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Modeling the effects of hydrology on gross primary productivity and net ecosystem productivity at Mer Bleue bog

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[1] The *ecosys* model was applied to investigate the effects of water table and subsurface hydrology changes on carbon dioxide exchange at the ombrotrophic Mer Bleue peatland, Ontario, Canada. It was hypothesized that (1) water table drawdown would not affect vascular canopy water potential, hence vascular productivity, because roots would penetrate deeper to compensate for near-surface dryness, (2) moss canopy water potential and productivity would be severely reduced because rhizoids occupy the uppermost peat that is subject to desiccation with water table decline, and (3) given that in a previous study of Mer Bleue, ecosystem respiration showed little sensitivity to water table drawdown, gross primary productivity would mainly determine the net ecosystem productivity through these vegetation–subsurface hydrology linkages. Model output was compared with literature reports and hourly eddy-covariance measurements during 2000–2004. Our findings suggest that late-summer water table drawdown in 2001 had only a minor impact on vascular canopy water potential but greatly impacted hummock moss water potential, where midday values declined to −250 MPa on average in the model. As a result, simulated moss productivity was reduced by half, which largely explained a reduction of 2–3 μmol CO_2 m^{-2} s^{-1} in midday simulated and measurement-derived gross primary productivity and an equivalent reduction in simulated and measured net ecosystem productivity. The water content of the near-surface peat (top 5–10 cm) was found to be the most important driver of interannual variability of annual net ecosystem productivity through its effects on hummock moss productivity and on ecosystem respiration.

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1. Introduction

[2] The water balance of peatlands is critical for their carbon (C) sequestration [*Lafleur et al.*, 2003, 1997; *National Wetlands Working Group*, 1997; *Shurpali et al.*, 1995]. However, there is considerable uncertainty as to how gross primary productivity (GPP), ecosystem respiration (ER) and net ecosystem productivity (NEP ≈ GPP − ER) depend on subsurface hydrology in peatland ecosystems [*Bubier et al.*, 2003]. In particular, understanding how variations in water table (WT) influence the relative importance of GPP and ER for variations in NEP is of critical concern. Several studies have suggested that bog ER changes little with WT variation [*Dimitrov et al.*, 2010c; *Dimitrov*, 2009; *Lafleur et al.*, 2005a], thus implying that variations in GPP are the main determinant of those in NEP. Yet, the mechanisms by which bog GPP is linked to changes in WT depth and peat water contents (θ) are not fully understood. In this study we use an ecophysiological model and field and laboratory observations to investigate these linkages.

1.1. Hydrological Effects on Peatland NEP and Its Components

[3] Several field studies have shown that peatland water status, as reflected by changes in water table, influences NEP through its components GPP and ER [*Sulman et al.*, 2009; *Strack and Waddington*, 2007; *Strack et al.*, 2006; *Lafleur et al.*, 2001; *Aurela et al.*, 2001; *Waddington and Roulet*, 2000; *Bubier et al.*, 1999; *Christensen et al.*, 1998; *Moore et al.*, 1998; *Alm et al.*, 1999, 1997]. The WT drawdown during drought has been widely reported to decrease NEP [*Lafleur et al.*, 1997; *Shurpali et al.*, 1995] or both NEP and GPP [*Strack et al.*, 2006; *Alm et al.*, 1999; *Joiner et al.*, 1999; *Schreader et al.*, 1998; *Shurpali and Verma*, 1998]. However, peatland communities have been found to respond in different ways to low WT and θ [*Bubier et al.*, 2003; *Aerts*,

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1999, 1995]. *Weltzin et al.* [2000] found that bryophyte and sedges enhanced their GPP under wetter conditions, while shrubs enhanced their GPP under moderately dry conditions. *Bubier et al.* [2003] reported a substantial reduction in GPP under dry conditions at a sedge-dominated fen, but smaller reduction in GPP under the same conditions at an adjacent bog dominated by evergreen (ericaceous) shrubs. They argued that this smaller reduction in bog GPP during moderately dry summer periods was a long-term adaptation of these evergreen species to water stressed conditions. The reason for such long-term adaptation has been attributed by different researchers to either drought tolerance or drought avoidance. For example, *Small* [1972a, 1972b] found that ericaceous shrubs at a dry peatland had high tolerance to moisture stress, while *Aerts* [1999, 1995] reported that wetland evergreens were able to conserve plant moisture under water-stressed conditions, thus to avoid GPP reduction with drought.

[4] The presence or absence of mosses plays a key role in the water and C budgets of peatlands. Water status of moss is more sensitive to water deficits than is that of vascular plants because mosses lack stomata to control their water loss to the atmosphere [*Clymo*, 1983; *Ingram*, 1983; *Richardson*, 1981]. Therefore, moss GPP is more sensitive to water deficits [*Clymo and Hayward*, 1982; *Proctor*, 1982] compared to vascular GPP. As a consequence, many authors have reported reduced moss GPP during dry periods [*Strack et al.*, 2006; *Weltzin et al.*, 2000; *Alm et al.*, 1999].

[5] The effects of peatland hydrology on ER have been widely debated [*Dimitrov et al.*, 2010c; *Dimitrov*, 2009]. Some researchers have found no dependence of ER on WT variation [*Blodau et al.*, 2007; *Lafleur et al.*, 2005a; *Moore et al.*, 2003; *Updegraff et al.*, 2001; *Bubier et al.*, 1998; *Silvola et al.*, 1996a, 1996b], while others have found a dependence but provide different explanations for it [*Sulman et al.*, 2009; *Strack and Waddington*, 2007; *Bubier et al.*, 2003; *Frolking et al.*, 2002, 2001; *Waddington et al.*, 2001; *Waddington and Roulet*, 2000; *Oechel et al.*, 1998; *Moore and Dalva*, 1993; *Alm et al.*, 1997; *Silvola and Ahlholm*, 1989]. *Dimitrov et al.* [2010c] attempted to reconcile these contradictory observations by suggesting a mechanism for maintaining conservative respiration in peatlands. Strong evidence for this mechanism was found by modeling C fluxes at the Mer Bleue bog in east-central Canada [*Dimitrov et al.*, 2010c], where an increase of soil respiration at depth with WT drawdown was offset by a decrease of respiration in near-surface (top 5–10 cm) peat and moss at drying hummocks. These findings were consistent with field experiments at the same site [*Lafleur et al.*, 2005a]. Although acting with different strengths in peatlands with different hydrological properties, this mechanism results in ER that may be largely independent of natural WT variations, unless the uppermost peat maintains its wetness during WT decline [*Dimitrov et al.*, 2010c].

1.2. Advances in Modeling of Hydrological and Topographical Effects on Peatland Carbon Balance

[6] Even though the large number of field studies above explain reasonably well various effects of subsurface hydrology on bog NEP and its components, a holistic understanding is hard to achieve experimentally due to confounding effects of temperature, nutrient availability, and plant communities and their phenology [*Roulet et al.*, 2007; *Lafleur et al.*, 2003; *Bubier et al.*, 2003]. The holistic understanding of hydrological effects on NEP is further complicated by differences in peatland type, changing environmental conditions, and lack of complete sets of measurements of water table, θ at depth and moss water content at different microtopographical forms (hummocks, hollows) at most peatland sites. Therefore, one way to investigate in detail the complexity of hydrological effects on NEP, and its components, is to use a process-based model capable of distinguishing these effects from those of soil temperature and nutrients, and of providing insight into interactions between various processes ongoing at different microtopographical forms of the peatland.

[7] Ecohydrological models couple hydrology and C dynamics in peatlands, but differ greatly among each other with respect to their hydrological schemes and the way they treat (if they do) terrain topography. Some of these models, such as MWM [*St-Hilaire et al.*, 2010], PCARS [*Frolking et al.*, 2002] and the peat accumulation model [*Hilbert et al.*, 2000], do not simulate soil hydrology, but instead use WT depth as a model input to estimate peatland productivity and respiration. Thus, even though MWM was applied separately to bog hummocks and hollows for comparative modeling of their CO_2 fluxes [*Wu et al.*, 2011], the model does not really simulate interconnections between local hydrology and microtopography. Other models employ empirical hydrological schemes [*Bond-Lamberty et al.*, 2007; *Zhang et al.*, 2002] or simulate one-dimensional (vertical) soil water flow neglecting its lateral components [*Comer et al.*, 2000; *Potter*, 1997]. All such models omit the complexity of the spatial hydrology, thus greatly simplifying its effects on ecosystem productivity.

[8] Sophisticated ecohydrological and biogeochemical models, such as BEPS [*Chen et al.*, 2007, 2005] and InTEC V3.0 [*Ju et al.*, 2006], couple simulated three-dimensional hydrology to peatland C balance. *Sonnentag et al.* [2008] further adapted BEPS to model the effects of site (mesoscale) topography on hydrology, and hence on CO_2 exchange at Mer Bleue bog. However, to the best of our knowledge, none of these models simulates hydrological and biological processes at the microtopographic level of peatland hummocks and hollows. Instead, peatland hydrology is represented through modeling of WT depth and θ referenced to an average soil surface at the mesoscale, as θ at depth in hummocks and hollows were not simulated due to an inherent inability to reference them to an undulating hummocky peat surface. Thus, the complex effect of water content distribution and redistribution throughout the hummock-hollow peat profile on ecosystem C balance is also oversimplified.

[9] In the past we have used the *ecosys* model [*Grant*, 2001], which couples hydrology, soil thermal regime, and C and energy balances of ecosystems, to study hourly dynamics of water table, θ and soil temperatures in hummocks and hollows of the Mer Bleue bog [*Dimitrov et al.*, 2010a, 2010b]. The effects of these hydrological and thermal controls on ER and its components at the same site was extensively studied by *Dimitrov et al.* [2010c], thereby contributing to the current research. Here we use the same model run to investigate the effects of water table and θ variations on GPP and NEP at the Mer Bleue bog.

Table 1. Weather Conditions for Mer Bleue Peatland, Mean Annual Air Temperature, and Total Annual Precipitation Measured at Macdonald-Cartier International Airport, and Total Precipitation Measured at Mer Bleue Bog From April Through September (Including Growing Season)

	Years						
Weather Records	1998	1999	2000	2001	2002	2003	2004
Mean annual air temp. [°C]	8.3	7.7	6.0	7.6	6.9	5.8	5.8
Total annual precipitation [mm]	875	919	977	793	889	978	907
Total precipitation April–Sept. [mm]	332	425	511	392	422	397	577

1.3. Objectives and Hypotheses

[10] In our earlier application of *ecosys* for Mer Bleue bog [*Dimitrov et al.*, 2010c] we found both simulated and measured ER to be little sensitive to WT drawdown and changes in peat θ. The main objective of our current research is to develop a better understanding of the effects of subsurface hydrology on bog GPP and NEP, as determined by interactions among the water table and soil and plant water contents at hummock and hollow locations. We then use this understanding to explain the interannual variability of bog NEP and its relationship to WT dynamics and near-surface θ. Our main hypothesis is that, given ER is relatively insensitive to WT drawdown, a decrease of near-surface θ in hummocks causes a decrease of bog GPP and NEP, mainly due to decrease of moss productivity at hummocks. At the same time moss productivity at hollows and vascular productivity at hummocks and hollows remains relatively unaffected by changes in subsurface hydrology. This hypothesis is investigated through the following processes in the model.

1.3.1. Vascular Water Relations

[11] Near-surface peat desiccation at bog hummocks during WT drawdown causes low soil water potential and high soil hydraulic resistance, which in turn causes low root water potential and reduced root water uptake. However, during WT drawdown peat layers below ~10 cm depth in hummocks and peat in hollows maintain relatively high soil water contents through sustained upward water flux along the potential gradients above the water table. These high soil water contents enable rapid root growth and thereby rapid root water uptake that compensates for the reduced root water uptake from the near-surface peat. Thus, with similar evapotranspiration demand, total root water uptake, and hence canopy water and turgor potentials, should vary little with widely varying WT.

1.3.2. Moss Water Relations

[12] Compared to vascular plant water uptake, moss water uptake in hummocks should be more sensitive to near-surface desiccation as *Sphagnum* rhizoids grow in the near-surface peat only [*Richardson*, 1981]. Therefore, a decrease in near-surface θ slows moss water uptake, forcing moss canopy water potential to decrease at hummocks. On the other hand, moss canopy water potential at hollows changes little during WT drawdown because the near-surface θ is sustained by capillary rise through the shallow fibric peat.

1.3.3. Vascular, Moss and Total Productivities

[13] Stable vascular turgor potential with contrasting WT depths in both hummocks and hollows leads to similar vascular CO_2 fixation rates directly by maintaining similar mesophyll water status and indirectly by maintaining similar stomatal resistances. The decrease of moss canopy water potential with WT drawdown and near-surface desiccation directly reduces moss CO_2 fixation rates at hummocks, while moss canopy water potential and CO_2 fixation rates at hollows are relatively unaffected by WT drawdown. Total bog GPP therefore decreases with WT drawdown and decreasing moss productivity on hummocks.

2. Site Description

[14] Mer Bleue bog is a large (~2800 ha), ombrotrophic bog, located about 15 km east of Ottawa in Ontario, Canada. The groundcover is mainly *Sphagnum* mosses and overstory vegetation is dominated by a low shrub canopy (20–30 cm height), with sparse sedges and herbaceous plants and some discontinuous patches of coniferous trees [*Lafleur et al.*, 2005a; *Frolking et al.*, 2002; *Moore et al.*, 2002]. Peat depth increases from 2 to 6 m from the periphery toward the center and is about 4–5 m deep around the eddy-covariance (EC) tower [*Lafleur et al.*, 2005b]. The bog surface has expressed hummock-hollow microtopography, dominated by hummocks with an average diameter of 1 m that comprise about 70% of the surface and an average relief between hummocks and hollows of 25 cm [*Lafleur et al.*, 2005b]. Mer Bleue is a dry peatland with WT varying between ~20 and ~70 cm below the hummock surface [*Lafleur et al.*, 2005a, 2005b]. Based on peat texture and Von Post degree of humification, fibric peat occupies the top 0–35 cm, then hemic peat at 35–45 cm, and sapric peat at >45 cm in hummocks, and respectively at 0–10 cm, 10–20 cm, and >20 cm in hollows [*Lafleur et al.*, 2005b; S. Admiral, personal communication]. Macroporosity of fibric peat in both hummocks and hollows was estimated to be 0.8 m^3 m^{-3} [*Dimitrov et al.*, 2010a; *Dimitrov*, 2009]. Weather conditions that affected the WT levels, hence subsurface peat hydrology, are given in Table 1 for years 1998–2004.

3. Methods

3.1. Model Development

[15] The key *ecosys* algorithms for modeling of plant water relations and gross primary productivity are described in the auxiliary material (Text S1), in which equations are given in Appendix I, their parameters with values and literature sources are given in Appendix II, and equation variables and indices are given in Appendix III.[1] Below we briefly summarize the key model algorithms used for testing the hypotheses of this study. The *ecosys* algorithms for

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[1] Auxiliary materials are available in the HTML. doi:10.1029/2010JG001586.

aboveground and belowground respiration of vascular plants and moss and for microbial respiration are described in *Dimitrov et al.* [2010c] and are also briefly referred to here for completeness, as ecosystem respiration is a major component of net ecosystem productivity. Equations for plant water relations, productivity and respiration are connected to simulated soil hydrology, directly through θ and soil water potential (ψ_S), and indirectly through aqueous and gaseous O_2 and their transfer and transport through water and gas phases in soil and roots [*Grant*, 2001].

3.1.1. Plant Water Relations

[16] The model solves for coupled heat and water transfer through the soil-root-canopy continuum. For each plant species, *ecosys* converges first for the canopy temperature and then for the canopy water potential (ψ_C) at which canopy transpiration/evaporation (E) equilibrates with root/rhizoid water uptake (U) plus changes of canopy water content (ΔS) (Text S1, equation (A.1)). E is controlled by canopy-surface resistance (r_C) and aerodynamic resistance (r_A) (Text S1, equation (A.3)). With vascular plants r_C is the canopy stomatal resistance, which declines exponentially with increase of turgor potential (ψ_t, calculated from ψ_C in (Text S1, equation (A.2)) from the maximum cuticular resistance ($r_{C\max}$) when $\psi_t \rightarrow 0$ MPa and stomata are closed down to the minimum stomatal resistance ($r_{C\min}$) when $\psi_C \rightarrow 0$ MPa (ψ_t approaching its maximum) and stomata are fully open (Text S1, equation (A.4.a)). Thus, vascular plants regulate their r_C and E during dry periods to mitigate the effects of low ψ_S on their ψ_C.

[17] As *Sphagnum* lacks stomata [*Kim and Verma*, 1996], moss r_C is assumed constant, thus independent from moss ψ_C (Text S1, equation (A.4.b)) following *Clymo and Hayward* [1982] and *Proctor* [1982], although other studies have shown that the moss r_C can vary [*Williams and Flanagan*, 1996]. Lack of stomatal control on moss ψ_C causes moss canopy vapor density to approach atmospheric vapor density at ambient relative humidity during soil drying [*Grant et al.*, 2001]. Thus, low ψ_S during dry periods reduces moss U, hence moss ψ_C and moss canopy vapor density, which results in a decline of moss E (Text S1, equation (A.3)) with WT drawdown and near-surface desiccation.

[18] The U for each plant species (Text S1, equation (A.6)) is the sum of water uptake by root/rhizoid surfaces in each soil layer of the rooting zone, calculated by equilibrating the water transport from soil to the roots (U') with the water transport from the roots to the canopy (U'') (Text S1, equation (A.7.a)). U is therefore constrained by radial resistances from soil to root/rhizoid surfaces (Ω_S), radial resistances from those surfaces to root/rhizoid axes (Ω_R) and axial resistances of root/rhizoid axes to the canopy (Ω_A) determined by root/rhizoid axes lengths and densities (Text S1, equation (A.7.b)). While Ω_R and Ω_A increase slightly with decreasing θ in each soil layer, Ω_S increases sharply, which slows U and lowers ψ_C when solving for the root water potential (ψ_r) (Text S1, equations (A.8)–(A.9)).

[19] Maintaining multiple soil layers allows the model to represent contrasting hydrological conditions through the peat profile, such as dry near-surface and deep waterlogged peat [*Dimitrov et al.*, 2010a]. Simulated moss rhizoids grow in near-surface peat only while vascular roots grow deeper due to larger shoot-root C transfers per plant that drive extension of primary root axes [*Grant*, 2001]. Thus, *ecosys* is capable to model drying/re-wetting effects on E and U by simulating growth and distribution of moss rhizoids at near-surface and vascular roots to depths constrained by O_2 in the peat profile [*Dimitrov et al.*, 2010c].

3.1.2. Gross Primary Productivity Controlled by Plant Water Relations

[20] *Ecosys* calculates GPP for each plant species as a sum of leaf CO_2 fixation rates (V_C) (Text S1, equation (B.1)) simulated by the Farquhar model [*Farquhar et al.*, 1980], modified by non-stomatal water deficit effects on V_C derived from ψ_C for vascular plants (Text S1, equation (B.3.a)) [*Grant and Flanagan*, 2007] and moss (Text S1, equation (B.3.b)) [*Clymo and Hayward*, 1982; *Proctor*, 1982]. The Farquhar algorithm for carboxylation (Text S1, equations (B.6)–(B.11)) was further coupled to the algorithm for CO_2 diffusion into leaves (V_G) (Text S1, equations (B.12)–(B.17)). V_G is limited by the leaf surface resistance to CO_2 (r_L) (Text S1, equation (B.13)). Vascular r_L to CO_2 and water vapor ($r_{L\text{ water vapor}} = 0.64 \times r_{L\text{ CO2}}$) is controlled by leaf stomatal aperture through ψ_t (Text S1, equation (B.14.a)). All $r_{L\text{ water vapor}}$ are aggregated by leaf surface area for each species to arrive at canopy r_C, thus linking simulations at leaf and canopy levels. Moss r_L is assumed constant (Text S1, equation (B.14.b)) as *Sphagnum* leaves do not have stomata [*Richardson*, 1981]. Thus, *ecosys* is appropriate for applying in peatlands with its ability to simulate hydrological effects on vascular GPP through stomatal and non-stomatal controls, and on moss GPP through non-stomatal control only.

3.1.3. Ecosystem Respiration Controlled by Hydrology

[21] *Ecosys* equations for decomposition of soil organic matter, and for respiration and growth of microbial and root populations, interact with those for soil hydrology through soil water content θ, and through aqueous and gaseous O_2 diffusion [*Grant*, 2001; summarized in *Dimitrov et al.*, 2010c]. Heterotrophic microbes control the rates of decomposition, the inhibitory effect of desiccation upon which is caused by increase of aqueous microbial concentrations with decrease of θ [*Dimitrov et al.* [2010c], equations (A.1) and (A.2)]. Microbial respiration depends on concentration of C decomposition products through Michaelis-Menten kinetics [*Dimitrov et al.* [2010c], equation (A.3)]. Root/rhizoid respiration depends on concentration of root/rhizoid nonstructural C products of photosynthesis and internal plant C transfer through Michaelis-Menten kinetics. Both microbial aerobic and root/rhizoid respiration are controlled by O_2 uptake with respect to O_2 demand [*Dimitrov et al.* [2010c], equations (A.4), (A.5), and (B.5)]. The O_2 uptake is driven by ambient aqueous O_2 concentrations which depend on O_2 convective-diffusive transport in aqueous and gaseous phases [*Dimitrov et al.* [2010c], equations (A.5) and (B.5)].

[22] Thus, with low WT and consequent near-surface drying, microbial respiration in the upper peat will be maintained low through limited availability of decomposition products caused by low θ. However, microbial and root respiration in deeper, well-aerated peat above the water table will be maintained high, sustained by rapid gaseous O_2 diffusion in peat air-filled pore space and consequent replenishment of aqueous O_2 in peat water-filled pore space.

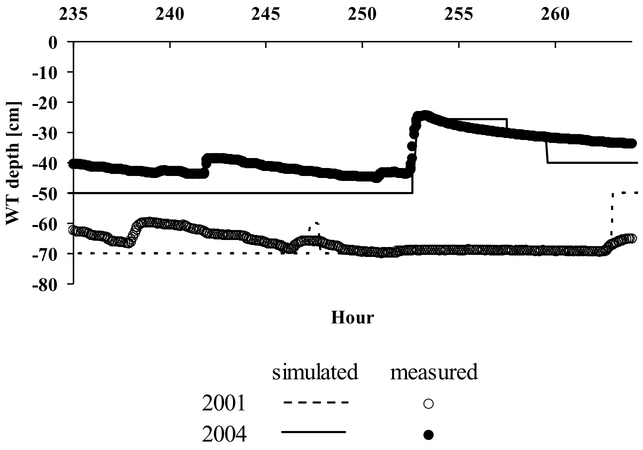

Figure 1. Hourly simulated and measured (potentiometric) WT depths from the hummock surface at Mer Bleue bog, DOY 235–264, dry year 2001 (lower simulated and measured) versus DOY 235–264, wet year 2004 (higher simulated and measured).

3.2. Field Measurements of Model Drivers, Carbon and Energy Fluxes

[23] To drive *ecosys*, half-hourly continuous measurements at 2 m above the canopy were provided from 1998 through 2004 for incoming short-wave radiation, air temperature, relative humidity, wind speed, and precipitation. Gap-filling for these measurements and corrections for winter precipitation at Mer Bleue bog from the Environment Canada weather station at Macdonald-Cartier Ottawa Airport (~15 km away) are summarized in *Dimitrov* [2009].

[24] To test *ecosys*, WT and θ were measured as described in *Dimitrov et al.* [2010a]. Eddy covariance measurements of net CO_2 exchange, partitioning into GPP and ER, as well as uncertainties in these measured and derived values, screening and gap-filling are described in *Lafleur et al.* [2003, 2001] and *Roulet et al.* [2007]. Screening and gap-filling of energy fluxes are summarized in *Dimitrov et al.* [2010b].

3.3. Model Experiment

[25] To test our hypotheses of the effects of varying WT and θ on NEP through GPP, a model transect of 6 grid cells, consisting of 3 hummocks and 3 hollows, was designed to represent the microtopography of Mer Bleue bog. The hourly model output generated from the third and fourth cells, representing bog hummocks and hollows, respectively, were used in comparisons with measured and literature data. The first and second, and the fifth and sixth cells were considered as boundary cells. Key soil properties for Mer Bleue bog are given in *Dimitrov et al.* [2010a, 2010c]. The model was initialized with the biological properties of shrub and moss [*Dimitrov*, 2009; see also *ecosys* library files] and spun up by repeating 15 times the 7-year weather record of 1998–2004 at Mer Bleue (section 3.2). Following *Ju et al.* [2006], the equilibrium during the model spin up was attained after 60–70 years, when changes in simulated C sequestration in the soil humic pool became stable over time.

3.4. Testing Modeled GPP and NEP Versus Field Studies

[26] NEP as represented by the EC-measured CO_2 exchange is assumed to be the difference between GPP and ER, i.e., NEP $\approx$ GPP $-$ ER, as these are the largest fluxes on average at Mer Bleue bog [*Roulet et al.*, 2007]. However, NEP in the model also includes methane and dissolved organic and inorganic C export, although these were not subjects of the field study. The initial analysis focused on two 30-day periods in August–September 2001 and 2004 (DOY 235–264) corresponding to low and high average WT, respectively, during which modeled GPP and NEP were compared against EC-derived GPP and NEP at hourly, hourly binned and daily time scales. Comparisons were not conducted earlier in the growing season because differences in WT dynamics were less pronounced. Annual aggregations of modeled GPP and NEP were then compared to EC-derived GPP and NEP for 2001 and 2004. Finally, interannual variability of modeled NEP for years 2000 to 2004 inclusive was related to changes in WT depth and near-surface peat θ, and compared to EC-derived annual NEP for the same years. Years 1998 and 1999 were omitted from the analysis due to incomplete meteorological records.

[27] Simulated hourly and daily GPP, NEP and latent heat flux (as another indicator of accurate modeling of plant productivity and water relations) were regressed on the EC-derived fluxes for the period 2000–2004. To evaluate goodness of fit, the coefficients of determination (R^2) and regression slopes and intercepts were considered. Absolute discrepancy between model output and measurements were evaluated by the root mean square deviation (RMSD) and relative discrepancy by Willmott's index of agreement [*Willmott*, 1981].

4. Results

[28] The period DOY 235–264 was dry in year 2001 (average WT ~ -67 cm) and wet in year 2004 (average WT ~ -38 cm), thus providing an opportunity to contrast bog GPP and NEP with low and high WT (Figure 1) and associated θ (Figures 2a and 2b) under similar meteorological forcing. During the hours of CO_2 fixation (GPP > 0) for these periods, similar average relative humidities ($65 \pm 16\%$ in 2001 and $76 \pm 12\%$ in 2004), air temperatures ($18.9 \pm 4.1°C$ in 2001 and $18.0 \pm 3.7°C$ in 2004) and wind speeds (2.4 ± 0.7 m s^{-1} in 2001 and 2.5 ± 0.7 m s^{-1} in 2004) minimized the effects of different vapor pressure deficits and boundary layer resistances (Text S1, equation (A.3)) on evapotranspiration. Therefore, differences in ψ_C and ψ_t during these periods were determined mostly by the differences in soil θ and ψ_S through plant water uptake (Text S1, equation (A.3.2)), so that differences in GPP were largely determined by the effects of subsurface hydrology. Hereafter, periods DOY 235–264 in 2001 and 2004 are referred by year only.

4.1. Effects of Soil Hydrology on Vascular Plant Water Relations

[29] In the model, deep WT drawdown in 2001 (Figure 1) reduced upward water flux along ψ_S gradients through the 20% micropore (matrix) fraction of the top 5–10 cm fibric peat in hummocks, causing severe drying (Figure 2a) as

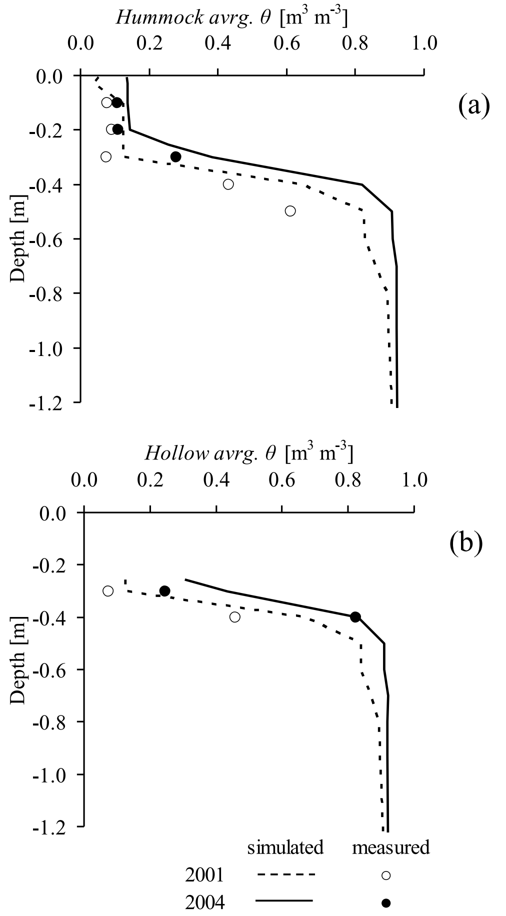

Figure 2. Average simulated and measured (TDR) soil water contents (θ) at depth in (a) hummocks and (b) hollows at Mer Bleue bog, DOY 235–264, dry year 2001 versus DOY 235–264, wet year 2004. Vertical axis refers to depth from hummock surface.

described in *Dimitrov et al.* [2010c]. Near-surface θ (upper 5–10 cm) decreased to ~0.03–0.05 $m^3\ m^{-3}$, i.e., <25% of the peat micropore fraction, resulting in near-surface desiccation. However, simulated θ was >0.12 $m^3\ m^{-3}$ at ~10 cm, i.e., >60% of the peat micropore fraction, so the peat remained wetter at and below that depth. At the bottom of the fibric peat, modeled and measured θ were close to saturation because of greater water retention and absence of macroporosity in hemic and sapric peat. Greater upward water flux from the higher WT in 2004 (Figure 1) resulted in higher near-surface hummock θ (Figure 2a) compared to that from the deep WT in 2001.

[30] Simulated θ and hence ψ_S and ψ_r were also driven by the diurnal evapotranspiration cycle, as well as by WT depth. To investigate representative ψ_S and ψ_r patterns at depth under contrasting WT, average ψ_S and ψ_r were calculated for each soil layer during 2001 and 2004 (Figures 3a and 3b). The low θ of near-surface peat micropores during 2001 caused strong reductions in near-surface ψ_S and ψ_r, while at the same time high micropore θ below 10 cm resulted in high ψ_S and ψ_r for the deeper fibric peat, hemic and sapric peat (Figure 3a). The high near-surface micropore θ during 2004 resulted in high ψ_S and ψ_r throughout the entire hummock peat profile. Near-surface ψ_r became less negative than ψ_S over the low WT in 2001 when the near-surface soil resistance Ω_S increased as θ decreased (Text S1, equation (A.9)). High Ω_S, in addition to the low near-surface ψ_S in 2001, resulted in a gradual reduction in U from the near-surface layers in hummocks. The direction of U eventually reversed (exudation) when ψ_r was less negative than ψ_S (Figure 3a), thus causing hydraulic lift in the model.

[31] In the model, reduced U at near-surface in 2001 was offset by increased U at depth, caused by high ψ_S (Figure 3a) and hence low Ω_S below 5–10 cm in the peat colonized by roots above the deeper water table. However, modeled root densities increased only marginally in the hemic and sapric peat above the water table (Figure 4), as root growth in the model was constrained by low soil O_2, consistent with experimental studies [*Nazaroff*, 1992]. Thus total vascular U, reduced at near-surface but increased at depth, was sufficient to sustain vascular E at high ψ_C and ψ_t over the lower WT in 2001 (Figure 5a). In comparison, the high WT during 2004 (Figure 1) resulted in high θ, ψ_S and ψ_r at all depths in the peat matrix (Figure 2a and Figure 3a), also causing total vascular U to sustain transpiration at high ψ_C and ψ_t (Figure 5a).

[32] Simulated ψ_C and ψ_t during the 2001 and 2004 periods were similar (Figure 5a) because U was similar in the zone of peak vascular root densities, i.e., between ~10–20 cm and 40 cm in the model (Figure 4) and in the field [*Murphy and Moore*, 2010; *Moore et al.* 2006, 2002]. This zone was below that of near-surface drying (upper 5–10 cm), hence was unaffected by the low WT in 2001. Similar vascular ψ_C and ψ_t under contrasting WT depths resulted in similar r_C (Figure 6a) and r_L (Text S1, equations (A.4.a) and (B.14.a)). Thus, contrasting subsurface hydrology had little effect on the simulated vascular water relations at hummocks.

[33] No near-surface drying was experienced at hollows, where the water table was close to the hollow surface and the shallow fibric peat was underlain by waterlogged deep peat. Thus ~70% of the fibric peat micropore fraction remained waterlogged in 2001, even though the near-surface bulk θ declined from that in 2004 (Figure 2b). In the model high hollow θ caused high ψ_S in peat micropores along the entire hollow peat profile in 2001 and 2004 (Figure 3b). Yet, simulated hollow ψ_C in 2001 was slightly lower than in 2004 (Figure 5b), and lower than the hummock ψ_C for both 2001 and 2004 (Figure 5a). That lower ψ_C was due to a combined effect of reduced θ in the upper 30–40 cm of hollow peat in 2001 (Figure 2b) and poorly developed vascular roots under low soil O_2 that raised Ω_R and Ω_A in the waterlogged hollow peat below 10 cm (model output not shown here). In the model, reduced θ in 2001 increased Ω_S [*Herkelrath et al.*, 1977] and decreased the active root length in contact with soil water, therefore increasing Ω_R and Ω_A [*Aguirrezabal et al.*, 1993].

[34] Increased Ω_S, Ω_R and Ω_A (Text S1, equations (A.7.a) and (A.7.b)) further reduced vascular U through the poorly developed roots in hollows, thus forcing lowered ψ_C to maintain vascular E at hollows in 2001 than in 2004 and at hummocks in 2001 and 2004 (Figures 5a and 5b). However, the slightly lower ψ_C was insufficient to lower ψ_t (Figure 5b) enough to trigger partial stomatal closure during the dry 2001. Instead, r_C at hollows was similar for both

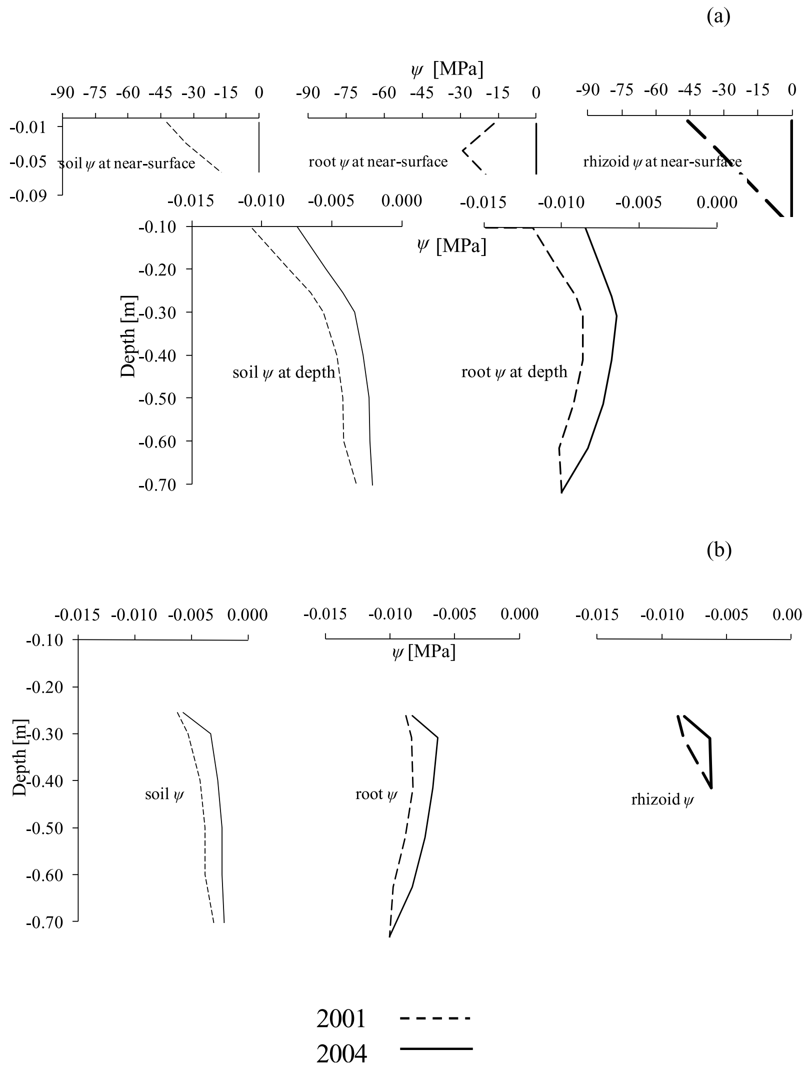

Figure 3. Average simulated water potentials (ψ): soil ψ, vascular root ψ and moss rhizoid ψ in (a) hummocks and (b) hollows at Mer Bleue bog, DOY 235–264, dry year 2001 versus DOY 235–264, wet year 2004. Vertical axis refers to depth from hummock surface.

2001 and 2004, and slightly greater than r_C at hummocks (Figures 6a and 6b), in spite of the small differences in ψ_C and ψ_t at hummocks and at hollows (Figures 5a and 5b). Compared to hummocks, higher hollow r_C was caused by higher values of the minimum canopy and leaf stomatal resistances (Text S1, equations (A.4.a) and (B.14.a)), through lower CO_2 fixation rates (Text S1, equations (A.5) and (B.15)). These lower CO_2 fixation rates were caused by slower nutrient uptake arising from reduced simulated microbial activity in hollows due to slower O_2 uptake in waterlogged peat, hence slower nutrient mineralization in the model that was ~24% and ~69% of that in hummocks during 2001 and 2004, respectively. Consequently, simulated vascular nutrient uptake in hollows was ~20% and ~35% of that in hummocks during 2001 and 2004, respectively. Lower soil temperatures in hollows [*Dimitrov et al.*, 2010b] further contributed to the slower nutrient mineralization and uptake in the model.

[35] Our simulations, indicating that vascular shrubs at Mer Bleue were not affected by water stress, were consistent with previous research at this site [*Moore et al.*, 2002; *Small*, 1972a, 1972b]. *Lafleur et al.* [2005b] found a little evidence of water stress in vascular plants at Mer Bleue bog, with first signs of slight reductions in shrub transpiration in the field detected when the water table reached its minimum depth at ~65–70 cm in hummocks in 2001.

4.2. Effects of Soil Hydrology on Moss Water Relations

[36] Moss U occurs in the upper ~10 cm of hummock and hollow peat, where rhizoids grow [*Clymo*, 1983; *Richardson*, 1981]. During periods of near-surface soil drying in hummocks as in 2001, low modeled moss U (Text S1, equation (A.7.a)), resulting from low near-surface ψ_S and ψ_r (Figure 3a), was insufficient to satisfy evaporative demand, which caused water loss and hence extremely low moss ψ_C (Figure 7a). These large ψ_C drops reduced differences between moss canopy and atmospheric vapor densities [*Grant et al.*, 2001], thus reducing moss E (Text S1, equation (A.3)) until soil rewetting allowed moss canopy vapor density and hence E to rise (Figure 8). High near-

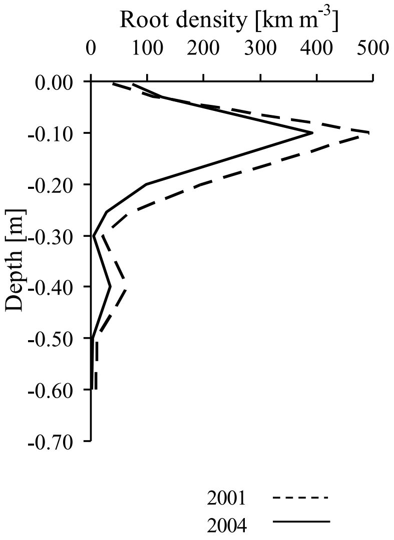

Figure 4. Average modeled root density at depth in hummocks, Mer Bleue bog, DOY 235–264, dry year 2001 versus DOY 235–264, wet year 2004. Vertical axis refers to depth from hummock surface.

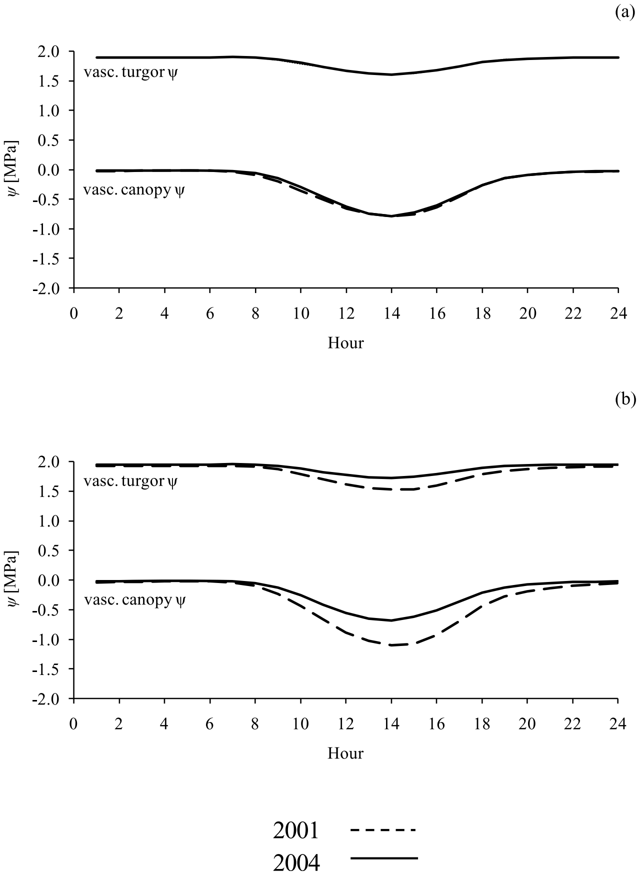

Figure 5. Hourly binned simulated vascular water potentials (ψ): canopy ψ and turgor ψ in (a) hummocks and (b) hollows at Mer Bleue bog, DOY 235–264, dry year 2001 versus DOY 235–264, wet year 2004.

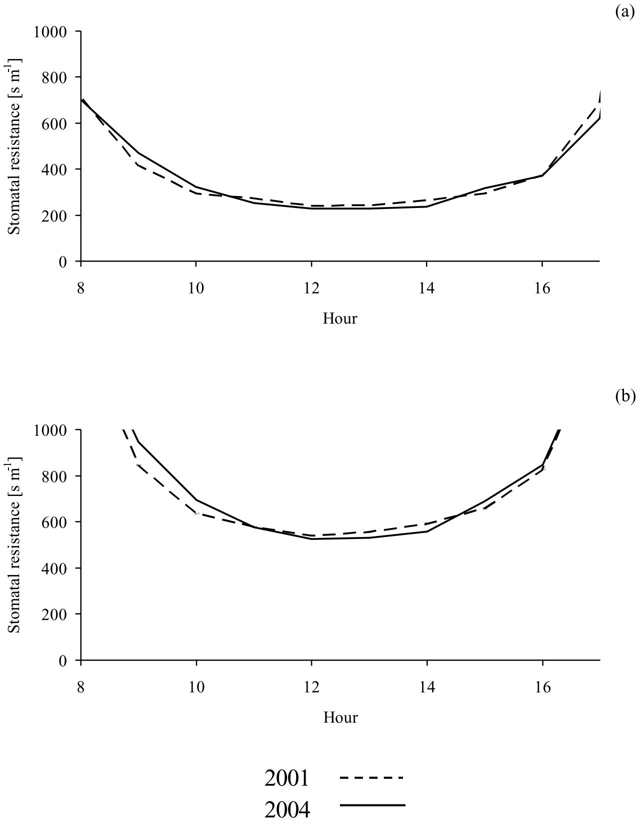

Figure 6. Hourly binned simulated vascular stomatal resistances in (a) hummocks and (b) hollows at Mer Bleue bog, DOY 235–264, dry year 2001 versus DOY 235–264, wet year 2004.

surface θ (Figure 2a) and ψ_S (Figure 3a) during 2004 resulted in much higher moss ψ_C in the model, compared to that during 2001 (Figure 7a).

[37] There were no pronounced effects of the water table and near-surface θ on hollow moss ψ_C in the model. Near-surface θ (Figure 2b) and ψ_S (Figure 3b) in hollows were sustained so that hollow moss ψ_C was unaffected by changes in soil hydrology during both periods (Figure 7b). However, with more hummocks than hollows at Mer Bleue bog (hummock: hollow surface area ratio of 7:3), the overall effects of water table and near-surface θ on simulated moss ψ_C were pronounced at the ecosystem scale. The simulated pattern of successive efflux events interspersed by periods of very low moss evaporation resulted in total moss E that was ~7% of vascular E over the low WT in 2001 and ~32% of vascular E over the high WT in 2004.

4.3. Vascular, Moss and Bog GPP During Periods of Contrasting Hydrology

[38] Simulated vascular and moss GPP at hummocks and hollows, total GPP by plant type (weighted for hummocks and hollows) and total bog GPP were investigated during the periods of contrasting hydrology WT in 2001 and 2004. Vascular and moss GPP were not measured separately so that species simulations could not be validated by independent tests. However, simulated total bog GPP was compared against EC-derived bog GPP.

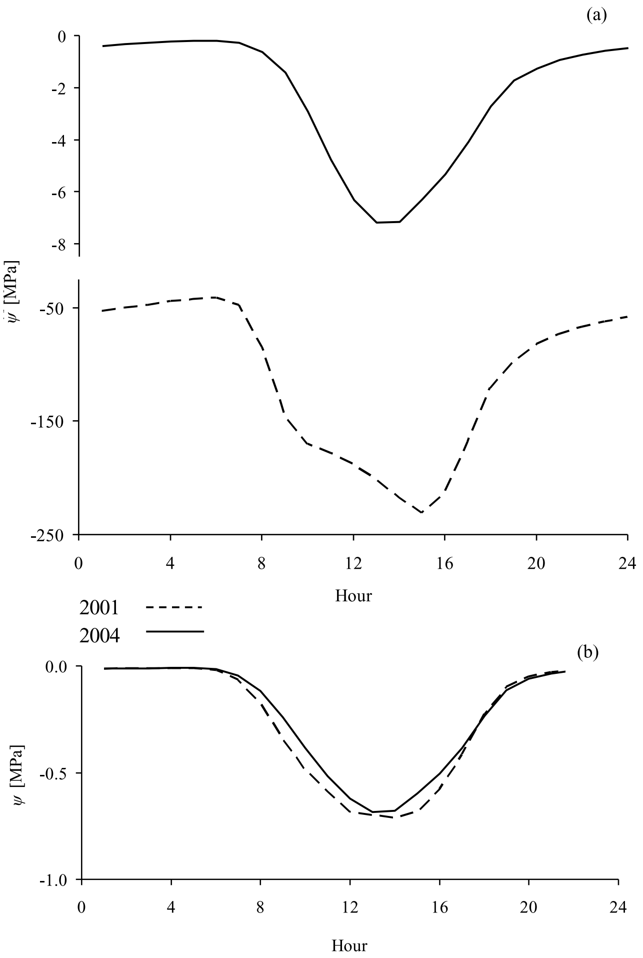

Figure 7. Hourly binned simulated moss canopy water potentials (ψ) in (a) hummocks and (b) hollows at Mer Bleue bog, DOY 235–264, dry year 2001 versus DOY 235–264, wet year 2004.

[39] In the model, similar vascular ψ_C and ψ_t under the contrasting WT and near-surface θ for hummocks and hollows (Figures 5a and 5b) resulted in similar stomatal (Text S1, equation (B.14.a)) and non-stomatal (Text S1, equation (B.3a)) effects on CO_2 fixation in vascular plant leaves (Text S1, equations (B.2), (B.12) and (B.13)), hence similar vascular GPP. Therefore, within the normal range of WT variation at Mer Bleue bog, subsurface hydrology had only minor effects on simulated vascular GPP. This finding was consistent with field studies at Mer Bleue [*Lafleur et al.*, 2005b; *Bubier et al.*, 2003]. Total vascular GPP and hummock vascular GPP during the drier 2001 were ~92% and ~90%, respectively of those during the wetter 2004 (Figures 9a and 9b), while hollow vascular GPP was similar for both periods (Figure 9c). The slightly lower hummock vascular GPP in the model during drier 2001 period was due to slower simulated mineralization in the upper most productive hummock peat (top 10–20 cm) caused by reduced heterotrophic respiration and microbial activity [*Dimitrov et al.*, 2010c]. Thus, with vascular root densities peaking at ~10–20 cm depth in the model (Figure 4) and in the field [*Murphy and Moore*, 2010; *Moore et al.*, 2006], simulated vascular nutrient uptake and leaf N concentration at hummocks were ~35% and ~10% less, respectively, in 2001 than in 2004.

[40] In the model moss ψ_C at hummocks was very low during 2001 (Figure 7a) which strongly reduced CO_2 fixation in moss leaves (Text S1, equations (B.2) and (B.3.b)), and hence moss GPP compared to 2004. These extremely negative ψ_C caused total moss GPP and hummock moss GPP during 2001 to decline to ~22% and ~49%, respectively of those during 2004 (Figures 10a and 10b). In contrast, moss GPP at hollows was similar for both periods (Figure 10c) because subsurface hydrology did not affect moss ψ_C (Figure 7b).

[41] Both simulated and EC-derived total bog GPP (vascular and moss) were lower during 2001 than during 2004 at hourly (Figure 11a), hourly binned (Figure 11b) and daily (Figure 11c) time scales. At the annual time scale, simulated bog GPP of 704 g C m^{-2} y^{-1} and EC-derived bog GPP of 691 C m^{-2} y^{-1} for 2004 were higher than simulated bog GPP of 656 g C m^{-2} y^{-1} and EC-derived bog GPP of 527 g C m^{-2} y^{-1} for 2001. Discrepancies between simulated and EC-derived annual GPP were mainly due to a more rapid rise in simulated GPP in May and early June, which was partially offset in 2004 by increased simulated GPP in July and early August.

4.4. ER During Periods of Contrasting Hydrology

[42] Recently, both modeling [*Dimitrov et al.*, 2010c; *Dimitrov*, 2009] and experimental research [*Lafleur et al.*, 2005a] have found ER at Mer Bleue bog to be relatively unaffected by changes in water table and peat θ. These findings are illustrated in Figures 12a and 12b for hourly and hourly binned CO_2 exchange, where the nighttime (negative) values represent ER. Even though the model had a tendency to underestimate ER for both 2001 and 2004 periods [*Dimitrov et al.*, 2010c], both simulated and measured ER fluxes were similar under contrasting simulated WT (Figures 12a and 12b and Figure 3). A decrease in near-surface microbial respiration in peat hummocks, resulting from WT drawdown and subsequent desiccation of the uppermost peat, offset an increase of soil respiration at depth with improved aeration. This resulted in average soil respiration of 0.85 μmol CO_2 m^{-2} s^{-1} in hummocks for both 2001 and 2004 periods in the model. However, increased hollow soil respiration with WT drawdown was offset by decreased aboveground moss respiration with near-surface desiccation in hummocks, which resulted in average ER of 2.01 μmol CO_2 m^{-2} s^{-1} and 2.23 μmol CO_2, respectively for 2001 and 2004 periods in the model.

[43] At the annual scale, modeled ER of 658 g C m^{-2} y^{-1} during the dry 2001 and 623 g C m^{-2} y^{-1} during the wet 2004 fitted within the confidence intervals of annual cumulative random errors of the EC-derived ER, which were 535 ± 134 g C m^{-2} y^{-1} for 2001 and 578 ± 145 g C m^{-2} y^{-1} for 2004. Details are given in *Dimitrov et al.* [2010c].

4.5. Explaining Bog NEP Through GPP and Subsurface Peat Hydrology

[44] Since ER was relatively unaffected by changes in water table and peat θ, simulated and EC NEP at hourly (Figure 12a), hourly binned (Figure 12b) and daily (Figure 12c) time scales during 2001 and 2004 periods closely followed the simulated and EC-derived bog GPP

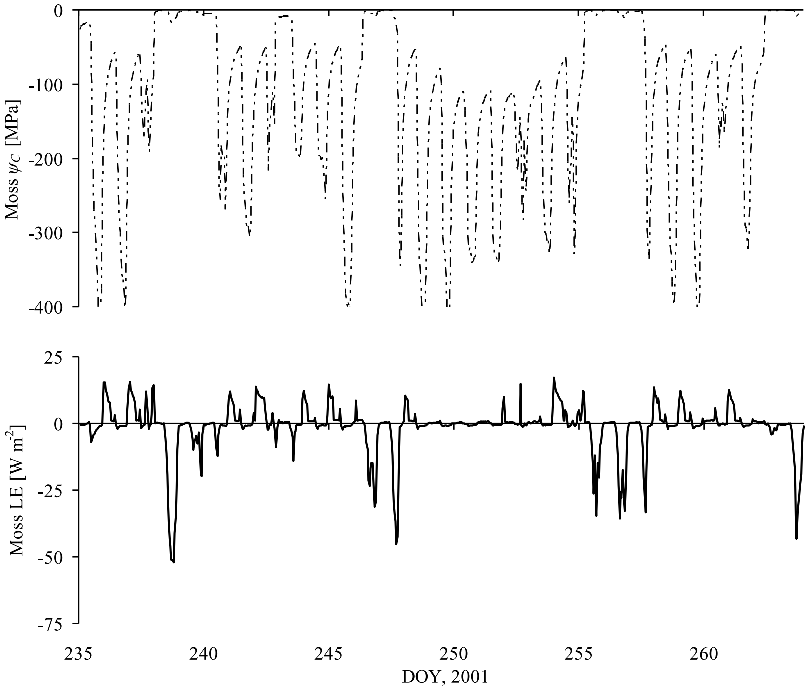

Figure 8. Hummocks, alternating patterns in time (DOY) of the simulated moss canopy water potential (ψ_C) and simulated moss latent heat flux (LE), Mer Bleue bog, DOY 235–264 during the dry year 2001. Negative LE values indicate direction to the atmosphere.

(Figures 11a–11c). However, both simulated and EC NEP (Figures 12a–12c) were lower during the dry 2001 period than during the wet 2004 period (Figure 1). At the annual time scale, simulated and EC-derived NEP were 83 and 102 g C m^{-2} y^{-1} with simulated and measured average WT of −41 and −38 cm during 2004. These were both higher than simulated and EC-derived NEP of −7 and 3 g C m^{-2} y^{-1} with simulated and measured average WT of −49 and −43 cm during 2001. These results supported our hypothesis that GPP was the main driver of NEP through variations in peat subsurface hydrology. Finally, during the period 2000–2004, simulated annual NEP consistently followed the EC-derived annual NEP (Figure 13).

4.6. Goodness of Fit and Evaluating Model Performance

[45] Simulated hourly GPP, NEP and latent heat flux were regressed on EC fluxes for the periods DOY 235–264 in 2001 and 2004 (Table 2 and Table 3) and for the entire period 2000–2004 (Table 4). Goodness of fit for simulated ER is given in *Dimitrov et al.* [2010c] and *Dimitrov* [2009]. All regressions were highly significant ($p < 0.0001$). High R^2, slopes close to 1.0 and intercepts close to 0, indicated good agreement between simulated and EC-derived GPP in both periods (Table 2). The comparison of NEP showed close agreement in 2001, but there was some bias (i.e., slope = 0.81) toward underestimating simulated NEP in 2004 (Table 3), even though the model captured the dynamics of hourly NEP during that period (Figure 12a). Regression statistics in Table 4 indicated that the model performed well for the entire period 2000–2004.

[46] Discrepancy between modeled and measured CO$_2$ efflux (NEP nighttime values) was less than the random error of EC measurements [*Dimitrov et al.*, 2010c]. To assess discrepancy between modeled and measured CO$_2$ influx (NEP daytime values), the random errors of EC-measured CO$_2$ influxes for these periods were calculated using relationships between these fluxes and their random errors of measurement developed for grassland sites of similar stature [*Richardson et al.*, 2006, Table 4]. These random errors were 1.04 μmol CO$_2$ m^{-2} s^{-1}, 1.46 μmol CO$_2$ m^{-2} s^{-1} and 1.08 μmol CO$_2$ m^{-2} s^{-1} respectively for DOY 235–264 in 2001, DOY 235–264 in 2004, and for the entire period 2001–2004. When compared to the corresponding RMSD values for these periods (Table 3 and Table 4), this indicated that at an hourly time scale the discrepancy between simulated and measured NEP was similar to the random error of EC-measured NEP for DOY 235–264 in 2001 and 2004, but higher than the random error of EC-measured NEP for the entire period 2000–2004 due to overestimated productivity in the early growing season by the model [*Dimitrov*, 2009].

[47] Simulated annual NEP was close to EC-derived NEP with a random error of ~7 g C m^{-2} y^{-1} for the period 2000–2004. That random error was computed using the above formulations for random error of flux measurement and accumulated to the annual time step using a procedure similar to that described for random uncertainty by *Richardson and Hollinger* [2007] but using the gap-filling procedure described by *Roulet et al.* [2007]. However, the annual EC-derived NEP is biased to different gap-filling strategies, which may result in potential increase/decrease of the measured NEP by another 5 to 33 g C m^{-2} y^{-1}/13 to 39 g C m^{-2} y^{-1} [*Roulet et al.*, 2007] that is well within the range of simulated annual NEP (Figure 13). This gave us some confidence that small biases at an hourly time scale did not propagate at an annual time scale.

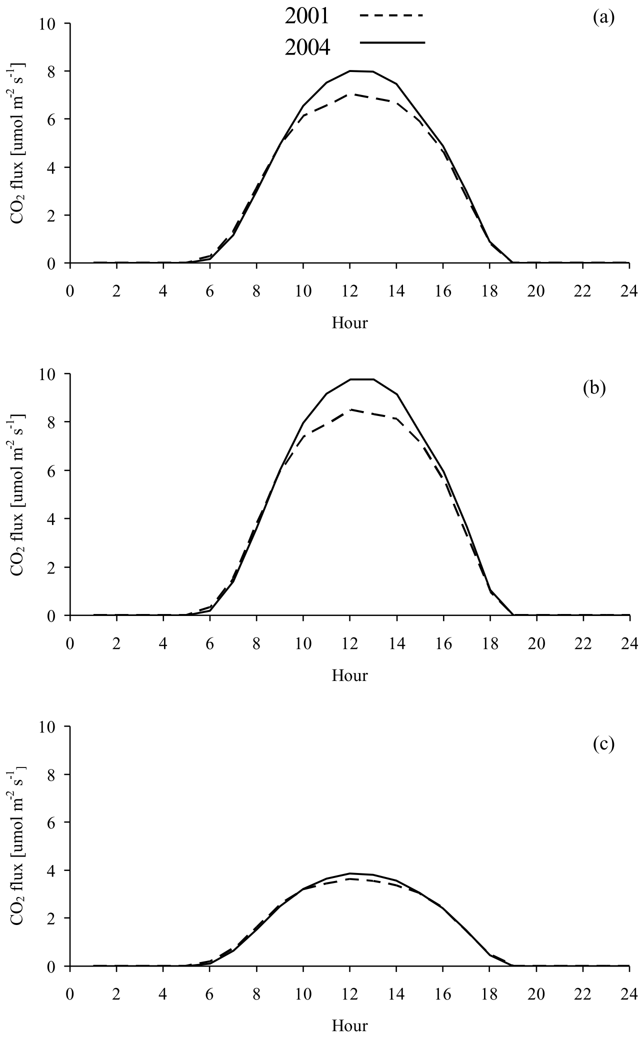

Figure 9. Hourly binned simulated (a) total vascular GPP (b) hummock vascular GPP, and (c) and hollow vascular GPP at Mer Bleue bog, DOY 235–264, dry year 2001 versus DOY 235–264, wet year 2004.

[48] RMSD for the latent heat flux during the entire period 2000–2004 (Table 4) was comparable to the maximum random error of 25.7 W m^{-2} of the EC latent heat flux (computed from the grassland relationship for LE from Table 4 of *Richardson et al.* [2006]) thus indicating that discrepancy between the model and measurements was similar to the random error of measurements. Furthermore, Willmott's indices of agreement close to 1 (Table 4) indicated low relative discrepancies between the model and data. Finally, we compared the modeled biomass and complete C budget based on average values for 2000–2004 with field estimates of the Mer Bleue bog biomass and C budget (Table 5) based on previous studies [*Roulet et al.*, 2007; *Moore et al.*, 2002] to show that most of the simulated C budget fluxes agreed well with the observed fluxes.

5. Discussion

[49] The main findings of this study, that GPP and NEP are sensitive to WT variation and that GPP drives NEP in the context of changing subsurface hydrology, were consistent with the field studies at Mer Bleue bog [*Lafleur et al.*, 2005a; *Moore et al.*, 2003] and other peatlands [*Strack et al.*, 2006; *Alm et al.*, 1999; *Joiner et al.*, 1999; *Schreader et al.*, 1998; *Shurpali and Verma*, 1998; *Lafleur et al.*, 1997] and build upon previous modeling work at the same site [*St-Hilaire et al.*, 2010; *Sonnentag et al.*, 2008; *Ju et al.*, 2006; *Frolking et al.*, 2002, 2001].

5.1. Findings of This Study in the Context of Experimental Research

[50] *Ecosys* simulations were consistent with findings that *Sphagnum* evaporation decreases with drought [*Kim and Verma*, 1996] and with WT decline below a critical depth that would reduce the water supply to the living moss [*Williams and Flanagan*, 1996; *Clymo and Hayward*, 1982]. Some authors have reported that a WT drop of only a few centimeters below some critical depth was enough to significantly reduce capillary rise to the *Sphagnum* surface and to substantially decrease *Sphagnum* evaporation in peatlands [*Lafleur and Roulet*, 1992; *Ingram*, 1983; *Romanov*, 1968]. Our study shows that WT drawdown can cause pronounced

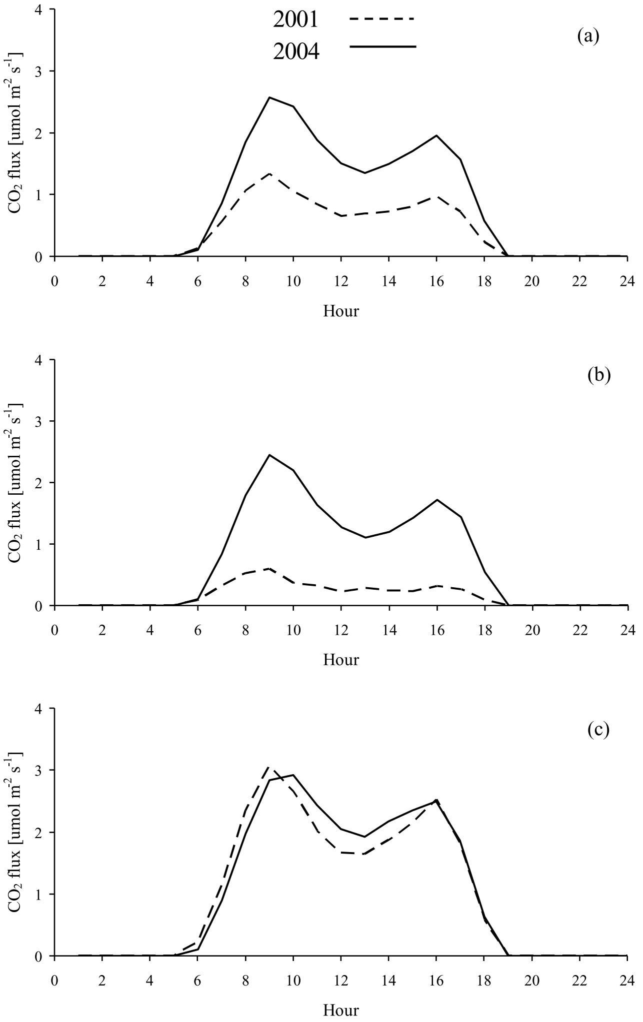

Figure 10. Hourly binned simulated (a) total moss GPP, (b) hummock moss GPP, and (c) hollow moss GPP at Mer Bleue bog, DOY 235–264, dry year 2001 versus DOY 235–264, wet year 2004.

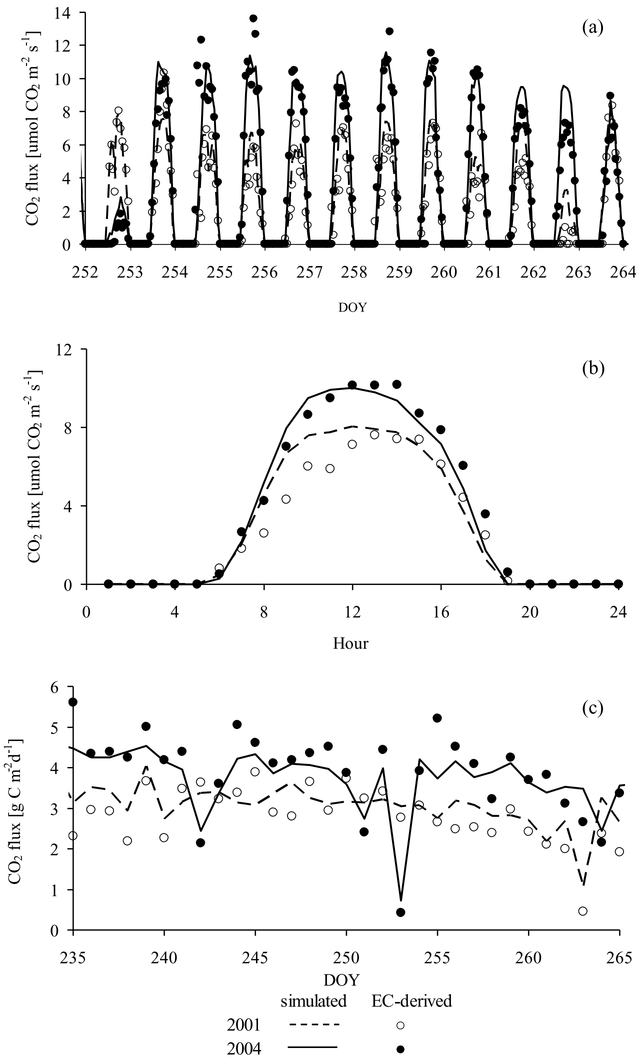

Figure 11. (a) Hourly simulated and EC-derived total bog GPP, (b) hourly binned simulated and EC-derived GPP, and (c) daily simulated and EC-derived GPP at Mer Bleue bog, DOY 235–264, dry year 2001 versus DOY 235–264, wet year 2004.

reduction in moss *E* and GPP, which is consistent with experimental research [*Weltzin et al.*, 2000; *Alm et al.*, 1999]. What we additionally show is that vascular plants can adapt to these conditions and maintain their GPP over a wide range of WT variation. This is consistent with *Bubier et al.* [2003], who reported limited response of GPP at the shrubby area of Mer Bleue bog and slight decline of GPP at a sedge fen.

[51] Our detailed results extend the above knowledge by providing an insight into the role of subsurface hydrology, as it is linked to the water table, and that changes in this hydrology, which drive near-surface soil moisture, are also an important driver of the peatland productivity and C exchange through different sensitivities of the moss and vascular productivities at different microtopographical positions. Thus, sensitivity of bog GPP and NEP to WT variation is attributed mainly to the sensitivity of hummock moss GPP to changes in near-surface peat θ, provided vascular vegetation and hollow moss are relatively insensitive within the level of natural WT variation seen over the study period.

5.2. Building Upon Previous Modeling Work at Mer Bleue Bog

[52] To put our simulations in the context of previous modeling studies at Mer Bleue bog and to discuss how we build upon that knowledge, we need to trace chronologically the modeling work at the site. Shortly after the large-scale field campaign commenced in 1998, the empirical model PDM [*Frolking et al.*, 2001] was written to simulate decomposition rates at Mer Bleue bog. PDM was later modified and expanded into PCARS [*Frolking et al.*, 2002] to simulate productivity and respiration at the same site. PCARS was further developed into MWM [*St-Hilaire et al.*, 2010] mainly by replacing the light use efficiency approach by biogeochemical approach for simulating photosynthesis [*Farquhar et al.*, 1980] and partitioning of the soil respiration into the oxic and anoxic peat zones. Although *Wu*

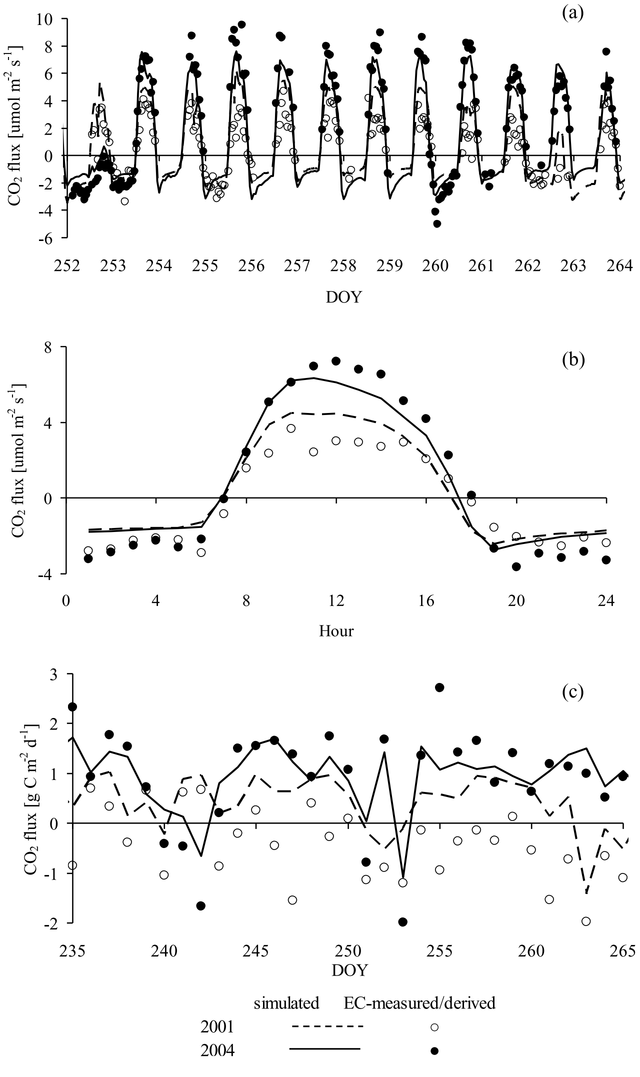

Figure 12. (a) Hourly simulated and EC-measured total bog NEP, (b) hourly binned simulated and EC-derived NEP, and (c) daily simulated and EC-derived NEP at Mer Bleue bog, DOY 235–264, dry year 2001 versus DOY 235–264, wet year 2004.

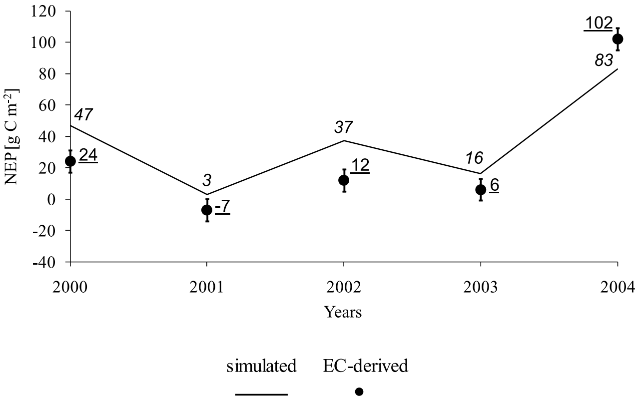

Figure 13. Simulated (italic) versus EC-derived (underlined) annual NEP and its interannual variability at Mer Bleue bog. Random errors (indicated by vertical bars) of EC-derived annual NEPs are determined from uncertainties in EC-measured CO_2 fluxes [*Richardson et al.*, 2006], accumulated to the annual time step [*Richardson and Hollinger*, 2007] by using the gap-filling procedure of *Roulet et al.* [2007].

et al. [2011] applied MWM separately for Mer Bleue hummocks and hollows to estimate their C fluxes, neither of these models simulated explicitly peatland hydrology at mesotopographic or microtopographic scales (see section 1.2).

[53] Subsequent application of the BEPS [*Sonnentag et al.* 2008; *Chen et al.* 2007, 2005] and InTEC [*Ju et al.*, 2006] models at Mer Bleue built upon modeling bog C balance by including some level of coupled hydrological and topographical control. However, InTEC is constrained to an annual time step and thus is unsuitable for simulating detailed seasonal hydrological responses, and although BEPS has a shorter time step (daily) it was adapted to only mesoscale topographic variation within the peatland [*Sonnentag et al.*, 2008], not to the hummock-hollow microtopography.

[54] Our simulations with *ecosys* [*Dimitrov et al.*, 2010c; this study] build upon simulations with BEPS [*Sonnentag et al.*, 2008] by increasing spatial resolution from mesotopography (BEPS, with assumed unified peat surface) to microtopography (*ecosys*, differentiating between hummocks and hollows). Also, our simulations with *ecosys* further build upon simulations with BEPS by increasing temporal resolution from daily (BEPS) to hourly (*ecosys*), which gives an opportunity to investigate the diurnal dynamics of modeled canopy water potentials, stomatal resistances, *E* and photosynthesis of plants under water stress. Furthermore, compared to BEPS, *ecosys* gives more holistic and process-oriented coupling of *E* to photosynthesis through plant water potentials that control directly vascular and moss productivities, and indirectly vascular productivity through controlling stomatal resistances.

[55] In contrast, BEPS couples *E* to photosynthesis of vascular plants through an empirical modifier of stomatal conductance that is a function of θ [*Chen et al.*, 2007, 2005], thus omitting the control from plant water status as affected by atmospheric conditions. An exception is the simulated moss in the version of BEPS adapted for peatlands [*Sonnentag et al.*, 2008], for which *E* and GPP are controlled by moss water content. Empirical root distribution in BEPS through a simple peat profile, consisting only of unsaturated and saturated zones, worked well at the mesoscale, but is unrealistic at the scale of hummocks and hollows. The ability of *ecosys* to

Table 2. Regression Statistics for Relation Between Simulated and EC-Derived Hourly GPP at Mer Bleue Bog for DOY 235–264 in 2001 and 2004

GPP [μmol CO_2 m^{-2} s^{-1}] for DOY 235–264 in 2001		
Statistics (n = 668)	*Units*	*Values (significance)*
Slope, *b*	—	0.93 ($p < 0.0001$)
Intercept, *a*	μmol CO_2 m^{-2} s^{-1}	0.40 ($p < 0.0001$)
R^2	—	0.81 ($p < 0.0001$)
GPP [μmol CO_2 m^{-2} s^{-1}] for DOY 235–264 in 2004		
Statistics (n = 742)	*Units*	*Values (significance)*
Slope, *b*	—	0.91 ($p < 0.0001$)
Intercept, *a*	μmol CO_2 m^{-2} s^{-1}	0.17 ($p < 0.01$)
R^2	—	0.91 ($p < 0.0001$)

Table 3. Regression Statistics for Relation Between Simulated and EC-Measured Hourly NEP at Mer Bleue Bog for DOY 235–264 in 2001 and 2004

NEP [μmol CO_2 m^{-2} s^{-1}] for DOY 235–264 in 2001		
Statistics (n = 334)	*Units*	*Values (significance)*
Slope, *b*	—	1.02 ($p < 0.0001$)
Intercept, *a*	μmol CO_2 m^{-2} s^{-1}	0.51 ($p < 0.0001$)
R^2	—	0.78 ($p < 0.0001$)
RMSD[a]	μmol CO_2 m^{-2} s^{-1}	1.19
NEP [μmol CO_2 m^{-2} s^{-1}] for DOY 235–264 in 2004		
Statistics (n = 386)	*Units*	*Values (significance)*
Slope, *b*	—	0.81 ($p < 0.0001$)
Intercept, *a*	μmol CO_2 m^{-2} s^{-1}	0.24 ($p < 0.001$)
R^2	—	0.90 ($p < 0.0001$)
RMSD[a]	μmol CO_2 m^{-2} s^{-1}	1.31

[a] RMSD is calculated between simulated and EC-measured hourly NEP influxes (daytime values), following *Richardson et al.* [2006].

Table 4. Regression Statistics for Relation Between Simulated and EC-Derived Hourly GPP, NEP, and LE at Mer Bleue Bog for the Period 2000–2004

GPP [μmol CO_2 m^{-2} s^{-1}]		
Statistics (n = 35931)	*Units*	*Values (significance)*
Slope, *b*	—	1.03 ($p < 0.0001$)
Intercept, *a*	μmol CO_2 m^{-2} s^{-1}	0.27 ($p < 0.0001$)
R^2	—	0.77 ($p < 0.0001$)
Willmott's index of agreement	—	0.91
NEP [μmol CO_2 m^{-2} s^{-1}]		
Statistics (n = 20336)	*Units*	*Values (significance)*
Slope, *b*	—	0.95 ($p < 0.0001$)
Intercept, *a*	μmol CO_2 m^{-2} s^{-1}	0.00 ($p < 0.0001$)
R^2	—	0.66 ($p < 0.0001$)
Willmott's index of agreement	—	0.89
RMSD[a]	μmol CO_2 m^{-2} s^{-1}	1.43
LE [W m^{-2}]		
Statistics (n = 16631)	*Units*	*Values (significance)*
Slope, *b*	—	0.98 ($p < 0.0001$)
Intercept, *a*	W m^{-2}	−3.85 ($p < 0.0001$)
R^2	—	0.81 ($p < 0.0001$)
Willmott's index of agreement	—	0.95
RMSD[a]	W m^{-2}	34.87

[a] RMSD is calculated between simulated and EC-measured hourly NEP influxes (daytime values), following *Richardson et al.* [2006].

Table 5. Simulated Carbon Budget Versus Estimated Carbon Budget at Mer Bleue Bog[a]

Carbon Stocks and Fluxes	Units	Simulated, *ecosys*	Measured and Derived
	I. Biomass carbon		
Aboveground biomass	g C m^{-2}	204	160^{b}
Belowground biomass	g C m^{-2}	91	173^{b}
Total biomass	g C m^{-2}	295	333^{b}
	II. Carbon fluxes		
GPP vascular	g C m^{-2} y^{-1}	499	440^{b}
GPP moss	g C m^{-2} y^{-1}	149	100^{b}
NPP vascular	g C m^{-2} y^{-1}	198	$160–245^{b}$
NPP moss	g C m^{-2} y^{-1}	87	$35–85^{b}$
NEP	g C m^{-2} y^{-1}	19	21.5 ± 39^{c}
Methane	g C m^{-2} y^{-1}	6	3.7 ± 0.5^{c}
Dissolved carbon	g C m^{-2} y^{-1}	6.4	14.9 ± 3.1^{c}
Methane + dissolved carbon	g C m^{-2} y^{-1}	12.4	$\sim 10^{a}$

[a] The estimated carbon budget of Mer Bleue bog was derived as a combination of measured (1998–1999) and predicted carbon fluxes and is described in detail in *Moore et al.* [2002]. The simulated carbon budget of Mer Bleue bog is aggregated as an average for the entire period 2000–2004 by weighting the model outcome by the proportional area covered by hummocks and hollows; years 1998 and 1999 were omitted because of incomplete meteorological records.

[b] From *Moore et al.* [2002].

[c] From *Roulet et al.* [2007].

model dynamically root distribution, driven by intraplant C transfers and root turgor, in a number of simulated soil layers gave a unique opportunity to model the effects of near-surface peat desiccation on vascular and moss productivities, revealing one of the major findings of our study.

5.3. Interannual Variability of Bog NEP

[56] *Lafleur et al.* [2003] argued that the interannual variability of NEP at Mer Bleue bog depends on complex interactions between WT dynamics, soil and atmospheric temperatures, photosynthetically active radiation, depth and duration of snowfall, soil freezing and plant phenological responses, all of which directly impact GPP in the course of the year. Among these factors they concluded that the water table is "still the most important determinant" of the interannual differences in growing season NEP and annual NEP at Mer Bleue bog, which supports previous findings on peatland CO_2 flux response to water deficits [*Alm et al.*, 1999; *Joiner et al.*, 1999; *Shurpali et al.*, 1995]. Our modeling results suggest that both the water table and θ in the upper 5 cm in hummocks are important determinants of NEP at Mer Bleue bog, as θ of the near-surface peat was found to be critically important for simulating GPP variation [this study] and ER [*Dimitrov et al.*, 2010c; *Dimitrov*, 2009], and may explain NEP even better than the water table alone. To illustrate this point, we consider the years 2004, 2002 and 2001 with the highest, an intermediate and the lowest measured and modeled annual NEP at Mer Bleue bog (Figure 13). For these years, the annual NEP values are better associated with average annual near-surface peat θ at 1, 5 and 10 cm depths in hummocks, rather than with average annual WT depths alone (Figure 14). This is partly because the water table is just one of the factors, which together with precipitation, evapotranspiration and peat properties (bulk density and porosity), determines θ and therefore, water availability in the most productive near-surface peat.

[57] Confounding effects between bog subsurface hydrology and environmental controls, such as incoming short-wave radiation and air temperature, complicate the NEP response to water table and near-surface peat θ when comparing individual years. Yet the effect of subsurface hydrology on bog NEP can be clearly distinguished among the effects of other environmental controls, measured at Mer Bleue during the period 2000–2004 as the near-surface peat θ has the strongest correlation with NEP, followed by the water table (Table 6). However, due to lack of measurements of peat θ above 10 cm depth, further experimental testing for Mer Bleue and other peatlands is needed to strengthen this hypothesis.

6. Conclusions

[58] The findings of this study are that GPP of bogs is most influenced by drought conditions through its moss component, particularly hummock mosses, which are highly susceptible to near-surface soil drying associated with WT drawdown. In contrast, GPP of vascular plants is relatively unaffected by WT drawdown because plant roots can compensate for reduced water uptake at near-surface by increasing root distribution and hence water uptake deeper

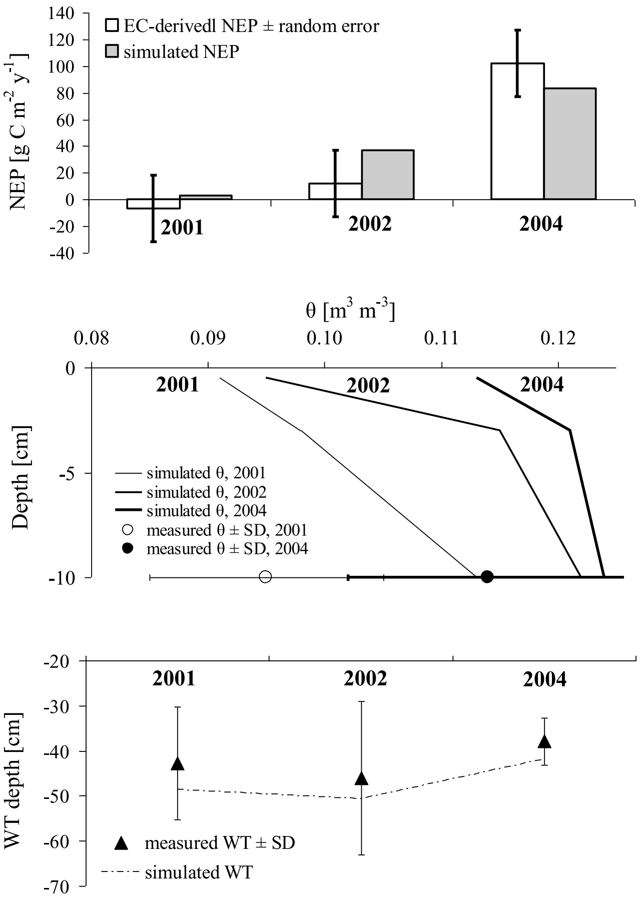

Figure 14. Interannual variability of NEP associated with average annual simulated and TDR-measured water contents (θ) in hummocks at 1, 5, and 10 cm below hummock surface, and with average annual water table (WT) depth, for years 2001, 2002, and 2004. No TDR θ at 10 cm were measured in 2002.

Table 6. Correlations Between Simulated Annual NEP (NEP_{sim}) and Simulated Annual Average Water Content of the Upper 5 cm in Hummocks (θ_{sim}); NEP_{sim} and Simulated Annual Average Water Table Depth (WT_{sim}); NEP_{sim} and Measured Annual Cumulative Incoming Short-Wave Radiation (SWR); NEP_{sim} and Measured Annual Average Air Temperature (T_{air}); EC-Derived Annual NEP (NEP_{mes}) and θ_{sim}; NEP_{mes} and Measured Annual Average Water Table Depth WT_{mes}; NEP_{mes} and SWR; NEP_{mes} and T_{air}, at Mer Bleue Bog for the Period 2000–2004

Correlations for NEP_{sim}	Correlation Coefficient, R	Correlations for NEP_{mes}	Correlation Coefficient, R
NEP_{sim} versus θ_{sim}	0.87	NEP_{mes} versus θ_{sim}[a]	0.84
NEP_{sim} versus WT_{sim}[b]	0.66	NEP_{mes} versus WT_{mes}[b]	0.56
NEP_{sim} versus SWR	0.01	NEP_{mes} versus SWR[c]	0.18
NEP_{sim} versus T_{air}	−0.62	NEP_{mes} versus T_{air}[c]	−0.54

[a] NEP_{mes} was correlated to θ_{sim} because there were no measured θ at 5 cm depth.

[b] WT_{sim} and WT_{mes} decline negatively from the soil surface.

[c] NEP_{sim} was correlated with measured SWR and T_{air}, as they both are model drivers and thus determine the simulated NEP.

in the soil. This, combined with previous research on ER at the site, suggests that GPP is the main determinant of seasonal and interannual variations in the overall bog-atmosphere CO_2 exchange (i.e., NEP). These results have important implications for future climatic impacts on bogs. Increased frequency of drought under warmer and drier climates will reduce the carbon sink of these ecosystems or convert them to overall CO_2 sources. Changes in moss species or distribution will play a significant role in bog response to changing climate. Given the vast stores of soil C in these ecosystems, climate carbon cycle models must be able to account for the integral role of mosses, as affected by changing hydrology, in northern peatland functioning.

Notation

Model Variables

E	canopy transpiration (vascular plants) or evaporation (moss), $m^3\ m^{-2}\ h^{-1}$
U	root/rhizoid water uptake, $m^3\ m^{-2}\ h^{-1}$
U'	water transport from the soil to roots/rhizoids, $m^3\ m^{-2}\ h^{-1}$
U''	water transport from the roots/rhizoids to canopy, $m^3\ m^{-2}\ h^{-1}$
ΔS	change of plant water content, $m^3\ m^{-2}\ h^{-1}$
r_A	aerodynamic boundary layer resistance, $s\ m^{-1}$
r_C	canopy stomatal resistance to water vapor, $s\ m^{-1}$
r_L	leaf stomatal resistance to CO_2 (or to water vapor, as $r_{L\ \mathrm{water\ vapor}} = 0.64 \times r_{L\ \mathrm{CO2}}$), $s\ m^{-1}$
θ	soil (peat) water content, $m^3\ m^{-3}$
ψ_C	canopy water potential, MPa
ψ_S	soil water potential, MPa
ψ_r	root water potential, MPa
ψ_t	turgor potential, MPa
Ω_A	axial resistances to water transport along primary or secondary root/rhizoid axes, $MPa\ h\ m^{-1}$
Ω_S	radial resistance to water transport from the soil to surfaces of roots/rhizoids, $MPa\ h\ m^{-1}$
Ω_R	radial resistance to water transport from the surfaces of roots/rhizoids to their, $MPa\ h\ m^{-1}$

Abbreviations

C	carbon
GPP	gross primary productivity, $\mu mol\ CO_2\ m^{-2}\ s^{-1}$
ER	ecosystem respiration, $\mu mol\ CO_2\ m^{-2}\ s^{-1}$
EC	eddy-covariance (technique)
NEP	net ecosystem productivity, $\mu mol\ CO_2\ m^{-2}\ s^{-1}$
RMSD	root mean square deviation
TDR	time domain reflectometry (technique)
WT	water table, cm or m

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References

Aerts, R. (1995), The advantages of being evergreen, *Trends Ecol. Evol.*, *10*, 402–407, doi:10.1016/S0169-5347(00)89156-9.

Aerts, R. (1999), Interspecific competition in natural plant communities: Mechanisms, trade-offs and plant soil feedbacks, *J. Exp. Bot.*, *50*, 29–37, doi:10.1093/jexbot/50.330.29.

Aguirrezabal, L. A. N., S. Pellerin, and F. Tardieu (1993), Carbon nutrition, root branching and elongation: Can the present state of knowledge allow a predictive approach at a whole-plant level?, *Environ. Exp. Bot.*, *33*, 121–130, doi:10.1016/0098-8472(93)90060-S.

Alm, J., A. Talanov, S. Saarnio, J. Silvola, E. Ikkonen, H. Aaltonen, H. Nykanen, and P. J. Martikainen (1997), Reconstruction of the carbon balance for microsites in a boreal oligotrophic pine fen, Finland, *Oecologia*, *110*, 423–431, doi:10.1007/s004420050177.

Alm, J., L. Schulman, J. Walden, H. Nykanen, P. J. Martikainen, and J. Silvola (1999), Carbon balance of a boreal bog during a year with an exceptionally dry summer, *Ecology*, *80*, 161–174, doi:10.1890/0012-9658(1999)080[0161:CBOABB]2.0.CO;2.

Aurela, M., T. Laurila, and J.-P. Tuovinen (2001), Seasonal CO_2 balances of a subarctic mire, *J. Geophys. Res.*, *106*, 1623–1637, doi:10.1029/2000JD900481.

Blodau, C., N. T. Roulet, T. Heitmann, H. Stewart, J. Beer, P. Lafleur, and T. R. Moore (2007), Belowground carbon turnover in a temperate ombrotrophic bog, *Global Biogeochem. Cycles*, *21*, GB1021, doi:10.1029/2005GB002659.

Bond-Lamberty, B., S. T. Gower, and D. E. Ahl (2007), Improved simulation of poorly drained forests using Biome-BGC, *Tree Physiol.*, *27*, 703–715.

Bubier, J. L., P. M. Crill, T. R. Moore, K. Savage, and R. K. Varner (1998), Seasonal patterns and controls on net ecosystem CO_2 exchange in a boreal peatland complex, *Global Biogeochem. Cycles*, *12*(4), 703–714, doi:10.1029/98GB02426.

Bubier, J. L., S. Frolking, P. M. Crill, and E. Linder (1999), Net ecosystem productivity and its uncertainty in a diverse boreal peatland, *J. Geophys. Res.*, *104*, 27,683–27,692, doi:10.1029/1999JD900219.

Bubier, J. L., G. Bhatia, T. R. Moore, N. T. Roulet, and P. M. Lafleur (2003), Spatial and temporal variability in growing season net ecosystem carbon dioxide exchange at a large peatland in Ontario, Canada, *Ecosystems*, *6*, 353–367.

Chen, J. M., X. Chen, W. Ju, and X. Geng (2005), Distributed hydrological model for mapping evapotranspiration using remote sensing inputs, *J. Hydrol.*, *305*, 15–39, doi:10.1016/j.jhydrol.2004.08.029.

Chen, X., J. M. Chen, S. An, and W. M. Ju (2007), Efects of topography on simulated net primary productivity at landscape scale, *J. Environ. Manage.*, *85*, 585–596, doi:10.1016/j.jenvman.2006.04.026.

Christensen, T. R., S. Jonasson, A. Michelsen, T. V. Callaghan, and M. Havström (1998), Environmental controls on soil respiration in the Eurasian and Greenlandic Arctic, *J. Geophys. Res.*, *103*(D22), 29,015–29,021, doi:10.1029/98JD00084.

Clymo, R. S. (1983), Peat, in *Ecosystems of the World, Vol. 4A, Mires: Swamp, Bog, Fen and Moor General Studies*, edited by A. J. P. Gore, pp. 159–224, Elsevier, New York.

Clymo, R. S., and P. M. Hayward (1982), The ecology of Sphagnum, in *Bryophyte Ecology*, edited by A. J. E. Smith, pp. 229–289, Chapman and Hall, London.

Comer, N. T., P. M. Lafleur, N. T. Roulet, M. G. Letts, M. Skarupa, and D. Verseghy (2000), A test of the Canadian Land Surface Scheme (CLASS) for a variety of wetland types, *Atmos. Ocean*, *38*, 161–179.

Dimitrov, D. D. (2009), Modelling of hydrological and thermal controls on CO_2 exchange at Mer Bleue bog, Ph.D. thesis, Dept. of Renewable Resources, Univ. of Alberta, Edmonton, Alberta.

Dimitrov, D. D., R. F. Grant, P. M. Lafleur, and E. R. Humphreys (2010a), Modeling the subsurface hydrology of Mer Bleue bog, *Soil Sci. Soc. Am. J.*, *74*(2), 680–694, doi:10.2136/sssaj2009.0148.

Dimitrov, D. D., R. F. Grant, P. M. Lafleur, and E. R. Humphreys (2010b), Modeling Peat thermal regime of an ombrotrophic peatland with hummock–hollow microtopography, *Soil Sci. Soc. Am. J.*, *74*(4), 1406–1425, doi:10.2136/sssaj2009.0288.

Dimitrov, D. D., R. F. Grant, P. M. Lafleur, and E. R. Humphreys (2010c), Modeling the effects of hydrology on ecosystem respiration at Mer Bleue bog, *J. Geophys. Res.*, *115*, G04043, doi:10.1029/2010JG001312.

Farquhar, G. D., S. von Caemmerer, and J. A. Berry (1980), A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species, *Planta*, *149*, 78–90, doi:10.1007/BF00386231.

Frolking, S., N. T. Roulet, T. R. Moore, P. J. H. Richard, M. Lavoie, and S. D. Muller (2001), Modeling northern peatland decomposition and peat accumulation, *Ecosystems*, *4*, 479–498, doi:10.1007/s10021-001-0105-1.

Frolking, S., N. T. Roulet, T. R. Moore, P. M. Lafleur, J. L. Bubier, and P. M. Crill (2002), Modeling seasonal to annual carbon balance of Mer Bleue Bog, Ontario, Canada, *Global Biogeochem. Cycles*, *16*(3), 1030, doi:10.1029/2001GB001457.

Grant, R. F. (2001), A review of the Canadian ecosystem model *ecosys*, in *Modeling Carbon and Nitrogen Dynamics for Soil Management*, edited by M. Shaffer, pp. 173–264, CRC Press, Boca Raton, Fla., doi:10.1201/9781420032635.ch6.

Grant, R. F., and L. B. Flanagan (2007), Modelling stomatal and non-stomatal effects of water deficits on CO_2 fixation in a semi-arid grassland, *J. Geophys. Res.*, *112*, G03011, doi:10.1029/2006JG000302.

Grant, R. F., P. G. Jarvis, J. M. Massheder, S. E. Hale, J. B. Moncrieff, M. Rayment, S. L. Scott, and J. A. Berry (2001), Controls on carbon and energy exchange by a black spruce–moss ecosystem: Testing the mathematical model *Ecosys* with data from the BOREAS experiment, *Global Biogeochem. Cycles*, *15*(1), 129–147, doi:10.1029/2000GB001306.

Herkelrath, W. N., E. E. Miller, and W. R. Gardner (1977), Water uptake by plants: II. The root contact model, *Soil Sci. Soc. Am. Proc.*, *41*, 1039–1043, doi:10.2136/sssaj1977.03615995004100060004x.

Hilbert, D., N. Roulet, and T. Moore (2000), Modeling and analysis of peatlands as dynamical systems, *J. Ecol.*, *88*, 230–242, doi:10.1046/j.1365-2745.2000.00438.x.

Ingram, H. A. P. (1983), Hydrology, in *Ecosystems of the World, Vol. 4A, Mires: Swamp, Bog, Fen and Moor General Studies*, edited by A. J. P. Gore, pp. 67–158, Elsevier, New York.

Joiner, D. W., P. M. Lafleur, J. H. McCaughey, and P. A. Bartlett (1999), Interannual variability in carbon dioxide exchanges at a boreal wetland in the BOREAS northern study area, *J. Geophys. Res.*, *104*(D22), 27,663–27,672, doi:10.1029/1999JD900136.

Ju, W., J. M. Chen, T. A. Black, A. G. Barr, H. McCaughey, and N. T. Roulet (2006), Hydrological effects on carbon cycles of Canada's forests and wetlands, *Tellus, Ser. B*, *58*, 16–30, doi:10.1111/j.1600-0889.2005.00168.x.

Kim, J., and S. B. Verma (1996), Surface exchange of water vapour between an open *Sphagnum* fen and the atmosphere, *Boundary Layer Meteorol.*, *79*, 243–264, doi:10.1007/BF00119440.

Lafleur, P. M., and N. T. Roulet (1992), A comparison of evaporation rates from two fens of the Hudson Bay Lowland, *Aquat. Bot.*, *44*, 59–69, doi:10.1016/0304-3770(92)90081-S.

Lafleur, P. M., J. H. McCaughey, D. W. Joiner, P. A. Bartlett, and D. E. Jelinski (1997), Seasonal trends in energy, water, and carbon dioxide fluxes at a northern boreal wetland, *J. Geophys. Res.*, *102*(D24), 29,009–29,020, doi:10.1029/96JD03326.

Lafleur, P. M., N. T. Roulet, and S. W. Admiral (2001), Annual cycle of CO_2 exchange at a bog peatland, *J. Geophys. Res.*, *106*(D3), 3071–3081, doi:10.1029/2000JD900588.

Lafleur, P. M., N. T. Roulet, J. L. Bubier, S. Frolking, and T. Moore (2003), Interannual variability in the peatland-atmosphere carbon dioxide exchange at an ombrotrophic bog, *Global Biogeochem. Cycles*, *17*(2), 1036, doi:10.1029/2002GB001983.

Lafleur, P. M., T. R. Moore, N. T. Roulet, and S. Frolking (2005a), Ecosystem respiration in a cool temperate bog depends on peat temperature but not on water table, *Ecosystems*, *8*, 619–629, doi:10.1007/s10021-003-0131-2.

Lafleur, P. M., R. A. Hember, S. W. Admiral, and N. T. Roulet (2005b), Annual and seasonal variability in evapotranspiration and water table at a shrub-covered bog in southern Ontario, Canada, *Hydrol. Processes*, *19*, 3533–3550, doi:10.1002/hyp.5842.

Moore, T. R., and M. Dalva (1993), The influence of temperature and water-table position on carbon dioxide and methane emissions from laboratory columns of peatland soils, *J. Soil Sci.*, *44*, 651–664, doi:10.1111/j.1365-2389.1993.tb02330.x.

Moore, T. R., N. T. Roulet, and J. M. Waddington (1998), Uncertainties in predicting the effect of climatic change on the carbon cycling of Canadian peatlands, *Clim. Change*, *40*, 229–245, doi:10.1023/A:1005408719297.

Moore, T. R., J. L. Bubier, P. M. Lafleur, S. Frolking, and N. T. Roulet (2002), Plant biomass, production and CO_2 exchange in an ombrotrophic bog, *J. Ecol.*, *90*, 25–36, doi:10.1046/j.0022-0477.2001.00633.x.

Moore, T. R., P. M. Lafleur, N. T. Roulet, and S. Frolking (2003), Dependency of ecosystem respiration in a cool temperate bog on peat temperature and water table, *Eos Trans. AGU*, *84*(46), Fall Meet. Suppl., Abstract #B22B–04.

Moore, T. R., P. M. Lafleur, D. M. I. Poon, B. W. Heumann, J. W. Seaquist, and N. T. Roulet (2006), Spring photosynthesis in a cool temperate bog, *Global Change Biol.*, *12*, 2323–2335, doi:10.1111/j.1365-2486.2006.01247.x.

Murphy, M. T., and T. R. Moore (2010), Linking root production to aboveground plant characteristics and water table in a temperate bog, *Plant Soil*, *336*, 219–231, doi:10.1007/s11104-010-0468-1.

National Wetlands Working Group (1997), *The Canadian Wetland Classification System*, 2nd ed., edited by B. G. Warner and C. D. A. Rubec, Wetlands Res. Branch, Univ. of Waterloo, Ontario, Canada.

Nazaroff, W. W. (1992), Radon transport from soil to air, *Rev. Geophys.*, *30*, 137–160, doi:10.1029/92RG00055.

Oechel, W. C., G. L. Vourlitis, S. J. Hastings, R. P. Ault Jr., and P. Bryant (1998), The effect of water table manipulation and elevated temperature on the net CO_2 flux of wet sedge tundra ecosystems, *Global Change Biol.*, *4*(1), 77–90, doi:10.1046/j.1365-2486.1998.00110.x.

Potter, C. S. (1997), An ecosystem simulation model for methane production and emission from wetlands, *Global Biogeochem. Cycles*, *11*(4), 495–506, doi:10.1029/97GB02302.

Proctor, M. C. F. (1982), Physiological ecology: Water relations, light and temperature responses, carbon balance, in *Bryophyte Ecology*, edited by A. J. E. Smith, pp. 333–381, Chapman and Hall, London.

Richardson, A. D., and D. Y. Hollinger (2007), A method to estimate the additional uncertainty in gap-filled NEE resulting from long gaps in the CO_2 flux record, *Agric. For. Meteorol.*, *147*, 199–208, doi:10.1016/j.agrformet.2007.06.004.

Richardson, A. D., et al. (2006), A multi-site analysis of random error in tower-based measurements of carbon and energy fluxes, *Agric. For. Meteorol.*, *136*, 1–18, doi:10.1016/j.agrformet.2006.01.007.

Richardson, D. H. (1981), *The Biology of Mosses*, Blackwell Sci., Oxford.

Romanov, V. V. (1968), *Hydrophysics of Bogs [Gidrofizika bolot (1961)]*, edited by A. Heimann, trans. N. Kaner, 299 pp., Israel Program for Sci. Trans., Jerusalem.

Roulet, N. T., P. M. Lafleur, P. J. H. Richard, T. R. Moore, E. R. Humphreys, and J. Bubier (2007), Contemporary carbon balance and late Holocene carbon accumulation in a northern peatland, *Global Change Biol.*, *13*, 397–411, doi:10.1111/j.1365-2486.2006.01292.x.

Schreader, C. P., W. R. Rouse, T. J. Giffis, L. D. Boudreau, and P. D. Blanken (1998), Carbon dioxide fluxes in a northern fen during a hot, dry summer, *Global Biogeochem. Cycles*, *12*(4), 729–740, doi:10.1029/98GB02738.

Shurpali, N. J., and S. B. Verma (1998), Micrometeorological measurements of methane flux in a Minnesota peatland during two growing seasons, *Biogeochemistry*, *40*, 1–15, doi:10.1023/A:1005875307146.

Shurpali, N. J., S. B. Verma, J. Kim, and T. J. Arkebauer (1995), Carbon dioxide exchange in a peatland ecosystem, *J. Geophys. Res.*, *100*(D7), 14,319–14,326, doi:10.1029/95JD01227.

Silvola, J., and U. Ahlholm (1989), Effects of moisture and temperature on the decomposition of milled and sod peat, in *International Symposium on Peat/Peatland Characteristics and Uses: Bemidji State University, May 16–19, 1989*, edited by S. A. Spigarelli, 622 pp., Cent. for Environ. Stud., Bemidji, Minn.

Silvola, J., J. Alm, U. Ahlholm, H. Nykanen, and P. J. Martikainen (1996a), CO_2 fluxes from peat in boreal mires under varying temperature and moisture conditions, *J. Ecol.*, *84*, 219–228, doi:10.2307/2261357.

Silvola, J., J. Alm, U. Ahlholm, H. Nykanen, and P. J. Martikainen (1996b), The contribution of plant roots to CO_2 fluxes from organic soils, *Biol. Fertil. Soils*, *23*, 126–131, doi:10.1007/BF00336052.

Small, E. (1972a), Photosynthetic rates in relation to nitrogen cycling as an adaptation to nutrient deficiency in peat bog plants, *Can. J. Bot.*, *50*, 2227–2233, doi:10.1139/b72-289.

Small, E. (1972b), Water relations of plants in raised *Sphagnum* peat bogs, *Ecology*, *53*, 726–728, doi:10.2307/1934791.

Sonnentag, O., J. M. Chen, N. T. Roulet, W. Ju, and A. Govind (2008), Spatially explicit simulation of peatland hydrology and carbon dioxide exchange: Influence of mesoscale topography, *J. Geophys. Res.*, *113*, G02005, doi:10.1029/2007JG000605.

St-Hilaire, F., J. Wu, N. T. Roulet, S. Frolking, P. M. Lafleur, E. R. Humphreys, and V. Arora (2010), McGill wetland model: Evaluation of a peatland carbon simulator developed for global assessments, *Biogeosciences*, *7*, 3517–3530, doi:10.5194/bg-7-3517-2010.

Strack, M., and J. M. Waddington (2007), Response of peatland carbon dioxide and methane fluxes to a water table drawdown experiment, *Global Biogeochem. Cycles*, *21*(1), GB1007, doi:10.1029/2006GB002715.

Strack, M., J. M. Waddington, L. Rochefort, and E.-S. Tuittila (2006), Response of vegetation and net ecosystem carbon dioxide exchange at different peatland microforms following water table drawdown, *J. Geophys. Res.*, *111*, G02006, doi:10.1029/2005JG000145.

Sulman, B. N., A. R. Desai, B. D. Cook, N. Saliendra, and D. S. Mackay (2009), Contrasting carbon dioxide fluxes between a drying shrub wetland in Northern Wisconsin, USA, and nearby forests, *Biogeosciences*, *6*, 1115–1126, doi:10.5194/bg-6-1115-2009.

Updegraff, K., S. D. Bridgham, J. Pastor, P. Weisshampel, and C. Harth (2001), Response of CO_2 and CH_4 emissions from peatlands to warming and water table manipulation, *Ecol. Appl.*, *11*, 311–326.

Waddington, J. M., and N. T. Roulet (2000), Carbon balance of a patterned boreal peatland, *Global Change Biol.*, *6*, 87–97, doi:10.1046/j.1365-2486.2000.00283.x.

Waddington, J. M., P. A. Rotenberg, and F. J. Warren (2001), Peat CO_2 production in a natural and cutover peatland: Implications for restoration, *Biogeochemistry*, *54*, 115–130, doi:10.1023/A:1010617207537.

Weltzin, J. F., J. Pastor, C. Harth, S. D. Bridgham, K. Updegraff, and C. T. Chapin (2000), Response of bog and fen plant communities to warming and water table manipulations, *Ecology*, *81*, 3464–3478, doi:10.1890/0012-9658(2000)081[3464:ROBAFP]2.0.CO;2.

Williams, T. G., and L. B. Flanagan (1996), Effect of changes in water content on photosynthesis, transpiration and discrimination against $^{13}CO_2$ and $C^{18}O^{16}O$ in *Pleurozium* and *Sphagnum*, *Oecologia*, *108*, 38–46, doi:10.1007/BF00333212.

Willmott, C. J. (1981), On the validation of models, *Phys. Geogr.*, *2*, 184–194.

Wu, J., N. T. Roulet, T. R. Moore, P. Lafleur, and E. Humphreys (2011), Dealing with microtopography of an ombrotrophic bog for simulating ecosystem-level CO_2 exchanges, *Ecol. Modell.*, *222*, 1038–1047, doi:10.1016/j.ecolmodel.2010.07.015.

Zhang, Y., C. Li, C. C. Trettin, H. Li, and G. Sun (2002), An integrated model of soil, hydrology, and vegetation for carbon dynamics in wetland ecosystems, *Global Biogeochem. Cycles*, *16*(4), 1061, doi:10.1029/2001GB001838.

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