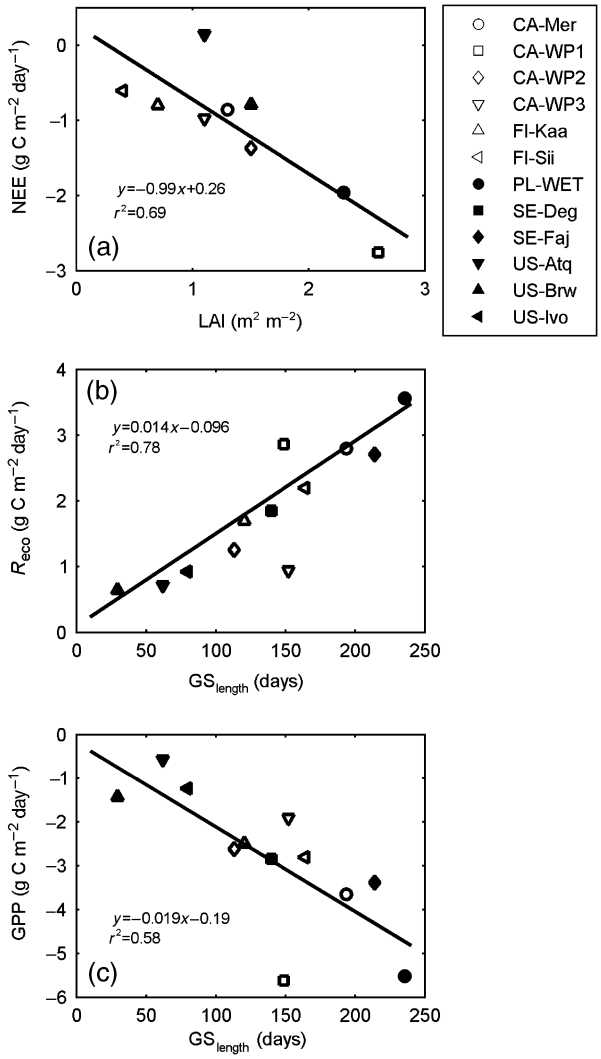

Fig. 3 Scatter plots of between-site summertime net ecosystem exchange (NEE) and LAI (a), ecosystem respiration (R_{eco}) and length of growing season (GS_{length}) (b) and gross primary production (GPP) and GS_{length} (c).

ined by expressing R_{eco} as a function of GPP according to a first-order polynomial of 4 week averages (Fig. 4). At exchange rates higher than c. 1 g C m^{-2} day^{-1} all sites fall below the 1 : 1 line, which can be expected as the sites act as net sinks for CO_2. We also observe a hysteresis loop between R_{eco} and GPP (Fig. 5), where the ratio R_{eco} to GPP, based on 4-week averages, is higher in fall than spring, suggesting that the seasonal trend in the two flux components is out of phase.

Discussion

The summertime NEE rates in the 12 peatland and wet tundra sites in this study revealed large differences between the sites. This contrasts results from Humphreys *et al.* (2006), who found similar mid-summer NEE rates in seven Canadian peatland sites, averaging -1.5 ± 0.60 g C m^{-2} day^{-1}. The differences may be partly attributed to the larger climatic differences between the sites included in the present study (Table 1), compared with the relatively small climate differences in the Humphreys *et al.* (2006) study, which was confined to peak growing season. Even though there was a relatively large range in average summer NEE between the peatlands and wet tundra in the present study, this range is still conservative compared with other ecosystems. In forests, annual GPP and R_{eco} are higher and the annual CO_2 sink strength is generally stronger (Valentini *et al.*, 2000; Janssens *et al.*, 2001; Law *et al.*, 2002). However, NEE of forests varies depending on stand age (Lindroth *et al.*, 2009); on this basis Limpens *et al.* (2008) argue that undisturbed peatlands should theoretically have less variable NEE. In addition, the vast amounts of organic C stored in peatlands illustrate that over long time scales (millennial) the cumulated C sequestration exceeds that of forests and other ecosystems. Our results show that in general the contemporary function of high-latitude peatlands is still as net sinks of CO_2; yet there are several earlier studies indicating that such ecosystems can act as net sources of CO_2, especially during unusually dry years (Oechel *et al.*, 1993; Shurpali *et al.*, 1995; Lafleur *et al.*, 1997; Alm *et al.*, 1999). To compare the contemporary total net C balance with the Holocene long-term C accumulation in peatlands (15–30 g C m^{-2} yr^{-1}: Gorham, 1991; Turunen *et al.*, 2002) both the land–atmosphere exchange of CH_4 and the C export through water runoff must be taken into account. Given the reported ranges of annual emissions of CH_4 (1–15 g C m^{-2}: Bubier *et al.*, 1993; Nilsson *et al.*, 2001, 2008; Huttunen *et al.*, 2003; Christensen *et al.*, 2007; Roulet *et al.*, 2007) and runoff C export (5–20 g C m^2: Roulet *et al.*, 2007; Nilsson *et al.*, 2008) the annual NEE sink strength reported here indicates that sites with at least 1 complete year of data in this study likely still constitute net sinks for atmospheric C.

Correlation analyses showed that R_{eco} generally had stronger relationships with environmental variables as compared with GPP, except for LAI (and pH on an annual scale), which correlated significantly with GPP and NEE, but not with R_{eco}. Humphreys *et al.* (2006) also found that vegetation indices were important for explaining the spatial variation in the CO_2 exchange in Canadian peatlands, as the maximum CO_2 uptake and ecosystem respiration at reference temperature correlated positively with LAI and aboveground biomass. It has been found for forests that LAI is a key variable for explaining both between-site and

Table 3 Stepwise regressions for between-site summer-time NEE, R_{eco} and GPP vs. environmental variables

	Independents						Model summary			
Dependent	#	Predictors	Coefficients	*t*	*P*	*VIF*	r^2	*F*	*P*	*n*
NEE	0	(constant)	1.316	3.360	0.015	–	0.894	25.349	0.001	9
	1	LAI	−1.069	−6.681	0.001	1.023				
	2	Prec	−0.005	−3.428	0.014	1.023				
R_{eco}	0	(constant)	−0.104	−0.221	0.831	–	0.747	20.659	0.003	12
	1	GS_{length}	0.014	4.545	0.003	1.000				
GPP	0	(constant)	1.206	1.664	0.147	–	0.862	18.661	0.003	9
	1	GS_{length}	−0.017	−4.018	0.007	1.063				
	2	LAI	−1.334	−3.483	0.013	1.063				

NEE, net ecosystem exchange; R_{eco}, ecosystem respiration; GPP, gross primary production; GS_{length}, length of growing season; LAI, leaf area index; Prec, precipitation sum.

Table 4 Correlation coefficients between average annual NEE and its components (R_{eco} and GPP) and ancillary data

	NEE	R_{eco}	GPP	T_{air}	PPFD†	Prec	WB	WTD	VPD	GDD	EVI	NDVI	GS_{length}	GS_{start}	GS_{stop}	LAI	pH
NEE	1	−0.59	0.87*[a]	−0.18	−0.36	0.51	0.85	0.49	−0.57	−0.11	0.16	−0.19	−0.30	0.37	−0.22	−0.96**	−0.96***
R_{eco}		1	−0.91**[b]	0.87*	0.83*	0.27	−0.45	−0.30	0.83*	0.86*	0.42	0.80*	0.92**	−0.90**	0.90**	0.74	0.52
GPP			1	−0.63	−0.69	0.09	0.67	0.48	−0.76	−0.58	−0.18	−0.59	−0.72	0.74	−0.67	−0.90*	−0.81*

*Correlation is significant at the $\alpha = 0.05$ level; **$\alpha = 0.01$ level; ***$\alpha = 0.001$ level (two-tailed significance test).
[a]$P = 0.110 \pm 0.009$ (SD); [b]$P = 0.179 \pm 0.015$ according to ten bootstrap simulations, respectively, accounting for the spurious correlation emanating from the derivation of GPP from the difference between NEE and R_{eco} (see 'Materials and methods').
†PPFD is summed over the growing season period (see 'Materials and methods').
NEE, net ecosystem exchange; R_{eco}, ecosystem respiration; GPP, gross primary production; T_{air}, average air temperature; PPFD, photosynthetic photon flux density; Prec, precipitation sum; WB, water balance sum; WTD, water table depth; VPD, vapour pressure deficit; EVI, enhanced vegetation index; NDVI, normalized difference vegetation index; GS_{start}, start day of growing season; GS_{length}, length of growing season; GS_{stop}, end day of growing season; LAI, leaf area index.

between-year variations in the CO_2 exchange (Schulze, 2006; Lindroth *et al.*, 2008). A high leaf area allows for high light absorption capacity on an ecosystem scale and thus high photosynthetic CO_2 uptake. The two sites with the highest LAI in this study (CA-WP1 and PL-WET, Table 1) had the highest GPP and largest annual CO_2 sink strength (Fig. 2). Both sites also had high pH, which was an important factor in determining annual GPP and NEE (Table 4). pH is not a direct driver of photosynthesis, but instead likely acts as an ecosystem indicator for conditions supporting the factors leading to high LAI and productivity, most importantly nutrient status (Bubier *et al.*, 1998).

The length of growing season period was an important variable in explaining the between-site variation in both R_{eco} and GPP (Tables 2–4, Fig. 3b and c). Many northern peatland and wet tundra ecosystems are limited by low temperatures and short growing seasons (Clymo, 1984; Aurela *et al.*, 2004); and a prolonged growing season due to global warming will allow for a longer period of photosynthesis and decomposition (Gorham, 1991). According to our results, the stimulating effect on GPP will be partly offset by a simultaneous increase in R_{eco}. However, GPP would increase more with a prolonged growing season as compared with R_{eco}; the slope of the regression line was −0.0193 and $0.0141\,g\,C\,m^{-2}\,day^{-1}$ per growing season day for GPP and R_{eco}, respectively (Fig. 3b and c). This finding is consistent with observations that long term C accumulation shows a significant north to south trend of increasing C accumulation at lower latitudes (Beilman *et al.*, 2009). However, the effect of higher temperature on the length of growing season period will be regulated by other factors such as light limitation, especially in the late part of the season, and water availability (Humphreys *et al.*, 2006; Aurela *et al.*, 2007). Increased GPP during growing season may also to some extent be offset by increased R_{eco} during the nongrowing season as a response to a warmer climate.

One of the main characteristics separating peatlands and wet tundra from upland ecosystems is the waterlogged conditions, which have been identified as a key feature allowing peatlands to function as persistent sinks for atmospheric CO_2, due to limited oxygen

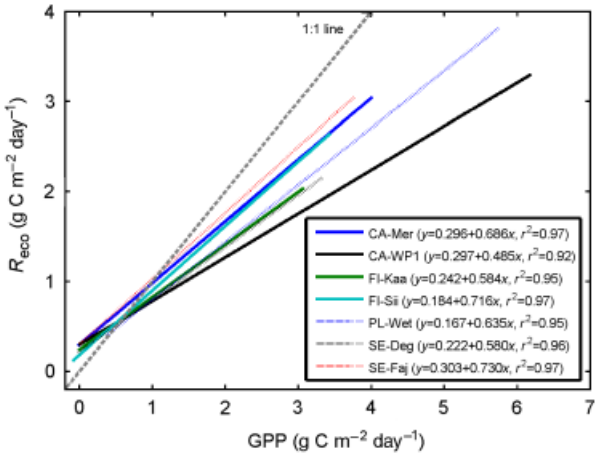

Fig. 4 First order polynomial curve fit of 4-week averages of ecosystem respiration (R_{eco}) as a function of gross primary production (GPP), for sites with full annual dataset. In this figure, GPP has a positive sign to simplify the interpretation. The length of the regression line indicates the data range for each site. An average year has been used for sites with >1 year of data.

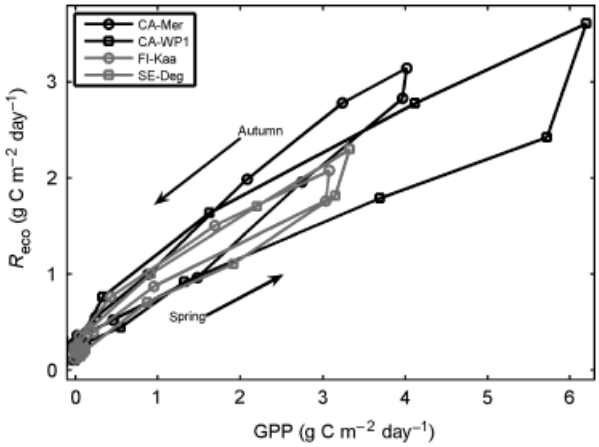

Fig. 5 Relationship between 4-week averages of ecosystem respiration (R_{eco}) and gross primary production (GPP) for CA-Mer, CA-WP1, FI-Kaa and SE-Deg. In this figure, GPP has a positive sign to simplify the interpretation. Within each site data points are connected in temporal order from the beginning to the end of the year (direction indicated by arrows).

diffusion into the soil restraining decomposition (Clymo, 1984). Even though there are considerable differences in climate, nutrient availability, species composition and ecosystem structure between the study sites (Table 1), all of them have suppressed decomposition due to the water-logged conditions to some extent. The observation in this study of higher between-site variation in GPP as compared with R_{eco} (coefficients of variation were 0.40 and 0.31 for GPP and R_{eco}, respectively), supports this argumentation. As a consequence, factors regulating annual plant photosynthesis are of crucial importance for the peatland and wet tundra C balance. The significant correlations between LAI and GPP illustrate that vegetation properties are important for the annual CO_2 exchange. It is known that the litter decay rates differ between various vegetation types; with increasing rates going from *Sphagnum* mosses to shrubs, graminoids and forbs (Aerts *et al.*, 1999; Moore *et al.*, 2007). A changing climate will bring about changes in northern peatland and wet tundra vegetation, and thus most likely also altering the CO_2 flux components, which will regulate the ecosystem response to higher temperatures and changes in local hydrology.

Neither WTD nor WB were found to be significant variables in explaining the variation in CO_2 flux components between sites. Many studies have found that dry conditions affect CO_2 fluxes in wetlands (Shurpali *et al.*, 1995; Lafleur *et al.*, 1997; Alm *et al.*, 1999; Aurela *et al.*, 2007; Lund *et al.*, 2007), and there are concerns that climate change will promote drying in many temperate and boreal peatlands (Tarnocai, 2006). Difficulties in comparing WTD between sites arise from the problem of determining zero datum, especially in topographically complex sites, as well as how representative a point measurement is for the fetch of the EC measurements. As a contrast, WB, which is the difference between precipitation and evapotranspiration, is an integrated measure but in the case of fens it does not take water discharge or recharge into account. Despite the lack of significant correlations in this study, it is well established that hydrology exerts a major control on peatland formation and functioning (Ivanov, 1981). The different peatland types, bog and fen, where the former is decoupled from the groundwater of the surrounding watershed and thus relies entirely on precipitation inputs to maintain its water balance, may react in different ways to changes in precipitation and evapotranspiration (Aurela *et al.*, 2004). Because of their dependence on precipitation, bogs should in general be more sensitive to drought conditions. However, relationships between NEE and WTD are complex and can not be generalized across various wetland types, possibly not even for a single type of wetland (Lafleur, 2009). Nonetheless, it is interesting to notice that precipitation explained a significant proportion of the spatial variation in summertime NEE, after variations in LAI had been accounted for (Table 3). This finding is consistent with the observations that precipitation interception by *Sphagnum* mosses importantly controls *Sphagnum* GPP, especially at low WTDs (Robroek *et al.*, 2009).

The scarcity of significant relationships for annual NEE and GPP with meteorological variables may have several explanations. Firstly, using annual averages may mask the effects of variables working on sub-annual time scales. Secondly, ecosystem response to meteorological variables is most likely different in various wetland types (Glenn *et al*., 2006). In forest ecosystems, Reichstein *et al*. (2007) showed that both GPP and R_{eco} in northern sites were temperature limited, whereas southern sites were limited by water availability. Valentini *et al*. (2000) found that the annual NEE of European forests increased with decreasing latitude, while annual GPP was fairly constant across sites and latitudes. These authors concluded that variations in R_{eco} were responsible for the between-site differences in forest NEE. In this study, as well as in Reichstein *et al*. (2007), a regular Pearson's correlation analysis showed that the between-site variation in NEE correlated significantly with GPP, but not with R_{eco}. However, according to the bootstrap simulation to reveal potential spurious correlation, the flux partitioning method affected this significant result. Still, the associated P value for the nonspurious correlation between NEE and GPP was lower than that between NEE and R_{eco} for both summertime (Table 2) and annual averages (Table 4). This observation, together with a higher between-site variation in GPP as compared with R_{eco} indicates that the spatial variation in NEE is more related to GPP than to R_{eco}.

The bootstrap approach for accounting for the spurious correlation between GPP and R_{eco} suggests that the flux partitioning method had an impact on relationships involving GPP and R_{eco}/NEE (Tables 2 and 4), thus caution is needed in interpreting such analyses. The influence of the flux partitioning method is likely affected by data set size. Indeed, the current scientific understanding of ecosystem functioning implies that a relationship between GPP and R_{eco} should exist. The CO_2 assimilation by photosynthesis ultimately leads to build-up of plant biomass and a general relationship between GPP and autotrophic respiration can therefore be expected (Janssens *et al*., 2001; Flanagan & Johnson, 2005). Autotrophic respiration has been estimated to represent 50–90% of the ecosystem respiration in peatlands (Frolking *et al*., 2002; Moore *et al*., 2002; St-Hilaire *et al*., 2008). Also the heterotrophic respiration should over longer periods of time be dependent on substrate quality and availability (Giardina & Ryan, 2000), which also suggests a relationship with GPP, although with a time lag (Janssens *et al*., 2001). It can be assumed that most of the heterotrophic respiration, especially in water-logged soils, originates from decomposition of relatively young organic matter (Christensen *et al*., 1999; Janssens *et al*., 2001). However, the ratio between young and old organic matter being exposed to aerobic decomposition is regulated by variations in WTD. EC data on R_{eco} cannot be separated into autotrophic and heterotrophic respiration without supporting measurements and modelling exercises (cf. Aubinet *et al*., 2009), which restricts the interpretation of the functional relationship between photosynthesis and respiration components.

The R_{eco} to GPP ratio (Fig. 4) was highest for FI-Sii and SE-Faj (>0.7). There were only 1–1.5 years of data available for these sites (Table 1), and during that time both sites experienced dry summers with drought periods suppressing GPP and increasing R_{eco} rates (Aurela *et al*., 2007; Lund *et al*., 2007). This indicates the impact of dryness on peatland and wet tundra CO_2 exchange, however, it can be assumed that in the absence of drought and for data sets collected under long periods of time when drought periods occurs only infrequently, ratios should generally be lower. The two bogs, CA-Mer and SE-Faj, generally seem to have larger ratios than the fens possibly resulting from lower productivity of the shrub dominated vegetation cover in these sites. The treed fen CA-WP1 had the lowest slope, which may be caused by high productivity of trees and limited heterotrophic respiration due to a high water table. In a study across several ecosystems and sites (Law *et al*., 2002), it was found that the R_{eco} to GPP ratio averaged 0.83, with higher ratios for forests (0.82–0.85) and lower for grasslands (0.74). The even lower average ratio of the sites in this study (0.63) can be attributed to factors such as low decomposition rates due to the wet conditions and the low decomposability of many peatland and tundra plants such as the *Sphagnum* mosses (Aerts *et al*., 1999; Moore *et al*., 2007). Hysterisis between R_{eco} and GPP (Fig. 5) resulted from the comparatively higher R_{eco} rates in the latter part of the growing season. This phenomenon was likely due to an increase in plant and microbial biomass as well as an increased fresh litter input in the late period, allowing for higher autotrophic and heterotrophic respiration rates (Sampson *et al*., 2007). Also a comparatively higher soil temperature during the autumn will lead to increased soil respiration. Such temperature effect is likely more pronounced in wetlands compared with upland ecosystems due to the greater thermal inertia of saturated soils. Soil temperatures in the sites in Fig. 5 were on average 3.3 °C higher between mid-July until mid-October compared with mid-April until mid-July. At the same time, GPP rates fall off quickly in autumn due to vegetation senescence and reduced incoming solar radiation. The water table may also play an important role here because it is often lower in autumn compared with spring, i.e., due to snow melt in the spring, allowing for higher aerobic decomposition rates.

Most models of the C sequestration in peatlands have focused on long time scales (Clymo, 1984; Hilbert *et al.*, 2000; Yu *et al.*, 2003), and were thus not constructed to capture within-site inter-annual variations or between-site differences in CO_2 exchange. Recently, as more data on the contemporary CO_2 exchange in peatlands and tundra have become available, models with a higher time resolution have been presented (Frolking *et al.*, 2002; Yurova *et al.*, 2007; St-Hilaire *et al.*, 2008). Based on the results in this study, GS_{length} and LAI are important drivers of spatial variation in peatland and wet tundra CO_2 exchange. These are variables that can be obtained from global climate grids such as the CRU data set (New *et al.*, 2002), and through remote sensing using, e.g. the Modis Land Product Subsets (http://daac.ornl.gov/MODIS/), thus providing a potential for extrapolation of the CO_2 exchange over the vast areas of northern peatlands and wet tundra. The ability to explain and correctly model the variability in CO_2 flux components in association with the environmental factors controlling it, will be essential to further improve both our present knowledge of current peatland and tundra C balance and our ability to simulate the response of wetlands at large to climate change.

Conclusions

In this study of 12 peatland and wet tundra sites spanning temperate to arctic climates we have found that the NEE of CO_2 and its components (GPP and R_{eco}) were highly variable between the sites. All sites with at least 1 year of complete data were net sinks for atmospheric CO_2. Variability in R_{eco} was lower compared with GPP, likely caused by the high water table suppressing decomposition rates and low decomposability of many peatland and wet tundra species. The length of growing season period correlated with both R_{eco} and GPP, and is thus a key factor determining spatial variation in these fluxes. This finding is important because global warming will prolong the growing season period and thus both R_{eco} and GPP. As both LAI and pH were found to have significant relationships with NEE and GPP, it is of major importance to study the effects of a changing climate on vegetation properties and nutrient conditions in various peatlands and wet tundra, and to include these factors in models of current and future wetland C exchange.

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