Two Bogs in the Canadian Hudson Bay Lowlands and a Temperate Bog Reveal Similar Annual Net Ecosystem Exchange of CO2

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Two Bogs in the Canadian Hudson Bay Lowlands and a Temperate Bog Reveal Similar Annual Net Ecosystem Exchange of CO$_2$

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Abstract

Two ombrotrophic bogs in Canada's Hudson Bay Lowlands (HBL), an area storing an estimated 33 Gt of soil carbon, are contrasted with the Mer Bleue temperate ombrotrophic bog approximately 1000 km to the southeast to assess the net carbon dioxide (CO$_2$) exchange between these ecosystems and the atmosphere. Peatlands in the HBL region may be impacted by not only climate change but also resource extraction practices that may cause drying of surrounding areas. Two years of eddy covariance CO$_2$ flux measurements show the two HBL bogs to be annual sinks for CO$_2$. Given random error and gap-filling uncertainties of 6 to 13 g C m^{-2} yr^{-1}, the annual budgets of 45 to 55 g C m^{-2} yr^{-1} for the HBL bogs did not differ significantly from the temperate bog's budget of 55 g C m^{-2} yr^{-1} (in the first year) despite differences in climate and vegetation composition and abundance. The temperate bog did have significantly greater net uptake of CO$_2$ (78 g C m^{-2} yr^{-1}) in the second study year. Component fluxes of photosynthesis and respiration were much smaller at the HBL bogs and speculated to be a result of less vascular vegetation. Less growing season CO$_2$ uptake at the HBL bogs was offset by less winter loss when compared to the temperate bog. The influence of mid-summer drying and lowered water tables was similar among all three bogs. Decreasing mid-summer net ecosystem productivity (NEP) appeared to be a result of reduced photosynthetic uptake rather than increased respiration. In the short-term, drying of the HBL peatlands might result in a decrease of their C sink strength.

Introduction

The peatlands of the Hudson Bay Lowlands (HBL) make up 90% of a 325,000 km^2 poorly drained plain located southwest of James Bay and Hudson Bay, Canada (Martini, 2006). This massive expanse of peatland is estimated to contain 33 Gt of soil carbon (C), equal to approximately 12% of all the organic C stored in Canadian soils (Tarnocai, 2000; Martini, 2006). Drying of the HBL peatlands may result from climate warming if enhanced evapotranspiration (due to warmer temperatures) is not offset by greater precipitation, although coastal areas of the HBL may also be subject to flooding with sea level rise (Tarnocai, 2006). Drying may also be a potential consequence of resource development such as mining that involves groundwater pumping (Whittington and Price, 2012). Our understanding of peatland C cycling processes in the HBL is therefore critically important due to the potential for large feedbacks to the climate system in response to climate change or other types of disturbances.

There are relatively few multi-year eddy-covariance CO$_2$ flux records for peatlands, particularly in northern boreal and subarctic climates similar to the HBL where mean annual temperatures are near 0 °C. Examples include the Kaamanen fen in Finland (Aurela et al., 2004; mean annual temperature [MAT] = –1.1 °C) with an average (± SD) annual net CO$_2$ uptake of 22 (± 20) g C m^{-2} yr^{-1} over 6 years; the Stordalen palsa mire in Sweden (Christensen et al., 2012; Olefeldt et al., 2012; MAT = –0.5 °C) with 66 (± 29) g C m^{-2} yr^{-1} over 8 years; and Degerö Stormyr fen in Sweden (Nilsson et al., 2008; MAT = 1.2 °C) with 52 (± 5) g C m^{-2} yr^{-1} over 2 years. In the West Siberian Plain, Zotino bog (Arneth et al., 2002; MAT = –1.5 °C) was estimated to have an average annual uptake of 23 (± 2) g C m^{-2} yr^{-1} over 2 years. In Canada, the two longest running peatland study sites include a boreal treed fen in the western part of the country (Flanagan and Syed, 2011;

MAT = 2.1 °C) with a relatively large uptake of 189 (± 47) g C m^{-2} yr^{-1} over 6 years, and the Mer Bleue low shrub bog in a temperate climate (e.g. Roulet et al., 2007; MAT = 6.0 °C) with a net CO$_2$ uptake of 40 (± 40) g C m^{-2} yr^{-1} over 6 years from 1998 to 2004.

The factors influencing differences in net ecosystem exchange of CO$_2$ (NEE) or net ecosystem productivity (NEP, defined here as the negative of NEE) among peatlands are attributed to the abiotic and biotic controls on the component fluxes of ecosystem respiration (ER) and gross ecosystem productivity or photosynthesis (GEP) including climate (air temperature, growing season length, thaw depth), vegetation (amount and composition), and peat characteristics. In a comparison study by Lund et al. (2010), which included a number of the peatlands listed above, it was striking how similar the seasonal and annual net CO$_2$ exchange was for Mer Bleue and the European boreal and subarctic peatlands despite greater ER and GEP and a considerably warmer climate at Mer Bleue.

Interannual variations in NEP can be relatively large as noted for the northern peatlands with multi-year records listed above. Temporal variability in annual NEP is often attributed to variations in weather and its effects on peatland hydrology, particularly water table depth as it affects both vascular and non-vascular plant productivity and autotrophic and heterotrophic (aerobic and anaerobic) respiration processes. With drying, some short-term responses may include greater aerobic decomposition (e.g. Sulman et al., 2010) and/or reduced productivity of the *Sphagnum* moss understory that relies on both precipitation and connectivity with the water table to keep moist and maintain photosynthesis (e.g. Robroek et al., 2009). Low water tables may also cause drought stress in vascular plants, particularly sedge species (Griffis et al., 2000; Bubier et al., 2003; Sonnentag et al., 2010). In contrast, lower water tables have also been shown to stimulate photosynthesis (Bubier et al., 2003; Sulman et al., 2010; Flana-

gan and Syed, 2011), possibly as a result of warmer soil temperatures, greater oxygen, and/or nutrient availability (Shaver et al., 1992). At Mer Bleue, GEP tends to decline with drier conditions (Sulman et al., 2010). Precipitation exclusion and laboratory experiments have shown that at very low capitulum water content, the productivity of the dominant *Sphagnum* moss species at Mer Bleue is reduced (Adkinson and Humphreys, 2010; Chong et al., 2012). Growing season ER may decline with drier conditions at Mer Bleue (Sulman et al., 2010) or may be relatively insensitive to water table variations (Lafleur et al., 2005). Dimitrov et al. (2010) used a comprehensive process model to illustrate how lower water tables at Mer Bleue may allow greater respiration at depth but not result in greater CO2 emissions to the atmosphere when offset by reduced near-surface respiration.

This study documents for the first time the net CO_2 budget for two HBL bogs over a two-year period. These CO_2 fluxes are compared with those measured over the same time period at the temperate Mer Bleue bog located approximately 1000 km to the southeast. These concurrent measurements are used to gain insight on the influence of climate and vegetation structure on the functioning of these peatlands. We hypothesize that the similarity in NEP that was observed for Mer Bleue and northern boreal peatlands in Europe will also hold true for the HBL bogs as a result of compensating factors. For example, shorter growing seasons and less vegetation at the HBL bogs may result in less CO_2 uptake in summer but we also expect less loss of CO_2 over the winter. The response of NEP to summer drought is also examined to see if net CO_2 uptake declines at the HBL bogs as it has been shown to do at Mer Bleue. Using Mer Bleue as a reference, the seasonal variations in NEP are examined to gain insight on how these HBL peatlands may respond in the short term to climate and other disturbances.

Methods

SITE DESCRIPTIONS

In 1990, detailed flux studies of several trace gasses were conducted at peatland sites in the southern HBL under the auspices of the Northern Wetland Study (NOWES) (e.g. Klinger et al., 1994). Eddy covariance measurements of energy fluxes and fluxes of CO_2 and CH_4 were established in a bog near the southwest end of Kinoje (Kinosheo) Lake (51°33′N, 81°49.5′W) (Neumann et al., 1994). In 2009/2010, micrometeorological towers were established in a low shrub bog at the north end of Kinoje Lake (51°35′N, 81°46′W) and in a bog-fen complex in the Attawapiskat River region of the HBL (52°41′N, 83°56′W) (Fig. 1). These sites were co-located with several intensive research efforts to examine historical hydrology, fire, and peatland carbon storage in the HBL (McLaughlin and Webster, 2014).
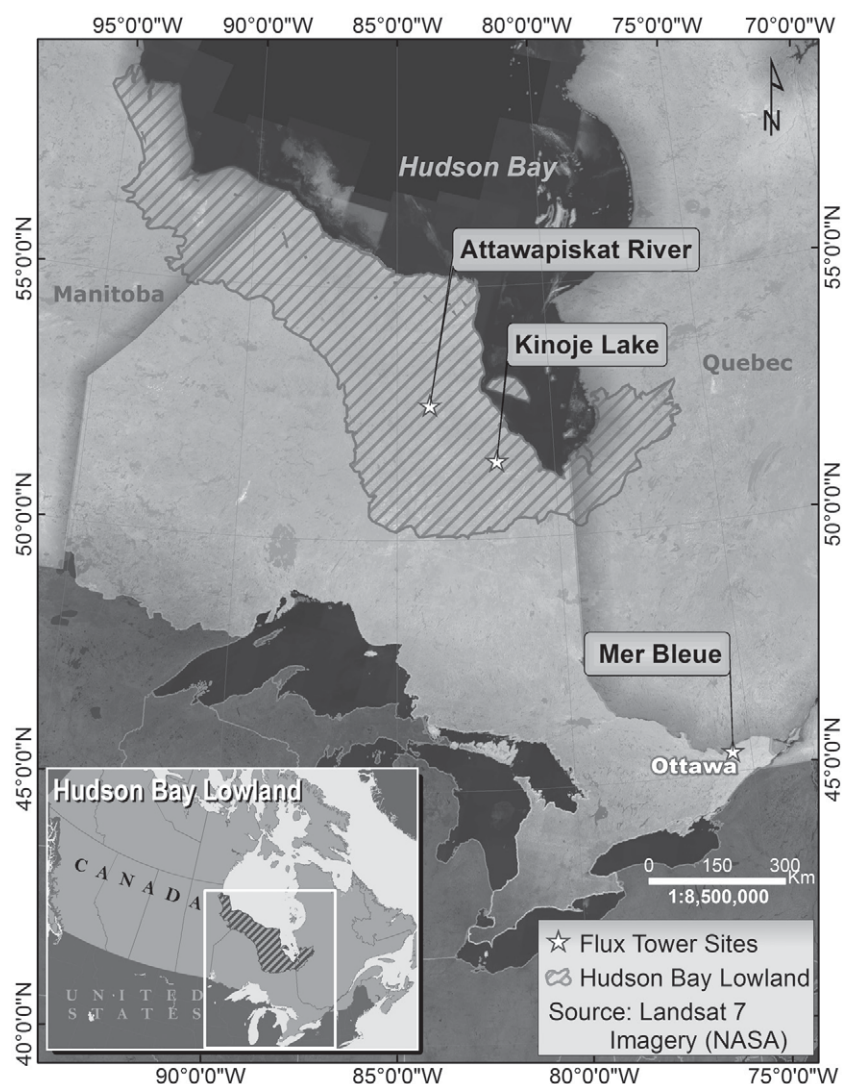

FIGURE 1.   Map locating the extent of the Hudson Bay Lowlands physiographic region and the three flux tower sites in Ontario, Canada.

The Attawapiskat River region is highly heterogeneous and is dominated by both bog and fen peatlands. The Attawapiskat River tower site (AR) discussed here is situated in a treed/low shrub bog (National Wetlands Working Group, 1997). In well drained areas, *Sphagnum* mosses including *S. fuscum,* (Schimp.) H.Klinggr., *S. rubellum* Wils., and *S. magellanicum* Brid. cover about 50% of the surface, while lichens account for the remaining 50% (the *Cladonia* group of lichens). The understory is dominated by *Chamaedaphne calyculata* (L.) Moench (Table 1). Lichens are virtually absent in low areas and instead the vegetation is dominated by *Sphagnum* species and sedges. Stunted black spruce [*Picea mariana*, (Miller) BSP], and to a lesser extent tamarack [*Larix laricina* (Du Roi) K. Koch] are found in hummock areas of the bog (Fig. 2). Other vegetation characteristics are outlined in Table 1. Peat thickness is just over 2 m near the center of the flux footprint area (McLaughlin, personal correspondence, 2012). The bog is surrounded by fen areas and networks of open pools with fetch from the tower restricted by these features ~450 m to the east and west and ~1000 m to the north and south.

The Kinoje Lake site (KL) is located 200 km to the south of AR. The region is dominated by low shrub bogs characterized by *Sphagnum* moss, some sedges, low ericaceous shrubs, and scattered *P. mariana*. In 1990, the bog where the NOWES flux tower was located was characterized by a patchwork of raised lichen [*Cladonia alpestris* (Opiz) Pouzar & Vezda] and moss (*Sphagnum* spp.) covered hummocks and wet hollows of lichen-rich peat, the latter often associated with surface pools of water (Neumann et al, 1994). Ericaceous shrubs and isolated stunted *P. mariana* trees were found on some hummocks. The mosses and lichens accounted for 75 to 90% of the living, non-woody biomass of the hummocks and 80% of the biomass of the moist hollows (Klinger et al, 1994). The bog at the new tower location is visually very similar (Fig. 2); *Sphagnum* accounts for 50–60% of the surface cover, while lichens and sedges account for the remaining cover (20–30% and 10–25%, respectively). Other vegetation characteristics are outlined in Table 1. The fetch from the tower is restricted to ~200 to 300 m between the south and southeast and to the west by trees along riparian areas but otherwise extends ~500 m. To the northeast of the tower, surface pools are common. At the NOWES flux tower site, peat depth ranged from 1.4 to 2.7 m. Basal peat ages ranged from about 3200 to 4100 years (Klinger et al., 1994).

The Mer Bleue site (MB) is located within a 2800 ha wetland complex in the Ottawa Valley–St. Lawrence Lowland (45°24′N, 75°30′W) just outside the city of Ottawa and about 1000 km south-

TABLE 1

Vascular vegetation characteristics for the three bog sites. Values are means ± 1 standard error. Values in parentheses for the density estimates are 95% confidence intervals.

	Attawapiskat River (AR)	Kinoje Lake (KL)	Mer Bleue (MB)
Plant area index	0.45 ± 0.08	0.35 ± 0.05	2.00 ± 0.18*
Tree density[1] (stems/ha)	446 (290, 689)	0	14+
Small tree density[2] (stems/ha)	1419 (1088, 1836)	929 (635,1361)	60+
Total above ground understory biomass (g m^{-2})	84.0 ± 17.7	104.2 ± 27.4	476.8 ±41.5^
Understory above ground biomass by species (g m^{-2})			
Andromeda glaucophylla Link.	1.3 ± 0.9	0 ± 0	0.5 ± 0.5
Chamaedaphne calyculata (L.) Moench	50.3 ± 15.6	28.9 ± 13.3	153.4 ± 34.3
Empetrum nigrum L.	0 ± 0	19.6 ± 18.4	0 ± 0
Graminoids	20.1 ± 3.9	39.6 ± 23.5	9.6 ± 3.4
Kalmia angustifolia L.	0.5 ± 0.4	5.5 ± 1.8	70.0 ± 12.3
Kalmia polifolia Wangenh.	2.1 ± 0.6	4.5 ± 1.8	0.7 ± 0.4
Larix laricina (understory) (Du Roi) K. Koch	0 ± 0	0 ± 0	0.8 ± 0.6
Maianthemum trifolium (L.) Sloboda	2.3 ± 1.6	0 ± 0	0.5 ± 0.2
Picea mariana (understory) (Miller) BSP	0.1 ± 0.1	0 ± 0	0 ± 0
Rhododendron groenlandicum (Oeder) Kron & Judd	1.6 ± 0.9	1.3 ± 0.9	75.6 ± 12.4
Rubus chamaemorus L.	3.5 ± 1.8	1.3 ± 0.7	0 ± 0
Sarracenia purpurea L.	0.6 ± 0.5	0.5 ± 0.5	0 ± 0
Vaccinium myrtilloides Michx.	0 ± 0	0 ± 0	118.0 ± 31.5
Vaccinium oxycoccus L.	1.5 ± 0.6	2.9 ± 1.8	12.6 ± 2.4

*Green leaf area index at MB has been reported using other methods as 1.3 (Moore et al., 2002) to 1.5 (Strilesky and Humphreys, 2012).
+Total count within a 150 m radius West through East around the flux tower in winter.
^ The total understory vegetation includes some species not listed here.
[1] Trees large enough to have a diameter >1 cm at 1.3 m height.
[2] Trees smaller than above but greater than 50 cm tall.

FIGURE 2. Summer images of (1) the treed/low shrub bog near Attawapiskat River in the Hudson Bay Lowlands (HBL), (2) the low shrub bog at Kinoje Lake in the HBL, and (3) the Mer Bleue low shrub bog near Ottawa, Ontario.

east of the HBL sites. The study area is located within a low shrub domed bog where peat thickness ranges from <0.3 m at the margins to >5 m at the center (Roulet et al., 2007). Bog development began 7100–6800 years ago (Roulet et al., 2007). The bog around the tower has a near-continuous ground cover of *Sphagnum* spp., mainly *S. capilifolium* (Ehrh.) Hedw. and *S. magellanicum*, with *Polytrichum strictum* Brid. and an overstory of ericaceous shrubs (Bubier et al., 2006). A few scattered trees are present in the flux tower footprint (*L. laricina, Betula populifolia* Marshall*,* and *P. mariana*) (Fig. 2). Further vegetation characteristics are outlined in Table 1. The area is relatively homogeneous for approximately 200 m in all directions. The area between 130° and 190° toward the tower structure, instrument huts (15 m away), and beaver pond (200 m away) is excluded from the analysis. Depending on direction, the bog beyond 250 m to 700 m from the tower becomes increasingly treed.

FLUX AND ANCILLARY MEASUREMENTS

The eddy covariance (EC) method is used to measure nearly continuous fluxes of CO_2 and energy exchange at all three peatland sites. The 30 min covariance of vertical velocity and the appropriate scalar entity is used to compute a flux. Vertical velocity was measured using sonic anemometers (models HS-50 at KL and AR and R3-50 at MB; Gill Instruments, Lymington, U.K.). For CO_2 fluxes, high frequency CO_2 mixing ratios were derived using measurements from infrared gas analyzers (models LI-7200 at KL and AR and LI-7000 at MB; LI-COR Inc., Lincoln, Nebraska, U.S.A. [LI-COR]). At MB, CO_2 mixing ratios were derived from instantaneous measures of CO_2 and H_2O mole fractions on air drawn down a 4 m sampling tube at 18 L min^{-1} resulting in a delay of 0.7 and 0.8 s relative to the sonic anemometer signals. At KL and AR, CO_2 mixing ratios were computed by the internal LI-7200 software (LI-COR) using high frequency temperature, water vapor, and pressure readings (Burba et al., 2012). All measurements were made at a rate of 10 Hz (KL and AR) or 20 Hz (MB). All high frequency eddy covariance data were captured and stored on the LI-7550 Analyzer Interface Unit (LI-COR) at KL and AR and on a personal computer at MB. Supporting structures varied among sites. At MB, EC instruments were mounted 3 m above the surface on a 1-m-long boom oriented to the N of a 5-m-tall triangular tower. At KL, the EC instruments were mounted on a stainless steel tripod 3 m above the surface, 75 cm from the tower mast, and oriented to the southeast. At AR, a 5 m scaffold structure supported a mast on which the EC instruments were mounted 7.5 m above the surface and 60 cm from the tower mast, oriented to the northwest. Sensors were

high enough so that any nearby trees were below these heights and could be considered within the flux footprint At all sites the daytime 80% cumulative flux footprint contour was typically <300 m upwind of the tower.

A suite of meteorological and soil parameters were measured at each monitoring tower to provide context to the flux measurements. Net radiation was measured using a net radiometer (CNR1 or CNR4, Kipp & Zonen, Delft, Netherlands), and incoming photosynthetically active radiation (PAR) and reflected PAR were measured using quantum sensors (LI-COR). Air temperature (T_{air}) and relative humidity were measured at 2, 3.2, and 4.7 m at MB, KL, and AR, respectively, using shielded and aspirated temperature humidity probes [HMP45C(212), Campbell Scientific Inc., Logan, Utah, U.S.A. (CSI)]. Rainfall was measured using tipping bucket rain gauges (TE252M, Texas Electronics Inc., Dallas, Texas, U.S.A.). Peat temperature was measured in two pits at each site (representing higher and lower microtopography) at 2, 5, 10, 20, 40 (or 50), and 100 cm with thermocouples (MB) or thermistors (CS107; CSI). Volumetric water content of the peat was also measured in 2 pits at 10, 20, 40, and 50 cm. Water table depth was measured at each tower using a pressure transducer within a well (OTT CS450; CSI). All meteorological and soil measurements were recorded at 2–5 s intervals and averaged every 30 min.

The density of trees >50 cm tall was determined at AR and KL using the variable area transect method (Parker, 1979). At MB, a winter field survey of every tree (above the ~50-cm-deep snow) in the northern half of a 150-m-radius area around the flux tower was carried out. Plant area index (including both leaf and stem area) was measured with an optical sensor (LAI-2000; LI-COR) near the time of peak biomass. Biomass of understory vascular vegetation was measured by destructively harvesting plants at the peat surface in eight 50 × 50 cm plots at AR and KL and at 30 plots at MB originally presented by Strilesky and Humphreys (2012).

FLUX DATA PROCESSING

A common procedure was used at all sites to compute fluxes, assess quality, and fill gaps in the data set. Fluxes of CO_2 were computed from the covariance of high frequency fluctuations from the mean CO_2 mixing ratio and vertical velocity (Webb et al., 1980) recorded over a 30 min period. A 3-axis coordinate rotation was applied in all cases. No spectral corrections were applied. Quality control of all turbulent fluxes included removing 30 min periods when vertical velocity or sonic temperature statistics indicated

the sonic anemometer transducers were obstructed by ice, for example. Similarly, the standard deviations of H_2O and CO_2 were filtered when possible by the sensor diagnostic signal and then limited to plausible values. When the nearest 30 min periods to an automatically rejected value or set of values also showed similar issues, these were rejected manually. Turbulent fluxes were also rejected when the difference between the values computed using block averaging differed by more than 100% from those computed using linear detrending. Flux measurements were then separated into day- and nighttime periods and were excluded when they exceeded 3 standard deviations from the mean value computed during a 30-day window.

The cold season was defined when the 3-day running mean (with no phase shift) of 5 cm soil temperature was below 0 °C. At night and during the cold season, a friction velocity threshold of 0.1 m s^{-1} was used to remove fluxes when turbulence was insufficient. NEP values indicating uptake of CO_2 greater than 0.48 mmol m^{-2} s^{-1} were also removed at night and during the cold season. This threshold was related to the standard deviation of the random measurement error associated with a flux of zero (given that photosynthetic uptake of CO_2 is not expected) for MB. Following Richardson et al. (2006) a relationship between CO_2 fluxes and the standard deviation of the random measurement error was developed for each site for the two study years. The relationships illustrate how the standard deviation of the random measurement error scales with the magnitude of the CO_2 flux. The relationships were similar among sites for both positive and negative fluxes and similar to a grassland site (Richardson et al., 2006) during daytime periods, but smaller standard deviations were observed at these bog sites at night.

NEE is calculated as the sum of CO_2 flux and the rate of change in storage below the eddy covariance instrumentation. NEP is defined as the negative of NEE such that positive NEP indicates net uptake of CO_2 by the peatland. Gaps of one and two 30 min intervals were linearly interpolated for all data traces. For NEP, longer gaps were filled using the following procedure for each study year. An exponential temperature response model (Lloyd and Taylor, 1994),

$$ER = R_{10}e^{308.56\left(\left[\frac{1}{56.02}\right]-\left[\frac{1}{T-227.13}\right]\right)},\qquad(1)$$

where R_{10} is the respiration rate at 10 °C, and T in K was determined using the negative of nighttime NEP (assumed to be equivalent to ecosystem respiration, ER) and 5 cm soil temperature for July and August of each year. Estimates of ER were calculated for all daytime 30 min intervals and missing nighttime 30 min periods outside of the cold season. To account for seasonal variations in ER due to factors other than soil temperature, such as phenology and soil moisture, modeled values of ER (Equation 1) were multiplied by a moving window parameter, calculated as the slope of the linear regression between modeled and measured ER values. Each window constituted 200 consecutive 30 min measurements (ranging between 7 days and 2 months) and was moved in an increment of forty 30 min measurements at a time. For daytime and nighttime periods during the cold season, missing NEP was filled with the mean NEP from 200 consecutive 30 min measurements. Next, daytime estimates of gross ecosystem production (GEP) during the non-cold season were estimated by adding measured and modeled ER to the negative of measured NEE. A rectangular hyperbolic relationship between GEP and PAR (e.g. Whiting, 1994),

$$GEP = \frac{GP_{max}\alpha PAR}{\alpha PAR + GP_{max}}\qquad(2)$$

where GP_{max} is the maximum photosynthesis and α is the photosynthetic efficiency, was evaluated for July and August of each year. GEP computed from this relationship was then adjusted to match the seasonal variations in GEP using the same procedure for ER above. Missing daytime NEP were filled using the difference between modeled GEP and ER.

Equations 1 and 2 were combined and parameterized for 10 day periods using only measured NEP, PAR, and T during the growing season to gain insight on seasonal variations in (GP_{max}) and (R_{10}) using non-linear least-squares regression (MathWorks Inc., 2008).

Systematic errors and biases associated with the choice of friction velocity threshold, empirical relationships, and driving variables chosen for the gap-filling routines, etc., were expected to influence the data sets in similar ways given the same procedures were used at all sites and both study years. To quantify the effect of random measurement errors on uncertainty in the parameterization of the gap-filling model (s_R) and the uncertainty associated with multi-day gaps (s_{LG}), a procedure similar to that of Richardson and Hollinger (2007) was carried out. First, a gap-free fully synthetic data set was developed using the gap-filling procedure described above. Gaps were inserted into these data sets to correspond to observed gaps in the measurements. A Monte Carlo procedure involved first adding artificial noise to the synthetic data set by randomly drawing a value from a Laplace distribution of the random flux measurement error. The random flux measurement error was a function of CO_2 flux and was described above. The gap-filing procedure was then carried out and the results used to gap-fill the data set. These steps were repeated 500 times. The standard deviation of the NEP, GEP, and ER sums for the year and seasonal periods of interest were calculated ($n = 500$).

The proportion of data missing or removed through quality control procedures amounted to 23, 29, and 37% at MB, AR, and KL, respectively. Much of this was due to power loss in winter at KL and AR (between 46 and 116 days during a particular winter), while MB had periodic power outages or computer issues lasting between 4 and 8 days that could occur at any time during the year. To assess the uncertainty in annual and seasonal CO_2 fluxes associated with the timing and duration of these long data gaps, 30% of the noise-free synthetic data set described above was replaced with random 30 min gaps, while a second version also received long gaps with the same length as observed at the sites. These steps were repeated for each site and each study year with the long gaps moving in increments of one day through the season in which the long gap occurred (see Fig. 3 for how seasons were defined). For example, at AR, an 89 day gap observed during the winter/spring of 2010/2011 was applied beginning November 2010 and shifted by one day 91 times. The standard deviation of the difference in annual and seasonal NEP, GEP, and ER calculated from these two data sets represented s_{LG}. The total uncertainty (s_{TOT}) was the sum of s_R and s_{LG} added in quadrature where 2 s_{TOT} represented an estimate of the 95% confidence intervals for total annual and seasonal NEP, GEP, and ER. Annual and seasonal fluxes were considered significantly different among sites when theses 95% confidence intervals did not overlap.

Results

There was remarkable similarity in annual NEP among the three bogs in year 1 despite significant differences in growing season weather, NEP, GEP, and ER (Tables 2 and 3; Fig. 3). In year 2, MB had much greater winter losses of CO_2 but a relatively productive spring and 1.6 to 1.9 times the growing season NEP compared to KL and AR (Fig. 3). This resulted in an annual uptake of CO_2 of 78 g C m^{-2} yr^{-1} compared to the 53 to 55 g C m^{-2} yr^{-1} at AR and KL, respectively. This difference exceeded the 95% confidence intervals associated with random measurement error and gap filling uncertainty and suggests there was significantly greater net CO_2 uptake at MB in year 2 (Table 3; Fig. 3).

An estimate of the photosynthetic potential (GP_{max}) (Table 4) and growing season GEP (Table 3) at MB was 2 to 3 times that of AR and KL. This may be attributable to the much greater vascular plant biomass at MB (Table 1). More biomass at MB likely also resulted in greater rates of autotrophic respiration. At MB, R_{10} was roughly 1.5 that of AR and KL. Since annual and growing season ER was about 2 to 2.5 times greater at MB, warmer conditions and possibly the lower water table (Fig. 4) and thus a greater volume of unsaturated peat may have also been important in driving these greater rates of respiration. During the growing season, these larger component fluxes at MB offset each other to result in daily NEP that was often similar to those of the northern sites; however, there was greater day-to-day variability at MB. For example, the average (± SD) daily NEP was 0.68 ± 0.51 g C m^{-2} d^{-1}, 0.57 ± 0.44 g C m^{-2} d^{-1}, and 0.74 ± 0.86 g C m^{-2} d^{-1} at AR, KL, and MB, respectively, during July and August during the two study years. On cloudy summer days in particular, MB could have a net loss of CO_2 as large as 1.5 to 2.5 g C m^{-2} d^{-1} as GEP dropped and ER remained relatively high. Similar weather resulted in net CO_2 loss no greater than 0.9 g C m^{-2} d^{-1} at KL and AR (Fig. 4, top panels). Differences in growing season NEP between the HBL peatlands and MB (Fig. 3; Table 3) were also due to differences in their seasonality. Daily NEP became positive much earlier in the year at MB, suggesting an earlier onset of the growing season by approximately 30 days

in year 1 and 50 days in year 2 (Fig. 3), as would be expected in this warmer climate with earlier snowmelt (Table 2). Daily NEP became negative nearly all at the same time in year 2 but earlier at MB in year 1 (Fig. 3).

Slightly greater growing season NEP at AR relative to KL appeared to be driven by greater growing season GEP at AR (Table 3). Greater GP_{max} was also observed at AR, particularly in year 1 (Table 4). Aboveground understory vascular biomass and plant area index were similar between the two sites, but AR had far more large trees (Table 1). It is possible these trees may have played a small but important role in driving these differences in ecosystem level GEP. There was effectively no difference in R_{10} or growing season ER between the two sites. This is in spite of warmer air temperatures and deeper mid-summer water table at KL, particularly in year 1 (Table 2; Fig. 4).

To account for differences in winter ER among sites, particularly in year 2, winter air and soil temperatures, snow depth and duration, and readings of soil moisture based on the dielectric permittivity of the soil were examined. Snow depth was similar at all 3 bogs and exceeded 50 cm in depth for at last some part of the winter in year 2. However, it fell earlier and remained longer at AR and KL (~140 to 165 days) relative to MB, where it lasted 80 and 100 days during year 1 and year 2, respectively. Despite air temperatures dipping below –30 °C at all three sites, peat temperature 1 m below the hummock surfaces only cooled to ~1.3 to 1.5 °C by the end of May at AR and KL. At MB, minimum temperatures at 80 cm and 150 cm were 1.9 and 3.9 °C at the end of April and early May in year 1 and 3.2 and 5.0 °C at about the same time in year 2. During both winters, peat remained unfrozen at 50 cm below the hummock surfaces at all three sites with minimum temperatures between 0.4 and 0.5 °C at AR and KL and between 0.4 °C (year 1) and 1.6 °C (year 2) at MB. Above this depth, a drop in the 20 cm soil moisture readings illustrated the time when a significant portion of the peat water froze at that depth. At MB, the peat at this depth was frozen for most of January and February in year 1 but only for a few weeks in February during the second winter. Less freezing may have been the cause for the

TABLE 2

Climate normals (CN) and selected weather observations (if available) for the three flux tower locations during study year 1 from 1 Nov 2010 to 31 Oct 2011 (Yr 1) and year 2 from 1 Nov 2011 to 31 Oct 2012 (Yr 2).

	Attawapiskat River (AR) 52.70°N, 83.94°W			Kinoje Lake (KL) 51.59°N, 81.77°W			Mer Bleue (MB) 45.41°N, 75.52°W		
	CN	Yr 1	Yr 2	CN	Yr 1	Yr 2	CN	Yr 1	Yr 2
Annual air temperature (°C)	–1.3	0.2	0.0	–1.1	1.4	1.3	6.0	6.6	6.7
May–August air temperature (°C)	13.4	13.1	13.4	12.0	13.7	14.3	18.0	18.2	18.6
November–April air temperature (°C)	–13.4	–11.2	–11.0	–12.4	–9.6	–9.6	–3.7	–3.2	–0.9
Annual precipitation (mm)	699.5	—	—	681.6	—	—	943.5	—	—
May–August rainfall (mm)	241.7	233.4	186.1	301.9	143.5	239.4	341.7	357.4	265.4
Final snow melt date (DOY)	—	120	90	—	112	98*	—	77	73
Climate normal data source (Environment Canada)	Lansdowne House, ON (1971–1989) 52°14′N, 87°53′W			Moosonee, ON (1971–2000) 51°16′N, 80°39′W			Ottawa MacDonald-Cartier Int'l Airport, ON (1971–2000) 45°19′N, 75°40′W		

*KL was temporarily snow-free for 4 days beginning on DOY 80.
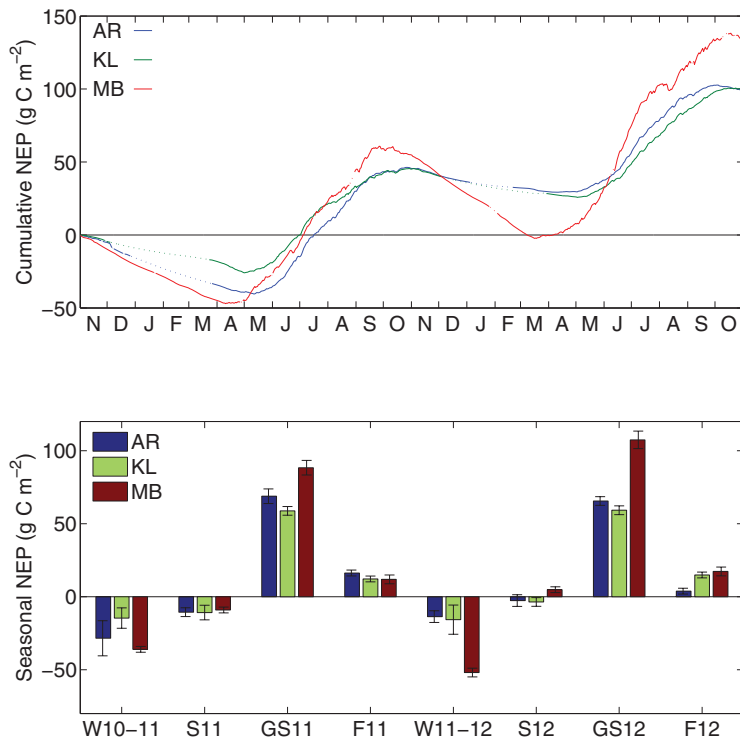
ON = Ontario.

DOY = Day of year.

FIGURE 3. Cumulative net ecosystem productivity (NEP) from November 2010 to the end of October 2012 at the Attawapiskat River (AR), Kinoje Lake (KL), and Mer Bleue (MB) bogs (top panel). Dashed lines indicate periods with gaps in the data of a day or more. Bottom panel depicts total NEP for this period for winter (W, November through February), spring (S, March and April), growing season (GS, May through August), and fall (F, September and October). The total uncertainty associated with random measurement errors and filling multi-day gaps in the dataset are presented as 95% confidence intervals (= 2 s_{TOT}) of the seasonal NEP, in g C m^{-2} for each period.

42% greater ER during MB's second vs. first winter. At AR and KL, the peat at 20 cm depth froze at both sites in both years for a much longer period relative to MB, from late December through early May and may be important in limiting the winter ER at AR and KL relative to MB (Fig. 3).

Differences in water table patterns between the two years were observed at all three sites (Fig. 4) and allowed us to examine the influence of drier peat conditions on NEP. In the first growing season, there was about 96 mm less rainfall at KL in year 1 compared to year 2 and just over a month where the water table remained 40 cm or more below the surface in year 1 (Table 2; Fig. 4). In year 2 at MB, a long dry period in the summer resulted in

a minimum water table depth of –78 cm, 26 cm deeper than the minimum water table depth of the previous year. At AR, there was just a subtle difference in water table depth patterns, with the low occurring mid-July in year 1 while the low occurred in mid-August in year 2 (Fig. 4).

The drier summers did not result in less NEP for any site (Table 3). There was no difference in total growing season NEP at KL or AR, while at MB it was greater during the drier year. Nevertheless, all sites showed evidence of a mid-summer decrease in daily NEP (Fig. 4, top panels) coinciding with the minimum water table depth from mid-July into early August. This timing also coincides with maximum 5 cm soil temperature (Fig. 4, bottom

TABLE 3

CO$_2$ exchange components (NEP: net ecosystem production, GEP: gross ecosystem production, ER: ecosystem respiration) for annual and growing season periods during study year 1 from 1 Nov 2010 to 31 Oct 2011 and year 2 from 1 Nov 2011 to 31 Oct 2012. The total uncertainty associated with random measurement errors and filling multi-day gaps in the data set are presented as 95% confidence intervals (=2 s_{TOT}) of the annual and growing season sum, in g C m^{-2} period^{-1}.

(g C m^{-2} period^{-1})	Attawapiskat River (AR)		Kinoje Lake (KL)		Mer Bleue (MB)	
	Yr 1	Yr 2	Yr 1	Yr 2	Yr 1	Yr 2
Annual						
NEP	46 ± 13	53 ± 6	45 ± 9	55 ± 11	55 ± 7	78 ± 7
GEP	323 ± 6	299 ± 6	295 ± 4	298 ± 4	651 ± 8	760 ± 8
ER	277 ± 14	246 ± 7	250 ± 10	243 ± 12	596 ± 11	682 ± 13
May through August						
NEP	69 ± 5	66 ± 3	59 ± 3	59± 3	88 ± 5	107 ± 6
GEP	243 ± 4	232 ± 3	222 ± 3	224 ± 4	466 ± 7	539 ± 7
ER	174 ± 5	166 ± 4	163 ± 4	165 ± 5	378 ± 9	432 ± 11

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TABLE 4

The mean (± 1 standard deviation) of the parameters for the light and temperature response function (Equations 1 and 2) at the three bog sites for the 10-day periods during the 2011 and 2012 growing seasons (May through August) ($n = 12$). GP_{max} is the maximum photosynthesis, α is the photosynthetic efficiency, R_{10} is the respiration rate at 10 °C, and R^2 is the range in coefficients of determination found for the parameterizations.

	Attawapiskat River (AR)		Kinoje Lake (KL)		Mer Bleue (MB)	
	Yr 1	Yr 2	Yr 1	Yr 2	Yr 1	Yr 2
GP_{max} ($\mu mol\ m^{-2}\ s^{-1}$)	5.2 (2.5)	4.9 (1.9)	4.4 (2.2)	4.5 (1.9)	10.7 (3.0)	12.4 (3.5)
α (mol CO_2 mol^{-1} PAR)	0.018 (0.009)	0.019 (0.009)	0.021 (0.011)	0.020 (0.012)	0.028 (0.008)	0.031 (0.007)
R_{10} ($\mu mol\ m^{-2}\ s^{-1}$)	1.2 (0.3)	1.2 (0.1)	1.0 (0.2)	1.0 (0.2)	1.5 (0.2)	1.7 (0.2)
R^2	0.50–0.86	0.66–0.89	0.32–0.84	0.64–0.93	0.81–0.95	0.78–0.92

panels). However, since the mid-summer drop in daytime NEP in year 1 at AR and KL and year 2 at MB was not accompanied by any difference in nighttime NEP (i.e. respiration) between years (Fig. 4, middle panels), this suggests the water table drawdown resulted in less photosynthesis rather than greater respiration (due to increased temperatures and/or more aerated peat) at all three sites. A similar temporal pattern was found for GEP and GP_{max} (data not shown) at all three sites.

Discussion

Two HBL peatlands have been shown here to be annual CO_2 sinks. The rate of CO_2 uptake, 1.7 g CO_2 m^{-2} d^{-1} (0.5 g C m^{-2} d^{-1}),

measured in 1990 by micrometeorological techniques for the period 25 June to 28 July 1990 (Neumann et al., 1994) was only slightly less than what we observed for the same dates in 2011 and 2012 (0.7 and 0.8 g C m^{-2} d^{-1}, respectively). For the same time period, air temperature was 1 and 1.5 degrees warmer in 2011 and 2012, respectively while rainfall over these three years was very similar, within 4 mm. However, since there is considerable year-to-year variability in peatland NEP (e.g. Roulet et al. 2007), any decadal-scale changes in CO_2 exchange are difficult to identify without long-term, continuous flux measurements at a given location.

Adding these two HBL sites to the body of literature that examines annual (or nearly annual) NEP or NEE of peatland ecosystems (e.g. Lindroth et al., 2007; Lund et al., 2010) slightly extends
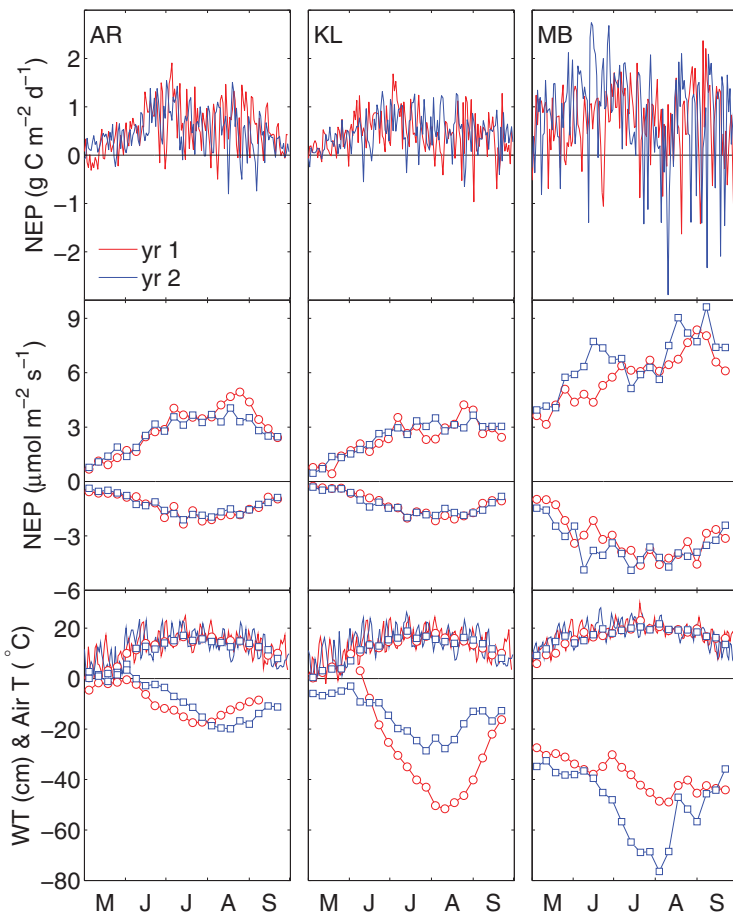

FIGURE 4. Daily total net ecosystem productivity (NEP) (top panels); 7-day average daytime NEP (positive values, middle panel) and nighttime NEP (negative values, middle panel); and average daily air temperature (Air T, lines), 7-day average 5-cm soil temperature (symbols) and daily (lines) and 7-day average water table depth (WT, symbols) for May through September 2011 and 2012 (bottom panel). In all panels, year 1 (2011) is shown in blue and/or as squares and year 2 (2012) is shown in red and/or as circles. Left panels are Attawapiskat River (AR) data, middle column panels are Kinoje Lake (KL) data, and right panels are Mer Bleue (MB) data.

the coverage of mean annual temperatures. AR and KL now join the Kaamanen fen in Finland (Aurela et al., 2004; –1.1 °C) and Zotino bog (Arneth et al., 2002; –1.5 °C) as the coolest non-tundra peatland sites. Lund et al. (2010) found that annual air temperature did not correlate with annual NEE (where MB was one of the study sites). Given the similarity in annual NEP between MB and our two HBL peatlands, at least in year 1, these results again support this finding. Mean annual NEP at KL and AR (50 g C m^{-2}) was greater than the average CO_2 uptake at Zotino bog (23 g C m^{-2}) and Kaamanen (22 g C m^{-2}) but fell within the 5-year range observed at Kaamanen (4 to 53 g C m^{-2}) and within the ranges observed at the Swedish peatlands with MAT near zero as described earlier (Christensen et al., 2012; Nilsson et al., 2008; Olefeldt et al., 2012). In terms of the longer record of annual NEP at MB, the HBL NEP also fell within its wide interannual range (10 to 140 g C m^{-2}) (Roulet et al., 2007).

Lund et al. (2010) did find a significant relationship between summer NEE (June–August) and LAI, although there was considerable scatter for sites with LAI < 2 (see Fig. 3a *in* Lund et al., 2010). This latter situation was also the case for the AR, KL, and MB sites where average (± SD) daily June–August NEP was 0.7 ± 0.5, 0.6 ± 0.5, and 0.8 ± 0.9 g C m^{-2} d^{-1} and was associated with LAI of 0.45, 0.35, and 2.0, respectively. Some studies have noted the importance of plant functional types in addition to LAI or total biomass in terms of explaining site to site variability in net CO_2 exchange. For example, consideration of the proportion of sedge biomass was important in explaining why MB, with about 1.5 times the green vascular plant biomass but little sedge biomass, had nearly identical net CO_2 exchange as a mesotrophic flark fen in northern Finland (Aurela et al., 2004) with ~47 g m^{-2} sedge biomass (Laine et al., 2012). In our study, the contribution of trees to the biomass at AR would likely have been significant. However, as found by Strilesky and Humphreys (2012), an overstory of stunted black spruce trees had relatively little impact on NEP of a treed bog near the MB site due to their relatively low productivity. For summer GEP and ER, Lund et al. (2010) found these correlated best, not with LAI, but with growing season length (see Fig. 3b and 3c *in* Lund et al., 2010). For example, the average growing season length at AR and KL for the two years was 146 days (based on consecutive 7-day average 5 °C air temperature limit). Lund et al.'s (2010) relationship predicts June–August GEP and ER to be ~3 and ~2 g C m^{-2} d^{-1}, respectively. Observed average (± SD) daily June–August GEP and ER were slightly less at 2.3 ± 0.6 and 1.7 ± 0.4 g C m^{-2} d^{-1} at AR and 2.2 ± 0.5 and 1.6 ± 0.5 g C m^{-2} d^{-1} at KL. For MB, the average 197 day growing season GEP and ER is predicted to be ~4 and ~2.7 g C m^{-2} d^{-1} using Lund et al.'s (2010) relationship, which is slightly less than observed values of 4.6 ± 0.9 and 3.8 ± 0.7 g C m^{-2} d^{-1}, respectively, in 2011 and 2012. Overall, the large-scale drivers of spatial variation in summer NEP identified by Lund et al. (2010) appear to apply to our HBL peatlands.

Some apparent spatial variations in peatland NEP may also be driven by different responses to summer drought events. With only two years of data, definitive responses of NEP to summers with low water tables are not possible. However, these first two years suggest a response similar to what has been observed at MB with more impact on GEP than ER. The relative insensitivity of MB's ER to water table variations during previous years has been demonstrated by Lafleur et al. (2005) and suggested to be a result of a number of compensating processes as illustrated using a comprehensive process model (Dimitrov et al., 2010). Dimitrov et al. (2010) suggested ER would be insensitive to decreasing

water table if microbial respiration in the near-surface desiccation zone decreased while root and microbial respiration in aerated peat below increased. Similarly, aerobic respiration in hollows could increase if autotrophic respiration of drying hummock *Sphagnum* decreased. In contrast, Sulman et al. (2010) combined growing season results from MB and from the South Fork bog in Wisconsin (U.S.A.) to show a tendency for ER to decrease in years with lower water tables and suggested that compensation processes would not be sufficient to offset the declining respiration by *Sphagnum*. Similar to our results, Sulman et al. (2010) found bog GEP tended to decrease with lower water table positions. With the dense shrub cover at MB contributing to the majority of CO_2 uptake in summer (Adkinson and Humphreys, 2010), a decline in GEP was likely evidence that vascular plant species, in addition to the *Sphagnum* spp., were suffering drought stress. However, it is important to note that conditions in early summer appeared to offset lower GEP in later summer such that growing season GEP in the drought year was greater than in the previous year at MB.

In terms of winter NEP, the longer winters and colder temperatures at the HBL peatlands resulted in peat that remained frozen longer, which may have led to the smaller winter losses of CO_2 despite peat temperatures above 0 °C at depth at all three sites. We also observed this relationship between years at MB with less loss during the colder first winter. Olefeldt et al. (2012) also highlighted the importance of freezing in peat in limiting ER. After achieving a maximum thaw depth of about 70 cm, the peat froze back entirely over the winter at Stordalen and, not surprisingly, CO_2 losses of 6 to 10 g C m^{-2} were slightly lower than at AR and KL.

As hypothesized, the similarity in annual NEP that was observed for MB and northern peatlands in Europe (e.g. Lund et al., 2010) was also observed for the HBL bogs as a result of compensating factors discussed above. Although these NEP values do not reflect the C lost as methane and dissolved organic C (DOC), we generally find that the annual net CO_2 exchange is often the dominant and most variable C flux in the net ecosystem C budget of a peatland (Roulet et al., 2007; Nilsson et al., 2008; Olefeldt et al., 2012) aside from some exceptions (Olson et al., 2013). Additional years of CO_2 flux measurements along with measurements of CH_4 and aquatic C fluxes for these HBL sites will help confirm the magnitude of these C sinks and their potential response to future drying.

Conclusions

The CO_2 sink strength of two HBL peatlands and a temperate peatland to the south (MB) was found to be remarkably similar despite large differences in climate, vegetation, and peat characteristics. Smaller growing season CO_2 uptake at the HBL peatlands was offset by less CO_2 loss through the winter months. A shorter growing season and less vascular vegetation biomass at the HBL peatlands may explain the lower GEP and ER at these sites. In winter, a longer period with frozen near-surface peat may have also limited ER at that time of year. Over the long term, shifts in climate and peatland moisture status would be expected to be accompanied by shifts in the composition of vegetation and changes in carbon cycling processes. In the short term during this two year study, it appeared that mid-summer water table drawdown temporarily decreased CO_2 uptake at all three bogs due to a decrease in photosynthesis rather than an increase in respiration.

Acknowledgments

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