

Spring photosynthesis in a cool temperate bog

TIM R. MOORE*, PETER M. LAFLEUR†, DIANE M. I. POON*, BENJAMIN W. HEUMANN*, J. W. SEAQUIST* and NIGEL T. ROULET*

*Department of Geography and Global Environmental & Climate Change Centre, McGill University, 805 Sherbrooke Street West, Montréal, QC, Canada H3A 2K6, †Department of Geography, Trent University, Peterborough, Canada ON K8P 2W6

Abstract

In northern ecosystems, the onset and growth of spring photosynthesis may have an important influence on the annual carbon (C) budget, yet the controls have not been clearly identified, especially for peatlands. We used a 5-year set of daily carbon dioxide (CO₂) exchange measurements derived from an eddy covariance tower located at Mer Bleue, an ombrotrophic bog near Ottawa, Canada, from March to May [day-of-year (DOY) 60–150], 1999–2003. We used half-hourly measured net ecosystem exchange minus modelled ecosystem respiration to estimate daily photosynthesis, as gross ecosystem production (GEP). The onset of GEP in each year was closely related to the thinning and disappearance of the snow cover, occurring between DOY 86 and 101. GEP increased during the spring, reaching 10-day average values of between 5 and 9 g CO₂ m⁻² day⁻¹ by the end of May. This increase was initially associated with moss activity (*Sphagnum* and *Polytrichum*), followed by the evergreen shrubs. Peat temperatures in the rooting zone (10–20 cm depth) and increases in shrub leaf nitrogen and chlorophyll *a* concentrations contributed to this rapid increase in GEP. Examination of moderate-resolution imaging spectroradiometer (MODIS) images over several years revealed that the temporal resolution (16-day composites) was inadequate to capture the onset of GEP but estimates of gross primary productivity and photosynthesis from MODIS 8-day composites for the most part followed the pattern and magnitude of CO₂ exchange observed at the tower.

Keywords: CO₂ exchange, MODIS, peatland, photosynthesis, remote sensing

Received 24 January 2006; revised version received 17 April 2006 and accept 19 June 2006

Introduction

In northern ecosystems, the onset of spring photosynthesis and carbon (C) uptake may have an important influence on the annual C budget. Myneni *et al.* (1997) have presented remote sensing evidence of an earlier spring and increased photosynthetic activity in northern ecosystems. In a boreal black spruce forest, Frohling (1997) showed through modelling that the timing and magnitude of spring played a large role in determining the annual C budget. Although phenological attributes of ecosystems have been determined (see Schwartz, 2003; Schwartz *et al.*, 2006), there are few studies of the development of photosynthesis as northern ecosystems emerge from the winter into spring and early summer.

During the spring, solar radiation loading can be high, but cold air or soil temperatures or slow development of

photosynthetic capacity may inhibit the ability of vegetation to utilize the radiation potential. The role of temperature on spring leaf-out in deciduous forests is well established (e.g. Hunter & Lechowicz, 1992), as is the development of their photosynthetic capacity (e.g. Black *et al.*, 2000). In five evergreen boreal forests, Tanja *et al.* (2003) found that air temperature was the trigger to the recovery of photosynthesis. On the other hand, several studies have identified soil temperature as a primary control on boreal conifer photosynthesis, through the inhibition of water uptake from frozen soils (e.g. Schwarz *et al.*, 1997; Jarvis & Linder, 2000). In a subalpine coniferous forest, Monson *et al.* (2005) noted a high variability in daily photosynthesis during spring and that air and soil temperature and melting snow were important controls. In a synthesis of data from temperate deciduous forests, Baldocchi *et al.* (2005) found that the timing of net C uptake [net ecosystem exchange (NEE) < 0] coincided with the date at which the mean daily soil temperature equals the mean annual air temperature.

Correspondence: Tim R. Moore, e-mail: tim.moore@mcgill.ca

Studies of the development of photosynthesis in peatlands are sparse. Bubier *et al.* (1998) discovered evidence of photosynthetic uptake of CO₂ beneath a spring snow pack in a boreal bog, presumably associated with the moss layer. Lafleur *et al.* (2001, 2003) have described the annual pattern of CO₂ exchange at Mer Bleue, a cool temperate bog, both within and among years, using data from an eddy covariance micrometeorological tower. There was a rapid rise in photosynthesis during the spring, but the controls on this have not been examined. Over a 6-year period (1999–2004) in the spring (March–May), NEE of CO₂ at the Mer Bleue site averaged $-33 \text{ g CO}_2\text{-C m}^{-2}$ (uptake by the peatland), ranging from -59 to $+15 \text{ g CO}_2\text{-C m}^{-2}$. At Mer Bleue, variations in the summer (June–August) NEE are the primary control on interannual variations in the CO₂ balance. In a subarctic fen in Finland (latitude 69°N), however, Aurela *et al.* (2004) showed that the timing of snowmelt and, thus, the spring uptake of CO₂ was the most important single determinant of the annual C balance.

Moderate-resolution imaging spectroradiometer (MODIS) data have been used to determine phenological attributes of vegetation. Zhang *et al.* (2004) recently used the normalized difference vegetation index (NDVI) and enhanced vegetation index (EVI) derived from the MODIS platform to identify the onset of spring green-up of vegetation in North America during 2001. MODIS was launched in late 1999 onboard the Earth Observing System platform Terra. Its purpose is to provide consistent information on vegetation condition, photosynthesis, and land cover at high temporal resolutions (1–16 days) and relatively high spatial resolutions (up to 250–1000 m) (Zhan *et al.*, 2002). There is great potential to use these data to provide information on ecosystem-level phenological patterns associated with climate change.

In this study, we examine the pattern of ecosystem uptake of CO₂ using eddy covariance data in a large ombrotrophic bog. We show the response of daily photosynthesis, expressed as gross ecosystem production (GEP) derived from measurements of NEE and modelled ecosystem respiration (ER), to environmental variables such as snow cover, temperature in the air and the peat and photosynthetically active radiation (PAR). We use data for a 90-day period in the spring (March–May, inclusive) over 5 years (1999–2003) to identify the primary controls on the onset and magnitude of spring GEP in this ecosystem. We then examine changes in the concentration of chlorophyll *a* and nitrogen (N) in the major plant species during 2003, as part of the 'spring greening'. Finally, we use MODIS satellite images of the site to determine changes in NDVI and EVI during the springs of 2000–2003 and compare MODIS estimates of gross

primary production (GPP) and photosynthesis (PSN) with the estimated photosynthesis at the tower.

Site and methods

The Mer Bleue peatland is a large, open low-shrub, raised bog, located 10 km east of Ottawa, ON, Canada (latitude 45.40°N, longitude 75.50°W). The climate of the region is cool continental, with a mean annual temperature of 6.0 °C and an annual precipitation of 944 mm (1971–2000 normals, Environment Canada). The vegetation in the raised section of Mer Bleue comprises hummocks occupied by the evergreen shrubs *Chamaedaphne calyculata*, *Ledum groenlandicum* and *Kalmia angustifolia*, along with the deciduous shrub *Vaccinium myrtilloides*; the shrubs are 20–30 cm high. The ground cover in hummocks is primarily *Sphagnum capillifolium* and *Sphagnum magellanicum* with some *Polytrichum strictum*. Hollows, about 20 cm lower than the hummocks, cover about 25% of the area and have a sparser cover of *K. angustifolia*, *L. groenlandicum* and *C. calyculata* with a moss layer dominated by *S. magellanicum* with some *S. angustifolium*. There is a sparse cover of the sedge *Eriophorum vaginatum* with rare trees such as *Larix laricina* and *Betula populifolia*. More details on the vegetation are included in Moore *et al.* (2002).

Environmental and CO₂ exchange measurements were made at a tower located about 300 m from the margin of the bog and with a footprint dominated by hummocks. CO₂ exchange was measured by the eddy covariance (EC) technique. Briefly, the measurement system consisted of a three-dimensional sonic anemometer (Solent R3, Gill Inst., Lymington, UK) and a fast response infrared gas analyser (LI6262, LI COR, Lincoln, NE, USA). The sonic anemometer and intake for the CO₂ sample were located at 3.2 m above the mean bog surface. Measurements of turbulence and CO₂ concentration are made every 0.01 s and covariance between the vertical wind velocity and CO₂ concentration is computed every 30 min. The turbulent flux of CO₂ is computed from this covariance, and subject to a variety of postprocessing corrections. The flux due to changes in CO₂ storage below the height of the instruments is estimated from the CO₂ concentration data and added to the turbulent flux to obtain NEE. Full details of the eddy covariance system, data handling and gap filling are described in Lafleur *et al.* (2003).

Photosynthesis is not measured by the eddy covariance system. Instead, we derived GEP, total photosynthetic flux ignoring photorespiration (also called GPP), from daytime (i.e. PAR > 0) eddy covariance measurements as follows. For each 30-min period GEP was computed as the difference between ER and NEE (i.e. GEP = ER – NEE), where a negative value of NEE

represents a net flux into the ecosystem and a positive value represents net release of CO₂; this sign convention and symbolism follows Law *et al.* (2002), Black *et al.* (2000) and others; in the remote sensing and ecosystem science convention, the sign is positive. Photorespiration is included in GEP, which is usually very small, so GEP is assumed to approximate GPP (Waring & Running, 1998). For the present analysis we use a daily time step, thus 30-min calculations of GEP were summed for each 24-h period to compute daily GEP.

ER for daytime periods was modelled as a function of 5 cm hummock soil temperature. The model was developed using night-time soil temperature and NEE, for example see fig. 8 in Lafleur *et al.* (2001). We acknowledge there are limitations to this approach, in that it might under-represent daytime ER because of enhanced autotrophic respiration. However, in light of a paucity of information on autotrophic processes, we are confined to this simple approach. Besides this potential systematic error, temperature–ER modelling involves a random error due to imperfect modelling and the measurement of NEE itself is subject to a random error due to sensitivity and application of the various components in the EC system. We used a relatively simple procedure to estimate the relative error in daily GEP as a result of these two sources. First, we assigned a somewhat conservative error in measured NEE (ϵ_{meas}) of 12%; this is typical of estimates from other studies (e.g. Law *et al.*, 2002). Secondly, we took the standard error of the estimate for the temperature–ER regression model (ϵ_{mod}) as the model error component. These errors are applied to each 30-min period of a day when a valid GEP was computed (i.e. GEP < 0). Following Barford (1985), the error in daily GEP (ϵ_{GEP}) is given as $\epsilon_{\text{GEP}} = (\sum_1^n (\epsilon_{\text{meas}}^2 + \epsilon_{\text{mod}}^2))^{0.5}$. ϵ_{mod} is usually much larger than ϵ_{meas} , thus, ϵ_{GEP} is highly dependent upon the temperature–ER regression model. Employing this technique we found the average relative error in daily GEP (i.e. $\epsilon_{\text{GEP}}/\text{GEP}\%$) was 35.4%, ranging from 6% to 183%. The mean absolute ϵ_{GEP} was $\pm 0.42 \text{ g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$. The relative daily error was generally larger early in the spring and decreased as GEP increased toward the late spring. The largest effect of this error on the results presented below is that the date of photosynthesis onset may be in error by 3–4 days, however, the comparisons in patterns of GEP between years are not greatly affected, nor are the comparisons with the remote sensing estimates. Finally, we accept that this is a rather crude treatment of the GEP error; much more sophisticated methods are currently under investigation (e.g. Hagen *et al.*, 2006), however no standard approach for error estimation of EC component fluxes has been devised yet.

Air temperature at a height of 2 m above the peat surface was recorded continuously, as were soil

temperatures at depths of 0.05, 0.10, 0.20 and 0.40 m beneath the peat surface in a hummock. Incoming PAR was measured with a quantum sensor. Signals from the sensors were monitored every 5 s and averaged every 30 min. These data were reduced to daily values by averaging all 30 min intervals collected from 00:00 to 24:00 hours of each day.

Snow depth was continuously measured at one location with a sonic ranging device. Periodic manual snow depth surveys were used to compute the average snow depth on the bog and the data from the continuous measurements were adjusted to the snow survey data to give a continuous record of average snow depth. Final snowmelt was estimated from measurements of solar albedo (ratio of reflected to incoming solar radiation) made from instruments on the tower. It was assumed snow cover was zero when the albedo was ≤ 0.20 .

We collected leaves from the major shrub and tree species and mosses (capitulum only for *Sphagnum*) at 3-week intervals in the spring of 2003. Half of the sample was oven-dried at 70 °C to determine moisture content, then ground through a Wiley mill and the C and N concentration determined on a elemental analyzer (CE Instruments NC 2500, Milano, Italy). The other half was frozen and analyzed fresh for chlorophyll *a* concentration using the methanol extraction and spectrophotometric determination method described by Porra *et al.* (1989).

We extracted 16-day MODIS composites of NDVI and EVI for a 3 × 3 pixel region centered on the tower for the spring periods covering 2000–2003. The spatial resolution of the 16-day composites is 250 m. A 3 × 3 mean was taken to ensure that errors due to pixel registration were minimized. Additionally, we extracted 8-day MODIS composites of GPP and net PSN centered on the tower for the spring periods covering 2001–2003. Data for year 2000 were not available because the instrument began recording on February 24 and had to undergo calibration before they could be made available. These data have a spatial resolution of 1000 m. The MODIS-derived fluxes were compared with the tower-derived estimates of GEP calculated for each of the 8-day MODIS compositing periods.

The NDVI and EVI are vegetation indices (and standard MODIS products) that are related to the chlorophyll content of green vegetation. The NDVI is computed as the difference between the near infrared and red reflectances divided by the sum of these reflectances, respectively. The EVI is similar to the NDVI but influences from background ‘noise’ (reflectance from bare soil, leaf litter, and the atmosphere) are minimized and it does not saturate at moderate biomass levels. Additionally, it is more sensitive to canopy structure (Huete *et al.*, 2002). A vegetation index composite is a summary of vegetation conditions for the

corresponding time period that more closely represents clear-sky views with a minimum of undesirable atmospheric and angular effects. Such a composite contains of pixels that are selected from different days through the period (Huete *et al.*, 2002).

MODIS GPP and PSN (net photosynthesis) are derived from the MOD-17 product whose core algorithm consists of a LUE (light-use efficiency) model that is parameterized with reflectance data via FPAR (fraction of absorbed photosynthetically active radiation) and a global network of climate stations (Heinsch *et al.*, 2003). Biome-specific maximum LUEs are read from a look-up table and are originally derived from independent runs of a biogeochemical model. The maximum LUEs are modified by vapor pressure deficit and temperature scalars that are computed from climate data provided by the Data Assimilation Office (DAO) at NOAA (National Oceanic and Atmospheric Administration). The photorespiration component of GEP is usually very small, so GEP is roughly equivalent to GPP (Waring & Running, 1998). In the MOD-17 algorithm, PSN is computed as GPP less leaf maintenance respiration and the maintenance respiration of fine root biomass, but does not include live-wood maintenance respiration or growth respiration. A composite for the productivity variables is an 8-day mean value derived from daily estimates.

Results

Patterns of photosynthesis and its controls

Results are presented for the period day-of-year (DOY) 60–150 for 5 years, 1999–2003. During these years, there was some variation in the mean monthly temperature and precipitation from March to May, compared with the long-term mean values (Table 1). The starting date of daily photosynthesis ranged from day 86 (2003) to day 101 (2001), with an average starting day of 93. By the end of May (day 150) daily photosynthetic rates

reached average values of between -4 and $-10 \text{ g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$ (Fig. 1). The mean daily GEP of the 5 years showed a strong ($r^2 = 0.93$, $P < 0.001$) linear increase from the onset, reaching an average of $-7.4 \text{ g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$ at the end of May and with an average daily change of $-0.11 \text{ g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$. Seasonal estimated cumulative GEP, to day 150, was -276 , -154 , -216 , -196 and $-218 \text{ g CO}_2 \text{ m}^{-2}$ for 1999–2003, respectively. There was a correlation ($r^2 = 0.71$, $P = 0.07$) between seasonal GEP and air growing degree-days (defined as the positive difference between air temperature and 5°C , Arora & Boer, 2005), but the relationship was insignificant ($r^2 = 0.15$, $P = 0.53$) for growing degree-days at a depth of 10 cm in the hummock.

The date at which the bog became a sink of CO_2 (daily $\text{NEE} < 0$), ranged from days 96 to 110, using the linear regression of NEE vs. DOY used by Baldocchi *et al.* (2005) for the period days 80–120 in each year. This was 4–24 days after the start of GEP, the larger differences occurring in 2002 and 2003. Soil temperature at a depth of 10 cm in a hummock at the dates when $\text{NEE} < 0$ ranged from 0.0 to 14.2°C , with an average of 3.8°C . These values are generally less than the mean annual air temperature of 6°C .

Snow cover, determined on a hummock, reached a maximum thickness of 0.4 – 0.6 m during the winter (Lafleur *et al.*, 2003, fig. 3) but had thinned to between 0.2 and 0.5 m by day 60. The snow cover lasted on average until days 90–101, except in 2000 when a thin ($< 0.10 \text{ m}$) cover persisted until day 124. There was a generally strong relationship between the disappearance of the snowpack and the start of GEP (within 4 days), except that in 2000 GEP started beneath a shallow snowpack ($< 0.10 \text{ m}$) that had existed from day 68, and in 2003 GEP continued after the return of a shallow (0.05 – 0.25 m) snowpack. Shallow to nonexistent snow cover in 2000 and thin snow cover early in March in 2002 did not trigger an early start to GEP.

Average daily air temperature (at 2.0 m) showed large variations from -15 to $+10^\circ\text{C}$ during the first half of

Table 1 Long-term (1971–2000) mean monthly temperature ($^\circ\text{C}$) and mean monthly precipitation (mm) for March, April and May and the values for 1999–2003, based on data from the Ottawa airport, located 10 km south-west of the Mer Bleue site

Month	Long-term mean	1999	2000	2001	2002	2003
March						
Temperature	−2.5	−2.8	1.8	−3.1	−3.0	−3.8
Precipitation	74	106	73	51	72	73
April						
Temperature	5.7	6.8	5.0	6.7	6.4	3.8
Precipitation	72	20	109	14	85	57
May						
Temperature	13.4	16.3	13.2	14.9	10.9	13.0
Precipitation	79	36	123	81	92	129

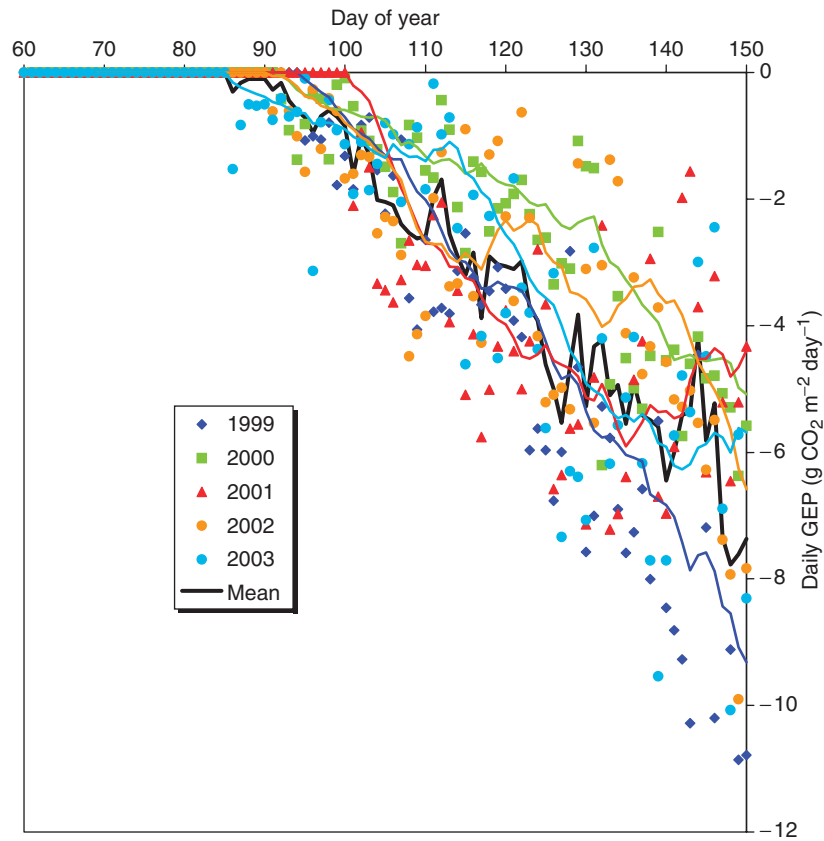


Fig. 1 Daily gross ecosystem production (GEP) at the Mer Bleue bog from day-of-year 60–150, 1999–2003. Lines represent the 10-day moving average based on the last date and the bold line represents the daily average of the 5 years.

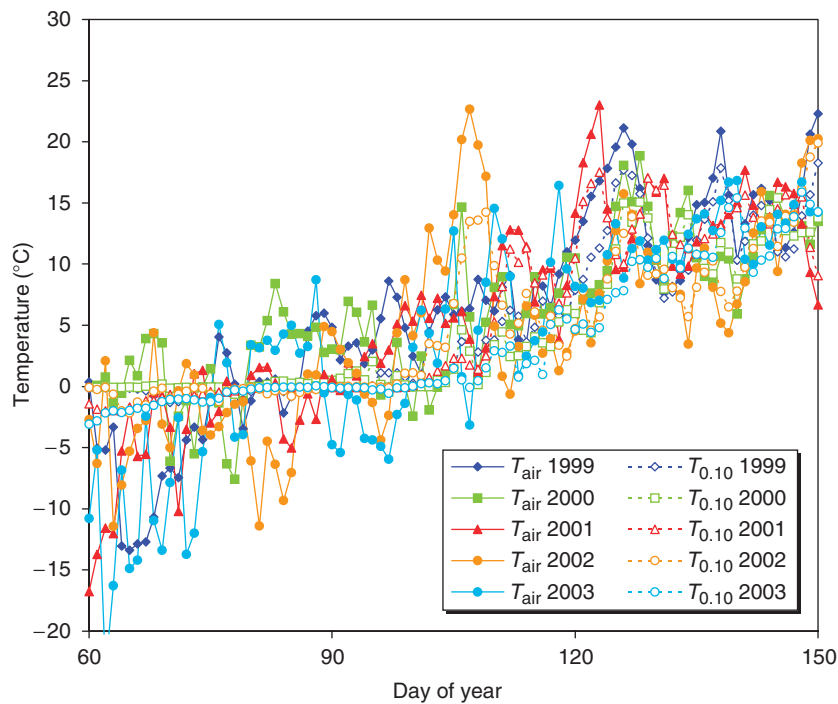


Fig. 2 Mean daily temperature at 2 m (T_{air}) and at 0.10 m beneath the peat surface in a hummock ($T_{0.10}$) for March–May, 1999–2003.

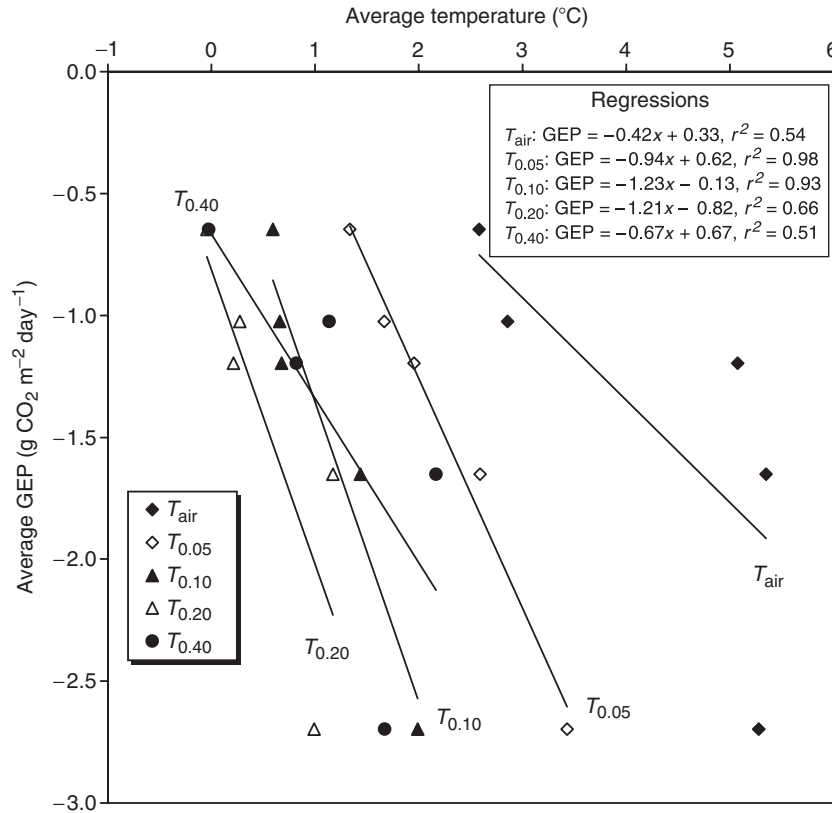


Fig. 3 Relationship between average daily gross ecosystem production (GEP) and average daily air and peat temperature at 0.05, 0.10, 0.20 and 0.40 m in a hummock ($T_{0.05}$, $T_{0.10}$, $T_{0.20}$ and $T_{0.40}$, respectively), for the 10 days after the start of GEP, 1999–2003.

the spring (Fig. 2), whereas daily temperature at a depth of 10 cm in the hummock increased from an average of -1.0°C at DOY 60–70 to 0.2°C at DOY 90–100, coinciding with the onset of GEP. Temperatures at a depth of 10 cm then rose rapidly from DOY 100–110, reaching an average value of 5°C . In the 10 days after the start of GEP, rates were small (average $-1.44\text{ g CO}_2\text{ m}^{-2}\text{ day}^{-1}$) compared with later in the spring, and ranged from $-0.65\text{ mg CO}_2\text{ m}^{-2}\text{ day}^{-1}$ in 2000 to $-2.70\text{ g CO}_2\text{ m}^{-2}\text{ day}^{-1}$ in 2001. These annual variations over the 5 years were positively correlated with both the average air and peat temperatures over this 10-day period ($r^2 = 0.51\text{--}0.98$), with the strongest correlation for peat temperatures at depths of 0.05 and 0.10 m (Fig. 3), suggesting that cold temperatures in the vascular rooting zone were a primary limitation on the development of shrub photosynthesis. The surface of the peat, with *Sphagnum capitulum*, was warmest, with temperatures close to or above the air temperature. *Sphagnum* mosses have no roots and, thus, their photosynthesis is independent of peat temperatures lower in the profile.

Within each of the 5 years after the start of GEP, the daily GEP rate was correlated with the air and soil

temperatures, with the strongest relationship observed with peat temperatures at 0.05 and 0.10 m (Table 2). The regression parameters were similar for 4 of the 5 years, the exception being 2001, which had a lower slope, a larger intercept and a weaker r^2 . This may have been caused by the unusually long-lasting snow cover, which delayed the onset of GEP. There was a strong correlation ($r^2 = 0.40\text{--}0.58$) between air and soil temperature and daily photosynthesis for the period from the start to day 150, when all 5 years were combined (Fig. 4).

Average daily PAR values were significantly related to GEP rates over the 5 years, though the relationship was not strong ($r^2 = 0.19$, $P < 0.001$). Temperatures and PAR were not strongly correlated ($r = 0.10\text{--}0.18$) for the period of GEP over the 5 years, allowing an examination of the influence of PAR on daily GEP rates. Inclusion of the daily average PAR value into the regression between GEP and temperature resulted in an improvement of the coefficient of determination by an average of 0.12 (Table 3), but temperature was the primary control on GEP rates during the spring. Using data from the onset of GEP in all years combined, peat temperature (hummock at 0.05 m) and daily PAR were able to explain 65% of the variation in daily GEP (Table 4).

Table 2 Regressions between daily GEP ($\text{g CO}_2 \text{m}^{-2} \text{day}^{-1}$) and mean daily temperature in the air at a height of 2.0 m (T_{air}) or in the hummock peat at depths of 0.05, 0.10, 0.20 or 0.40 m ($T_{0.05}$, $T_{0.10}$, $T_{0.20}$ and $T_{0.40}$, respectively) after the onset of photosynthesis

	T_{air}			$T_{0.05}$			$T_{0.10}$			$T_{0.20}$			$T_{0.40}$		
	b	c	r^2	b	c	r^2	b	c	r^2	b	c	r^2	b	c	r^2
1999	-0.40	-0.60	0.50	-0.43	-0.87	0.62	-0.43	-1.32	0.64	-0.48	-1.61	0.61	-1.00	0.27	0.70
2000	-0.23	-0.65	0.45	-0.27	-0.51	0.64	-0.28	-0.75	0.65	-0.30	-1.21	0.65	-0.43	-1.18	0.73
2001	-0.10	-3.21	0.08	-0.18	-2.34	0.24	-0.17	-2.62	0.22	-0.18	-2.80	0.21	-0.37	-2.17	0.31
2002	-0.22	-1.42	0.41	-0.34	-0.48	0.70	-0.36	-0.57	0.74	-0.41	-0.73	0.71	-0.67	0.01	0.57
2003	-0.28	-1.31	0.48	-0.41	-0.69	0.77	-0.43	-1.00	0.78	-0.47	-1.63	0.68	-0.72	-1.64	0.64
All years	-0.26	-1.24	0.40	-0.34	-0.77	0.59	-0.34	-1.07	0.59	-0.37	-1.48	0.55	-0.57	-1.24	0.53

Regression parameters include slope (b) and constant (c) and coefficient of determination (r^2).
GEP, gross ecosystem production.

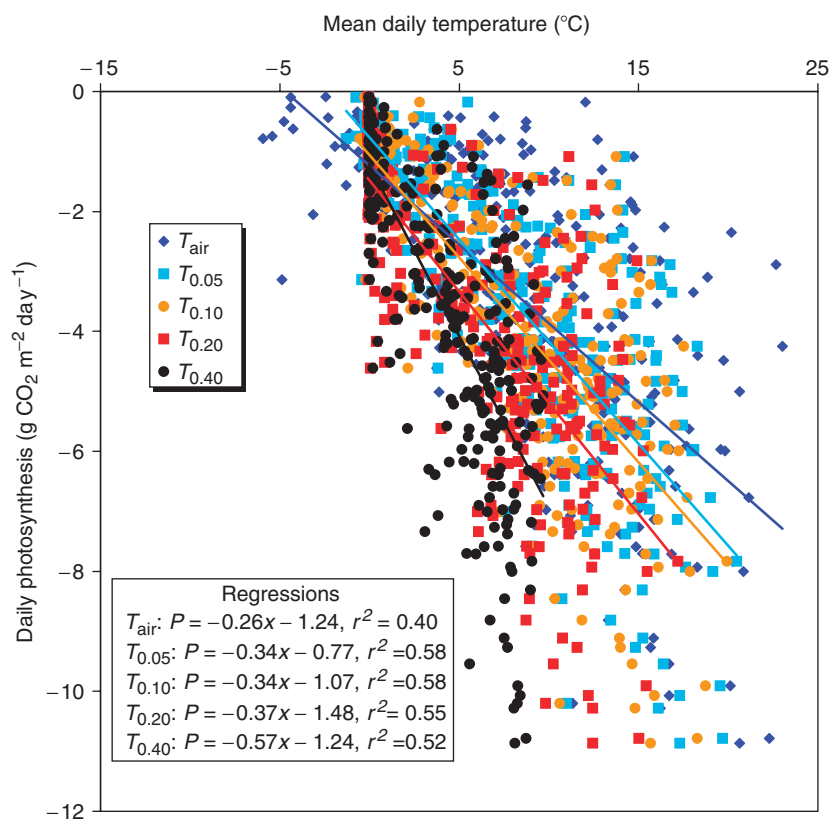


Fig. 4 The relationship between daily gross ecosystem production (GEP) and mean daily temperature in the air (T_{air}) and at four peat depths (0.05, 0.10, 0.20 and 0.40 m) in a hummock ($T_{0.05}$, $T_{0.10}$, $T_{0.20}$ and $T_{0.40}$, respectively), from the onset of observed GEP to day 150, 1999–2003 combined.

Nitrogen and chlorophyll a concentrations and mass

Concentrations of N (Fig. 5) in the leaves of the evergreen shrubs (*C. calyculata*, *K. angustifolia*, *L. groenlandicum*) in the spring of 2003 were low, ranging from 1.0% to 1.4%, and showed a modest increase from the first sampling date in early April (DOY 94) to early June (DOY 165). N concentrations were also low

and stable (0.9–1.1%) in the needles of *P. mariana*, collected from the bog margin, but were high (2–3%) in the leaves and needles of the scattered deciduous trees (*B. populifolia* and *L. laricina*) and the deciduous shrub (*V. myrtilloides*), which appeared at the end of May. N concentrations were low and stable (0.8–1.0%) in the mosses, *P. strictum*, *S. capillifolium* and *S. magellanicum*.

Concentrations of chlorophyll *a* showed a more substantial change over the spring than for N (Fig. 6). In the evergreen shrubs, concentrations rose from 0.7 to 1.0 mg g⁻¹ in early spring to 1.3 to 1.8 mg g⁻¹ in early June and those in the deciduous species were also high (1.8–2.8 mg g⁻¹). Concentrations in the *Sphagnum*

Table 3 Increase in coefficient of determination (*r*²) with inclusion of average daily PAR into regression of daily GEP against air temperature at 2 m (*T*_{air}) and peat temperature at depths of 0.05, 0.10, 0.20 and 0.40 m in a hummock (*T*_{0.05}, *T*_{0.10}, *T*_{0.20} and *T*_{0.40}, respectively), for 1999–2003

	<i>T</i> _{air}	<i>T</i> _{0.05}	<i>T</i> _{0.10}	<i>T</i> _{0.20}	<i>T</i> _{0.40}
Without PAR	0.412	0.588	0.582	0.552	0.532
With PAR	0.543	0.683	0.687	0.687	0.654

GEP, gross ecosystem production; PAR, photosynthetically active radiation.

Table 4 Regression between daily GEP (g CO₂ m⁻² day⁻¹) after the annual onset of GEP against daily temperature at a depth of 0.10 m in hummock (*T*, °C) and average daily PAR (μmol m⁻² s⁻¹), using data from all years (*n* = 289)

Variables	Equation	<i>r</i> ²	<i>S</i> _{ey}
<i>T</i>	<i>P</i> = -0.343 <i>T</i> - 1.06	0.582	1.59
<i>T</i> + PAR	<i>P</i> = -0.320 <i>T</i> - 0.004PAR + 0.52	0.687	1.38

*S*_{ey} standard error of the estimate; GEP, gross ecosystem production; PAR, photosynthetically active radiation.

mosses were low (0.1–0.3 mg g⁻¹) but higher in the *P. strictum* moss (0.3–1.5 mg g⁻¹).

Most of the increase in new biomass (new leaves on shrubs, occurrence of deciduous tissues) occurs from late May onwards (C. Isernhagen and E. Humphreys, personal communication), so most of the spring increase in photosynthesis derives from tissues that were present at the start. An indication of the change in photosynthetic capacity of the vegetation within the bog over the spring period can be derived from the combination of the foliar and moss biomass, obtained from thirty 0.5 m × 0.5 m quadrats located near the tower sampled at peak biomass in late summer. Shrub leaf biomass averaged 180 g m⁻² while that of the mosses (*P. strictum* and the capitulum of *S. capillifolium* and *S. magellanicum*) was 159 g m⁻² (Bubier *et al.*, 2006). Tree biomass is insignificant within the tower footprint and is not included in these estimates. About 60% of the N is contained in the shrub leaves, the remainder being in the mosses, whereas about 80% of the chlorophyll *a* is contained in the shrub leaves. The aerial foliar and moss N content was estimated to rise from 3.0 g m⁻² in early April to 3.9 g m⁻² in early June. The increase in estimated foliar and moss chlorophyll *a* content was greater, from 0.15 g m⁻² in early April to 0.35 g m⁻² in early June. Thus, the mass of N and chlorophyll *a* in photosynthetic tissues increased by 30–150% in the spring.

Remote sensing

Maximum NDVI levels range from 0.72 to 0.74 and occurred during the final compositing period, beginning

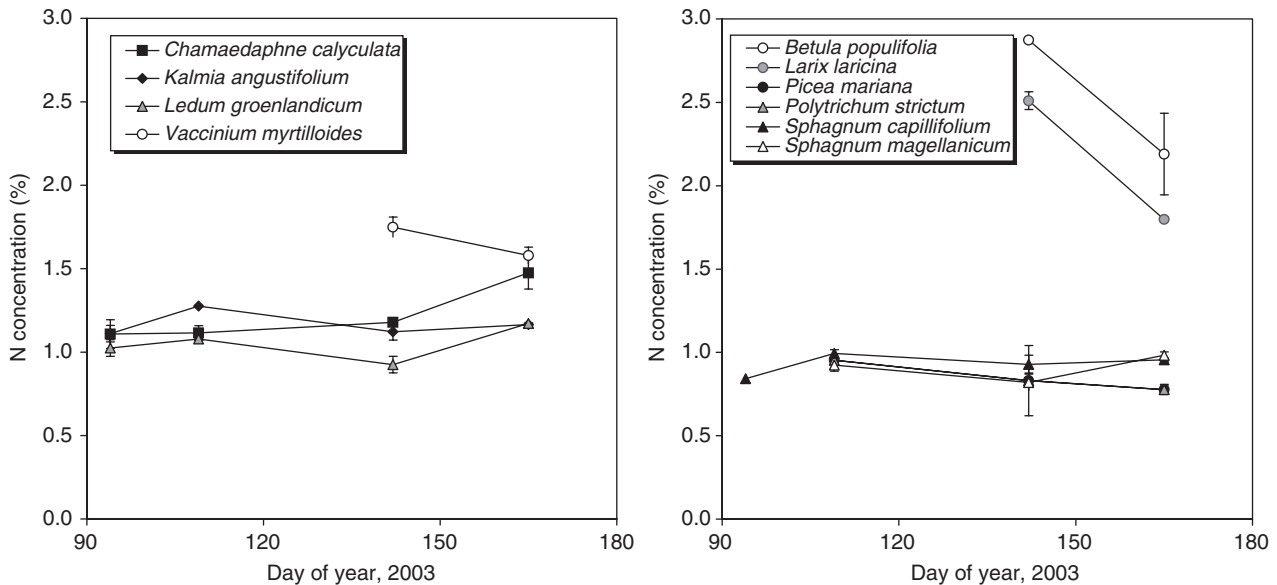


Fig. 5 Concentration of N in leaves of shrubs and trees and *Sphagnum* capitulum and *Polytrichum strictum*, spring 2003.

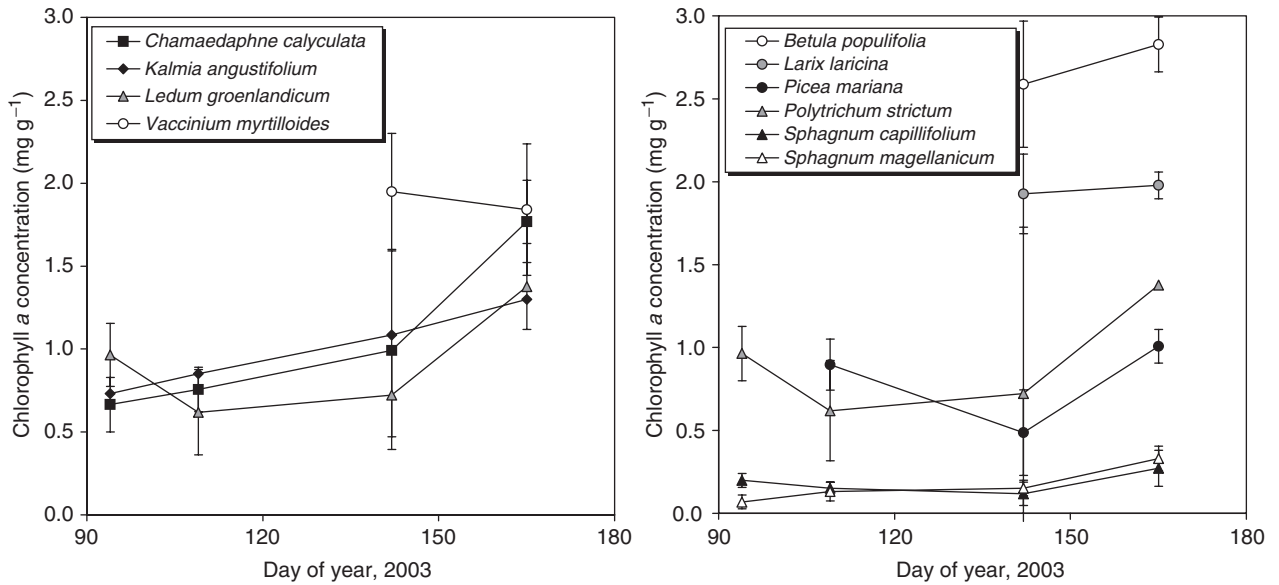


Fig. 6 Concentration of chlorophyll *a* in leaves of shrubs and trees and *Sphagnum* capitulum and *Polytrichum strictum*, spring 2003.

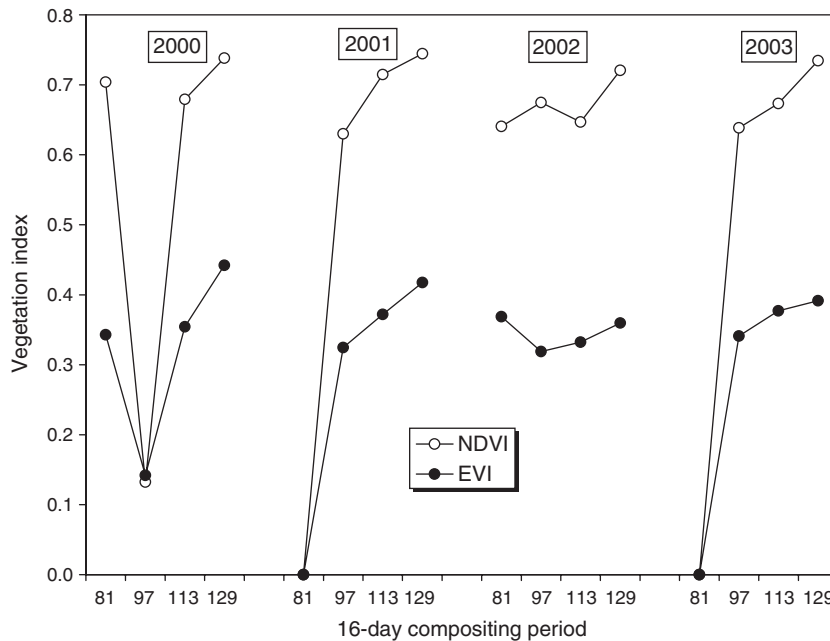


Fig. 7 MODIS-derived estimates of normalized difference vegetation index (NDVI) and enhanced vegetation index (EVI) for 16-day compositing periods corresponding to days 81–129 for 2000–2003. The dates indicated are the start of the compositing period.

with day 129 (Fig. 7). Spring profiles for EVI are lower in magnitude and maxima are reached during the final compositing periods for years 2000, 2002, and 2003, and ranged from between 0.44 for year 2000 and 0.39 by 2003. For both NDVI and EVI, spring trajectories start from 0 in years 2001 and 2003. A sudden decrease was detected in year 2000 for the second compositing period.

There is a strikingly good correspondence between the MODIS-derived GPP and PSN, and tower-derived

GEP estimates both terms of their magnitudes and their spring profiles (Fig. 8). For years 2001 and 2003, all estimates begin near $0 \text{ g CO}_2\text{-C m}^{-2} \text{ day}^{-1}$ and rise steeply thereafter. For 2001, maximum values reach 1.8, 2.1 and $2.9 \text{ CO}_2\text{-C m}^{-2} \text{ day}^{-1}$ for PSN, GEP and GPP (sixth compositing period), while for 2003, maxima are reached at the fifth compositing period for PSN and GPP (1.4 and $1.9 \text{ CO}_2\text{-C m}^{-2} \text{ day}^{-1}$) before falling off, while GEP continues to rise to $1.6 \text{ CO}_2\text{-C m}^{-2} \text{ day}^{-1}$. For

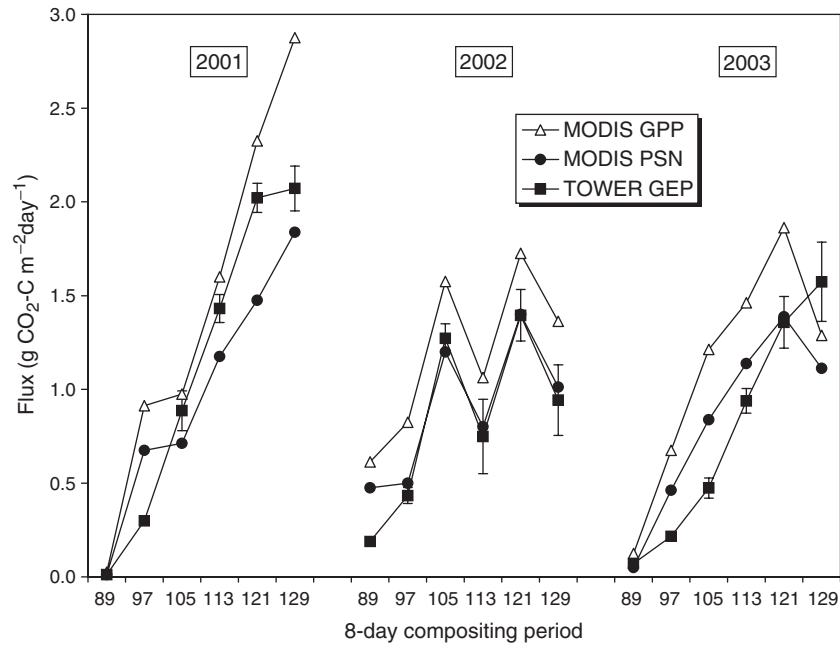


Fig. 8 MODIS-derived estimates of gross primary production (GPP) and photosynthesis (PSN) compared with the tower-derived gross ecosystem production (GEP) observations (and their standard deviation shown as error bars) for 8-day compositing periods from day 81 through 129, 2001–2003 (no data were available for 2000). The dates indicated are the start of the compositing period.

2002, productivity profiles start substantially above 0 and fluctuate considerably, achieving maxima at the fifth compositing period for all three measures, before falling off. According to these metrics, 2002 was also the least productive.

Discussion

Several approaches have been taken to define the seasonal start and development of ecosystem photosynthesis. In evergreen forests, Tanja *et al.* (2003) defined the start of photosynthesis in five boreal coniferous forests as the date when the half-hourly NEE first falls below 20% of the maximum summer NEE. On the other hand, Gu *et al.* (2003) developed daily maximum photosynthetic rates to define phenological characteristics of forest and grassland ecosystems, from which they derived a spring photosynthesis development velocity. We have taken the estimated daily photosynthesis, or GEP, based on the difference between observed daily NEE and computed daily ER, both of which have errors. From our calculations the mean error in daily GEP is $\pm 0.42 \text{ g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$; this is a relatively small amount and has its greatest effect during the early spring and does not change the conclusions from this study. One unaccounted for source of error is that daytime ER flux modelled from night-time data leads to a systematic overestimation (perhaps as much as 15%, because of daytime inhibition of leaf respiration; Janssens *et al.*,

2001), which then translates through to the computed photosynthesis term as an overestimation. Although we have no means of verifying this uncertainty at our site, it should not greatly change our interpretation of the patterns of photosynthesis development. Although it would affect the comparison of absolute fluxes derived from the MODIS imagery, again it would not greatly affect the seasonal patterns shown in Fig. 8.

The results from this peatland show that GEP starts immediately after the disappearance of a snow cover, and can continue if a thin snow cover reappears. Although the shrub leaves are above the snowpack, the initial GEP is likely associated with the mosses, which have no roots and can photosynthesize as soon as they thaw and receive light. Using two *Sphagnum* species from a New York peatland, Titus & Wagner (1984) showed that photosynthesis at a PAR of $500 \mu\text{mol m}^{-2} \text{ s}^{-1}$ was temperature dependent, but the rates at 2–3 °C were half of that at 20 °C. Moreover, during the spring, the mosses are likely to be close to their optimum moisture content, derived from snowmelt and precipitation, a high water table and low rates of evapotranspiration, $<2 \text{ mm day}^{-1}$ (Lafleur *et al.*, 2005). Using the results from *Sphagnum nemorum*, a hummock species similar to the dominant *S. capillifolium* at Mer Bleue, the photosynthetic rates observed by Titus & Wagner (1984) under laboratory conditions (optimum moisture content and light) are equivalent to $1.6 \text{ g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$, with a moss biomass of 159 g m^{-2} (Bubier *et al.*, 2006). This is close to the average

GEP recorded over the first 2–3 weeks after the disappearance of the snow cover (Fig. 1). Moore *et al.* (2002) also reported fast *Sphagnum* growth in the early spring.

Although the peatland contains evergreen shrubs, their leaves are initially brown and show significant increases in foliar N and especially chlorophyll *a* during the spring (Figs 5 and 6). The strong relationship between photosynthetic capacity and N concentration has been demonstrated for plants within Mer Bleue by Small (1972) and for fens and bogs and biomes in general by Reich *et al.* (1999). The frozen soil in the rooting zone of the shrubs may inhibit water uptake and photosynthesis during the early part of the spring, as has been suggested for evergreen trees in the boreal forest (e.g. Jarvis & Linder, 2000) though the pattern may not be general, as reported for five forest sites by Tanja *et al.* (2003). Using a shrub foliar mass of 180 g m^{-2} (Bubier *et al.*, 2006) and average evergreen foliar photosynthetic rates from Small (1972), the shrub photosynthetic capacity at 20°C is about $13 \text{ g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$ and perhaps half of that at 10°C , which is the average spring temperature. Combined with the moss photosynthesis rates, these values are similar to the GEP recorded by the tower during the second half of the spring (Fig. 1). The combination of the moss and shrub components creates a continual increase in GEP during the spring (Fig. 1) and there appears to be no clear critical threshold temperature. The relationship between temperature and photosynthetic uptake can be complex (see a review by Öquist & Huner, 2003) and Tanja *et al.* (2003) and Monson *et al.* (2005) have noted that in evergreen systems the spring recovery can be reversible, after a cold spell. In our bog, most of the photosynthetic biomass can be regarded as evergreen, in mosses and shrubs, with the deciduous shrubs and trees (e.g. *V. myrtilloides* and *L. laricina*) not producing leaves and needles until the end of May.

Radiation on a daily basis appears to be relatively unimportant in the spring development of GEP in this peatland. The low compensation and light saturation points for *Sphagnum* are well established: Titus & Wagner (1984) report values of about 55 and $500 \mu\text{mol m}^{-2} \text{ s}^{-1}$, respectively, for *S. nemorum*. Light saturation at $600\text{--}900 \mu\text{mol m}^{-2} \text{ s}^{-1}$ was reported for shrub leaves from Mer Bleue (Small, 1972) and the light saturation observed at the tower falls in the range of $600\text{--}700 \mu\text{mol m}^{-2} \text{ s}^{-1}$ (Letts *et al.*, 2005), similar to that reported for other northern bogs (e.g. Frolking *et al.*, 1998).

In this peatland, the rapid start of GEP after snowmelt also entails a rapid conversion of the ecosystem from a net source to a net sink of CO_2 (i.e. $\text{NEE} < 0$). This occurred an average of 11 days after the start of GEP, and the average daily temperature at 10 cm in the peat at this date is similar to the mean annual temperature,

suggesting that the relationship established by Baldocchi *et al.* (2005) for deciduous forests may be more broadly applicable. The rate of increase in GEP during the spring, averaging $0.1 \text{ g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$, is less dramatic than for deciduous forests, as suggested by Gu *et al.* (2003) for an evergreen forest.

It is not possible to identify the onset of CO_2 uptake ($\text{NEE} = 0$) using MODIS vegetation indices (16-day composites) or productivity estimates (8-day composites). This is likely because the coarse temporal resolution of these products cannot detect the rapid change in this ecosystem from a net source to a net sink of CO_2 . Furthermore, it is unlikely that such a rapid switch from source to sink would lead to a discernible change in the spectral properties of a plant canopy. These indices should be better able to detect the onset of photosynthesis but the signal would be difficult to differentiate from an increase in their values associated with the melt of the snow pack. It is less likely that MODIS FPAR product would not be able to detect the presence of moss on the bog surface (Connolly, 2006).

The sudden decrease in year 2000 corresponds to a series of snowfall events recorded at the Ottawa airport from days 97 to 103. Snow depth on the bog ranged from 5.5 to 23.3 cm throughout the compositing period. Values near zero for the first compositing periods of 2001 and 2003 are associated with snow cover, while for 2002 the snow pack had completely disappeared by the middle of the first compositing period. It is worth noting that snow depth measurements at Mer Bleue are not strictly absolute measures. For snow depths $< 20 \text{ cm}$, the tops of the hummocks may be visible as systematic measurement for both hummocks and hollow were not conducted for all years. Secondly, recorded snow depth is interpolated from a sensor that measures depth continuously at one spot, which is complemented by sporadic snow depth data from other locations on the bog surface.

The very good correspondence between variations in MODIS GPP and PSN and tower-derived GEP may arise from two factors acting in isolation or combination; snowfall events and the influence of the DOA climatology in the MOD-17 algorithm through the temperature scalar. For 2001 and 2003, snow pack was recorded at Mer Bleue during the first compositing period while the snow had already melted for the corresponding period in 2002. Snow cover would lead to very low FPAR estimates. A number of snowfall events (recorded at the Ottawa airport) may have led to the downturn in all productivity estimates during the fourth compositing period of 2002. The down-regulation of photosynthesis in the MOD-17 algorithm is partly controlled by low temperatures (Heinsch *et al.*, 2003). The relative decrease in productivity for the third

compositing period of 2001 corresponds to a series of nights where below freezing temperatures were recorded at the Ottawa airport, though there is no corresponding drop in productivity associated with tower-derived GEP. No snow was recorded for this period. There does not seem to be a clear explanation for the mismatch between MODIS and tower productivity at the end of the series for 2003. The close correspondence in the magnitudes of, and variability in springtime productivity estimates from MODIS and the tower are encouraging for tracking patterns in spring-time photosynthesis dynamics in this ecosystem, albeit with a precision limited to the compositing periods applied to the data.

There is evidence of warmer springs: at the Ottawa International Airport, 15 km southwest of the Mer Bleue peatland, the March–May mean temperature has risen by an average of 0.21 °C per decade from 1939 to 2004. Rising spring temperatures elsewhere have been linked to changes in phenology and remote sensing attributes (e.g. Myneni *et al.*, 1997; Zhang *et al.*, 2004; Goetz *et al.*, 2005; Schwatz *et al.*, 2006) and NEE is related to growing season length across ecosystems (Churkina *et al.*, 2005). Given our finding of the strong relationship between spring GEP and snow disappearance and temperature in the Mer Bleue bog, will warming have a profound effect on the annual C budget, as has been suggested by Aurela *et al.* (2004) in a Finnish peatland?

We suggest that the impact of warmer springs on the annual C budget or NEE of this bog will not be strong, for several reasons. First, an earlier spring at the southerly location of Mer Bleue (45°N) may not result in stronger utilization of solar radiation, as may occur at more northerly locations, for example 69°N (Aurela *et al.*, 2004) and 60–67°N (Tanja *et al.*, 2003). Second, warmer peat temperatures induce greater ER, which would compensate for increased GEP. From 1999 to 2003, March–May GEP was strongly correlated with ER ($r = -0.98$, $P = 0.004$) and to a lesser extent with NEE ($r = 0.94$, $P = 0.016$). Third, the annual C budget at the Mer Bleue bog is strongly related to the NEE during the summer and early fall (Lafleur *et al.*, 2003). From 1999 to 2003, the June–August NEE ranged from –206 to –328 (average 266) g CO₂ m⁻². Drier summers had smaller NEE values and an earlier spring may increase the summer drying and negate any increased spring NEE.

Acknowledgements

This project has been supported by funds from the NSERC Strategic Grant Program, NSERC Discovery Grants Program and the NSERC/CFCAS/BIOCAP Canada Fluxnet Canada Research Network. We thank the National Capital Commission for permission to use Mer Bleue and Gershon Rother for his assistance over the last 7 years.

References

- Arora VK, Boer GJ (2005) A parameterization of leaf phenology for the terrestrial ecosystem component of climate models. *Global Change Biology*, **11**, 39–59.
- Aurela M, Laurila T, Tuovinen J-P (2004) The timing of snow melt controls the annual CO₂ balance in a subarctic fen. *Geophysical Research Letters*, **31**, doi: 10.1029/2004GL020315.
- Baldocchi DD, Black TA, Curtis PS *et al.* (2005) Predicting the onset of net carbon uptake by deciduous forests with soil temperature and climate data: a synthesis of FLUXNET data. *International Journal of Biometeorology*, **49**, 377–387.
- Barford NC (1985) *Experimental Measurements: Precision, Error and Truth*, 2nd edn. John Wiley, New York.
- Black TA, Chen WJ, Barr AG *et al.* (2000) Increased carbon sequestration by a boreal deciduous forest in years with a warm spring. *Geophysical Research Letters*, **27**, 1271–1274.
- Bubier JL, Crill PM, Moore TR *et al.* (1998) Seasonal patterns and controls on the net ecosystem CO₂ exchange in a boreal peatland complex. *Global Biogeochemical Cycles*, **12**, 703–714.
- Bubier JL, Moore TR, Crosby G (2006) Fine-scale vegetation distribution in a cool temperate bog. *Canadian Journal of Botany*, **84**, 910–923.
- Churkina G, Schimel D, Braswell BH *et al.* (2005) Spatial analysis of growing season length control over net ecosystem exchange. *Global Change Biology*, **11**, 1–11.
- Connolly J (2006) *A biogeographical study of peatlands using geographical information systems and remote sensing*. PhD thesis, University College Dublin, Dublin, Ireland.
- Frolking S (1997) Sensitivity of spruce/moss boreal forest net ecosystem productivity to seasonal anomalies in weather. *Journal of Geophysical Research*, **102**, 29053–29064.
- Frolking S, Bubier JL, Moore TR *et al.* (1998) Relationship between ecosystem productivity and photosynthetically active radiation for northern peatlands. *Global Biogeochemical Cycles*, **12**, 115–126.
- Goetz SJ, Bunn AG, Fisje GJ *et al.* (2005) Satellite-observed photosynthetic trends across boreal North America associated with climate and fire disturbance. *Proceedings National Academy of Sciences*, **102**, 13521–13525.
- Gu L, Post WM, Baldocchi D *et al.* (2003) Phenology of vegetation photosynthesis. In *Phenology: An Integrative Environmental Science* (ed. Schwartz M.D.), pp. 467–485. Kluwer Academic Publishers, Dordrecht, the Netherlands.
- Hagen SC, Braswell BH, Linder E *et al.* (2006) Statistical uncertainty of eddy flux-based estimates of gross ecosystem carbon exchange at Howland Forest, Maine. *Journal of Geophysical Research*, **111**, D08S03, doi: 10.1029/2005JD006154.
- Heinsch FA, Reeves M, Bowker CF (2003) *User's Guide, GPP and NPP (MOD 17A2/A3) Products, NASA MODIS Land Algorithm*. <http://www.forestry.umd.edu/ntsg/>
- Huete A, Didan K, Miura T *et al.* (2002) Overview of the radiometric and biophysical performance of the MODIS vegetation indices. *Remote Sensing of Environment*, **83**, 195–213.
- Hunter AF, Lechowicz MJ (1992) Predicting the timing of budburst in temperate trees. *Journal of Applied Ecology*, **29**, 597–604.
- Janssens IA, Lankreijer H, Matteucci G *et al.* (2001) Productivity overshadows temperature in determining soil and ecosystem

- respiration across European forests. *Global Change Biology*, **7**, 269–278.
- Jarvis P, Linder S (2000) Constraints to growth of boreal forests. *Nature*, **405**, 904–905.
- Lafleur PM, Roulet NT, Admiral S (2001) The annual cycle of CO₂ exchange at a boreal bog peatland. *Journal of Geophysical Research*, **106**, 3071–3081.
- Lafleur PM, Roulet NT, Bubier JL *et al.* (2003) Interannual variability in the peatland-atmosphere carbon dioxide exchange at an ombrotrophic bog. *Global Biogeochemical Cycles*, **17**, doi: 10.1029/2002GB001983.
- Lafleur PM, Hember RA, Admiral SW *et al.* (2005) Annual and seasonal variability in evapotranspiration and water table at a shrub-covered bog in southern Ontario, Canada. *Hydrological Processes*, **19**, 3533–3550.
- Law BE, Falge E, Gu L *et al.* (2002) Environmental controls over carbon dioxide and water vapour exchange of terrestrial vegetation. *Agricultural and Forest Meteorology*, **113**, 97–120.
- Letts M, Lafleur PM, Roulet NT (2005) On the relationship between cloudiness and net ecosystem carbon dioxide exchange in a peatland ecosystem. *Ecoscience*, **12**, 53–59.
- Monson RK, Sparks JP, Rosenstiel TN *et al.* (2005) Climatic influences on net ecosystem CO₂ exchange during the transition from wintertime carbon source to springtime carbon sink in a high-elevation, subalpine forest. *Oecologia*, **146**, 130–147.
- Moore T, Bubier JL, Frohking S *et al.* (2002) Plant biomass and production and CO₂ exchange in an ombrotrophic bog. *Journal of Ecology*, **90**, 25–36.
- Myneni RB, Keeling CD, Tucker CJ *et al.* (1997) Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature*, **386**, 698–702.
- Öquist G, Huner NPA (2003) Photosynthesis of overwintering evergreen plants. *Annual Review of Plant Biology*, **54**, 329–355.
- Porra RJ, Thompson WA, Kriedemann PE (1989) Determination of accurate extinction coefficients and simultaneous equations for assaying chlorophylls *a* and *b* extracted with four different solvents: verification of the concentration of chlorophyll standards by atomic absorption spectroscopy. *Biochimica et Biophysica Acta*, **975**, 384–394.
- Reich PB, Ellsworth DS, Walters MB *et al.* (1999) Generality of leaf trait relationships: a test across six biomes. *Ecology*, **80**, 1955–1969.
- Schwartz MD (ed.) (2003) *Phenology: An Integrative Environmental Science*. Kluwer Academic Publishers, Dordrecht, the Netherlands.
- Schwartz MD, Ahas R, Aasa A (2006) Onset of spring earlier across the northern Hemisphere. *Global Change Biology*, **12**, 343–351.
- Schwarz PA, Fahey TJ, Dawson TE (1997) Seasonal air and soil temperature effects on photosynthesis in red spruce (*Picea rubens*) saplings. *Tree Physiology*, **17**, 187–194.
- Small E (1972) Photosynthesis rates in relation to nitrogen recycling as an adaptation to nutrient deficiency in peat bog plants. *Canadian Journal of Botany*, **50**, 2227–2233.
- Tanja S, Berninger F, Vesala T *et al.* (2003) Air temperature triggers the recovery of evergreen forest photosynthesis in spring. *Global Change Biology*, **9**, 1410–1426.
- Titus JE, Wagner DJ (1984) Carbon balance for two *Sphagnum* mosses: water balance resolves a physiological paradox. *Ecology*, **65**, 1765–1774.
- Waring RH, Running SW (1998) *Forest Ecosystems: Analysis at Multiple Scales*, 2nd edition. Academic Press, San Diego, CA.
- Zhan X, Sohlberg RA, Townshend JRG *et al.* (2002) Detection of land cover changes using MODIS 250 m data. *Remote Sensing of Environment*, **83**, 336–350.
- Zhang X, Friedl MA, Schaaf C *et al.* (2004) Climate controls on vegetation phenological patterns in northern mid- and high-latitudes inferred from MODIS data. *Global Change Biology*, **10**, 1133–1145.