Patterns in Vegetation and CO_2 Dynamics along a Water Level Gradient in a Lowland Blanket Bog

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ABSTRACT

The surface of bogs is commonly patterned and composed of different vegetation communities, defined by water level. Carbon dioxide (CO_2) dynamics vary spatially between the vegetation communities. An understanding of the controls on the spatial variation of CO_2 dynamics is required to assess the role of bogs in the global carbon cycle. The water level gradient in a blanket bog was described and the CO_2 exchange along the gradient investigated using chamber based measurements in combination with regression modelling. The aim was to investigate the controls on gross photosynthesis (P_G), ecosystem respiration (R_E) and net ecosystem CO_2 exchange (NEE) as well as the spatial and temporal variation in these fluxes. Vegetation structure was strongly controlled by water level. The species with distinctive water level optima were separated into the opposite ends of the gradient in canonical correspondence analysis. The number of species and leaf area were highest in the intermediate water level range and these communities had the highest P_G. Photosynthesis was highest when the water level was 11 cm below the surface. Ecosystem respiration, which includes decomposition, was less dependent on vegetation structure and followed the water level gradient more directly. The annual NEE varied from −115 to 768 g CO_2 m^{-2}, being lowest in wet and highest in dry vegetation communities. The temporal variation was most pronounced in P_G, which decreased substantially during winter, when photosynthetic photon flux density and leaf area were lowest. Ecosystem respiration, which is dependent on temperature, was less variable and wintertime R_E fluxes constituted approximately 24% of the annual flux.

Key words: peatland; photosynthesis; respiration; net ecosystem exchange; vegetation composition; spatial variation; water table.

INTRODUCTION

Blanket bogs are locally important ecosystems in areas with high and regular rainfall, for example in Ireland, Scotland, and costal areas of England and Norway. In Ireland, blanket bogs cover approximately 12% of the land area and their carbon (C) stock is estimated to be 0.57 Pg or 28% of the total Irish soil C stock (Tomlinson 2005). Globally peat-

lands are an important C store. Since the last Ice Age, northern peatlands have accumulated 270–455 Pg of atmospheric C (Gorham 1991; Turunen and others 2002). At present, pristine peatlands are, in general, a small sink of carbon dioxide (CO_2) (Gorham 1991; Turunen and others 2002) and a considerable source of methane (CH_4) (Bartlett and Harriss 1993). The annual C budget of a peatland depends on the environmental conditions and interannually a peatland can change from being a sink to a source of C (Waddington and Roulet 2000; Lafleur and others 2003).

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Studies carried out in peatlands of the boreal, arctic and cold temperate climate zones have shown that the CO_2 exchange is dependent on vegetation structure and environmental factors such as hydrological conditions and weather phenomena (Alm and others 1997; Lafleur and others 2003). In ombrotrophic bogs CO_2 exchange varies spatially (Waddington and Roulet 2000), as the surface is often a continuum of different vegetation communities commonly classified as microforms, namely hummocks, lawns and hollows (Lindsay 1995). These vegetation communities are supported by different water levels that affect their species composition, biomass (Moore and others 2002), and photosynthetic capacity (Bubier and others 2003). The response of CO_2 fluxes to environmental variables varies between communities (Bubier and others 2003). Therefore, an understanding of the interaction between different vegetation communities and climate is a vital prerequisite for the incorporation of peatlands into models of global C cycling (Belyea and Malmer 2004).

Ireland has a humid temperate climate that is characterized by cool summers and mild winters, with only moderate seasonality (Collins and Cummins 1996). The proximity of the Gulf Stream exerts a moderating influence on the climate. This provides conditions that are extremely favorable to peat formation. The major difference compared to more northern and continental regions is the lack of snow cover and soil frost during winter. As a result the evergreen plants and mosses are able to function during the winter period. Only a few studies of CO_2 fluxes have been carried out in peatlands in this region (Sottocornola and Kiely 2005; Laine and others 2006). Consequently, the nature of CO_2 exchange of blanket bogs is not well understood.

The surface structure and vegetation composition of lowland blanket bogs, which are located in flat to moderately sloping terrain, resemble that of raised bogs (Guinan and others 1998). However, the high oceanic rainfall (>1250 mm per annum) and frequent rain days (>270 days per annum), required for the existence of these bogs, constitutes an important input of nutrients (Doyle 1982). Similar to raised bogs, the different vegetation communities in blanket bogs support different CO_2 exchange dynamics (Laine and others 2006) but the interaction between the factors controlling CO_2 fluxes and their spatial variation is poorly understood. In Ireland, the longer growing season and mild winters may produce higher annual productivity. However, plant and soil respiration during winter

may be high compared to peatlands in more northerly regions (Wilson and others 2007a). This emphasizes the need to investigate the contribution of wintertime CO_2 fluxes to the annual CO_2 balance, in this maritime temperate climate.

In this study, we measured the CO_2 exchange along a water level and vegetation gradient in a lowland blanket bog. The use of the chamber method allowed us to study homogenous vegetation communities and to analyze the flux responses to varying environmental variables. These measurements captured both spatial and temporal variation in the components of CO_2 exchange: gross photosynthesis (P_G), ecosystem respiration (R_E) and net ecosystem exchange (NEE). Our aims were: (1) to characterize the vegetation structure along the water level gradient; (2) to quantify the controls on P_G and R_E along the gradient and (3) to investigate the temporal variation in CO_2 exchange.

MATERIALS AND METHODS

Site Description

The study site was located in an extensive lowland blanket bog in Co Kerry, Ireland (51°55′N, 9°55′W). During 2003, 2004 and 2005 the annual rainfall was 2510, 2356 and 2459 mm y^{-1}, respectively. In this maritime climate the abundant fog may contribute to the moisture conditions. In the same period, the average air temperature for the warmest month, July and the coldest month, February was 14.6 and 6.1°C, respectively.

The surface of the bog is a continuum of vegetation communities ranging from dry hummocks to permanently inundated hollows. Hummocks were covered by a dense bryophyte carpet (*Sphagnum* spp., *Racomitrium lanuginosum*) and had *Molinia caerulea* and dwarf shrubs *Calluna vulgaris* and *Erica tetralix* as dominant vascular plant species. The lawn level vegetation ranged from dense stands of *M. caerulea* and *Schoenus nigricans* in drier areas, to wet areas dominated by *Rhynchospora alba* that had a shorter growing season than most other plant species in the area. Moss cover was sparse in lawns. Inundated hollows supported bryophytes (*Sphagnum cuspidatum, S. auriculatum*) and a scattered vegetation of *R. alba, S. nigricans* and *Eriophorum angustifolium*.

Study Site

The study site was established in June 2003. Eighteen stainless steel collars (0.6 m × 0.6 m × 0.15 m) were inserted into the peat to cover the spatial

Table 1. Characteristics of Sample Plots

Sample plot	HU1	HU2	HU3	HU4	HU5	HU6	HL1	HL2	HL3	HL4	HL5	HL6	LL1	LL2	LL3	LL4	LL5	LL6	HO1	HO2	HO3
Drosera rotundifolia	0.5												0.5			0.5	0.5	0.1		0.2	
Drosera intermedia								1											0.1	0.1	0.1
Erica cinerea	3	2	1	3	3	3	3	2		3	3	3									
Eriophorum angustifolium					1									1	1	1	0.5	0.5			
Molinia caerulea	5	5	12	6	7	10	10	10	7	5	4	8	3	2	4	2	2	1		0.5	0.5
Narthecium ossifragum	3	2	2	4	10	15	5	7	7	3	2	4		0.5	2	1	0.5	0.5	0.5		
Rhynchospora alba				1	3	3	25	3	10	17	35		25	20	15	20	20	3	0.5	2	0.1
Schoenus nigricans		15	2				1	7	1		8		3								
Calluna vulgaris	4	8	4	7	8	4	7	4	3		1	6	1		1						
Menyanthes trifoliata																				15	10
Carex limosa																		0.1	0.1	0.1	0.1
Moss cover	100	60	97	96	91	22	27	22	6	54	8	53	10	2	1	6	15	2	25	15	10
WT_{MED}	−15	−14	−14	−13	−12	−11	−7	−6	−5.5	−4	−3	−3	−3	−2	−2	−1.5	−1.5	0	2.5	3.5	7
VGA_{MAX} 2003	0.7	1.5	0.6	0.9	1.1	1.1	1.5	1.1	1.0	1.1	1.0	0.9	0.7	0.9	0.9	0.9	0.7	0.6	0.1	0.4	0.5
VGA_{MAX} 2004	0.9	2.1	0.9	0.6	1.2	1.2	1.7	1.8	1.3	1.2	1.1	1.2	0.6	0.9	0.8	1.0	0.9	0.7	0.1	0.4	0.5

Percentage cover of the five most abundant vascular plant species, total moss cover (%), median water level (WT_{MED}, cm below surface) and maximum vascular green area (VGA_{MAX}, $m^2 m^{-2}$) in years 2003 and 2004 are shown.

variation in vegetation from hummocks to low lawns. In March 2004, three additional sample plots were established to widen the range to include hollow vegetation. The sample plots were divided into four groups: hummocks (HU), high lawns (HL), low lawns (LL) and hollows (HO). In each group, we coded the sample plots from 1 to 6 according to their median water level (WT_{MED}). The sample plot characteristics are given in Table 1.

## CO$_2$ Flux Measurements

Carbon dioxide exchange measurements were made using a closed transparent plexiglas chamber (0.6 m × 0.6 m × 0.33 m). The chamber was vented and included a cooling system (Alm and others 1997). The CO$_2$ concentration inside the chamber was monitored with a portable infrared gas analyzer (EGM-4, PP Systems, UK). The instantaneous net CO$_2$ exchange (NEE) was first measured under a stable ambient illumination at 15 s intervals over a 60–240 s period. This was then repeated with the chamber covered with an opaque canvas cover, to measure the instantaneous ecosystem respiration rate (R_E). The CO$_2$ flux rates were calculated from the linear change in gas concentration as a function of time. We used the ecological sign convention for NEE, in which net flux from the biosphere to the atmosphere is negative. Gross photosynthesis (P_G) was calculated as the sum of flux rate values measured in light (NEE) and dark (R_E). Both P_G and R_E are presented here as positive values.

To relate the gas fluxes to prevailing environmental conditions, the photosynthetic photon flux density (PPFD, μmol m^{-2} s^{-1}, PAR-1, PP-Systems, UK) and air temperature (*T*) inside the chamber were recorded simultaneously with NEE readings. At the same time, water level (WT), relative to the sample plot surface, was measured. For sample plots HU1, HU2, HL2, HL4, LL4 and LL5, we used measurements carried out from July 2003 to August 2005; for sample plots HO1, HO2 and HO3 measurements were from March 2004 until August 2005. For the other 12 sample plots measurements were made from July 2003 to September 2004.

Vegetation

We used Vascular Green Area index (VGA, m m^{-2}) in the P_G and R_E models to describe the changes in gas fluxes that were related to seasonal dynamics of plant growth. The VGA was calculated for each sample plot according to Wilson and others (2007b) and Laine and others (2006). We counted the number of leaves of each vascular plant species
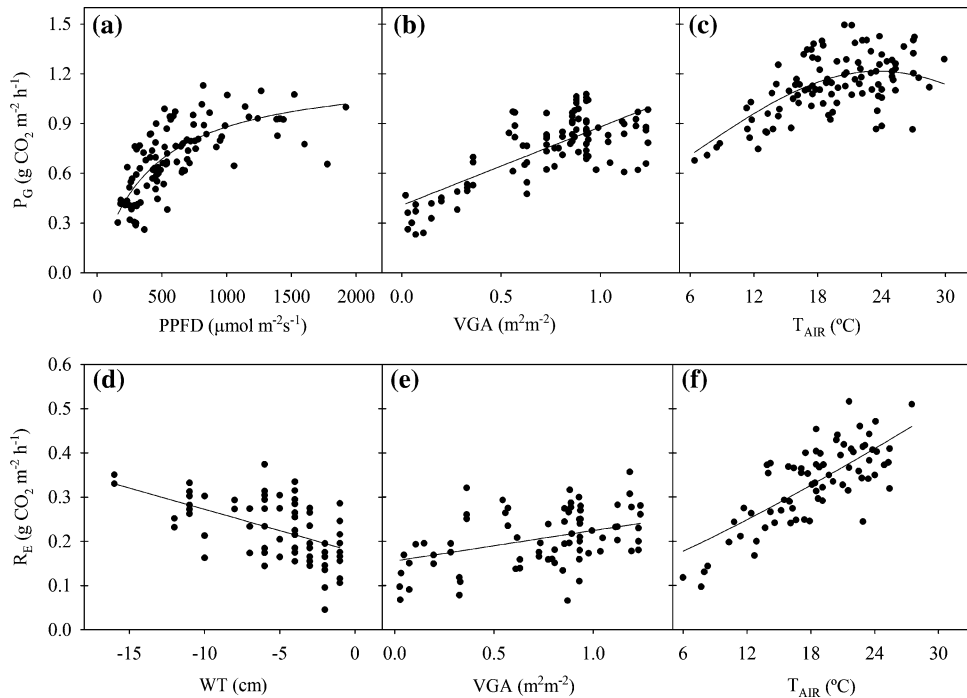
Figure 1. Environmental controls on P_G and R_E using sample plot HL6 as an example. Response of P_G to (**A**) photosynthetic photon flux density (PPFD), (**B**) vascular green area (VGA) and (**C**) air temperature (T_{AIR}). Response of R_E to (**D**) water level (WT), (**E**) VGA and (**F**) T_{AIR}. During 2003–2004 measured P_G values were adjusted to (**A**) VGA = 1 and T_{AIR} = 10°C, (**B**) PPFD = 1000 μmol m^{-2} s^{-1} and T_{AIR} = 10°C, (**C**) PPFD = 1000 μmol m^{-2} s^{-1} and VGA = 1 using equation (1). During 2003–2004 measured R_E values were adjusted to (**D**) WT = −5 cm and VGA = 1, (**E**) T_{AIR} = 10 °C and VGA = 1, (**F**) T_{AIR} = 10 and WT = −5 cm using equation (2). The regressions lines in figures are based on the form of response between P_G/R_E and environmental variable used in the models.

present in each sample plot at 2–4 week intervals throughout the study period. We then multiplied this by leaf size, which was determined by measurement of the leaves of selected individual plants of each species on the same dates as the leaf numbers were counted. For each sample plot, non-linear regression analysis was used to interpolate the green area (GA) of each species between measurements. This was done to describe the seasonal dynamics in the growth of the species. We used GA models described in Laine and others (2006). Daily VGA was calculated by summing the GA values of each species within the sample plot.

In addition, the vegetation composition of the sample plots was surveyed in August of 2003 and 2004 by estimating the abundance (cover) of each species (%). The nomenclature of vascular plants, mosses and liverworts follows Stace (1997) and Smith (2004, 1990), respectively. We used constrained ordination to characterize the moisture gradient in vegetation. Canonical Correspondence Analysis (CCA) using CANOCO for Windows 4.5 program (Ter Braak and Smilauer 1998) was performed for plant community data gathered in Au-

gust 2004. We applied median, mean, minima and maxima water level as explaining variables. A Monte Carlo permutation test was performed to evaluate the significance of the model and the partial effect of each explaining variable. In addition, vegetation properties such as VGA, moss cover, VGA + moss cover, VGA / moss cover and number of species were included in CCA as supplementary variables.

Modelling of CO_2 Exchange Components

To describe the different responses of varying plant communities along the moisture gradient, we parameterized the CO_2 exchange component (P_G, R_E) models separately for each sample plot. Following the approach of Tuittila and others (2004), we used a multiplicative model format in which the sub-models, representing the responses of fluxes to different environmental variables, were multiplied by each other. We examined the distribution of residuals of the individual response functions and models to validate the model formats and to choose the terms and parameters necessary for the models.

Table 2. Estimated Parameter Values, Goodness of Fit (R^2) and Standard Error of the Estimates (SEE) for the Model of Gross Photosynthesis (P_G) of Sample Plots

	P_{MAX} (g CO_2 m^{-2} h^{-1} VGA unit^{-1})	k_{PPFD} (μmol m^{-2} s^{-1})	s (VGA unit, m^2 m^{-2})	T_{opt} (°C)	T_{tol} (°C)	b (cm^{-1})	R^2	SEE (g CO_2 m^{-2} h^{-1})
HU1	1.33 (0.15)	328.17 (79.34)	0.41 (0.08)	25.51 (1.51)	18.10 (2.68)	–	0.83	0.14
HU2	0.69 (0.08)	349.03 (61.55)	1.02 (0.22)	24.32 (0.90)	13.83 (1.27)	–	0.79	0.20
HU3	1.21 (0.08)	358.14 (84.32)	0.78 (0.16)	23.48 (1.16)	13.63 (1.74)	–	0.79	0.15
HU4	1.48 (0.24)	642.12 (129.71)	0.49 (0.08)	19.98 (0.97)	11.96 (1.57)	–	0.84	0.11
HU5	0.97 (0.10)	383.75 (66.31)	0.90 (0.13)	23.94 (1.09)	13.71 (1.86)	–	0.91	0.12
HU6	1.50 (0.17)	527.82 (87.09)	0.39 (0.08)	18.79 (5.53)	27.78 (14.94)	–	0.84	0.14
HL1	0.86 (0.10)	398.03 (83.99)	0.45 (0.13)	23.35 (0.86)	10.84 (1.21)	–	0.84	0.14
HL2	0.66 (0.07)	283.02 (57.87)	1.02 (0.19)	26.40 (0.82)	13.27 (1.03)	–	0.81	0.18
HL3	0.83 (0.11)	329.52 (74.47)	0.75 (0.17)	23.64 (1.01)	12.24 (1.72)	–	0.81	0.15
HL4	0.89 (0.06)	415.98 (52.45)	0.54 (0.06)	25.80 (1.17)	18.71 (2.02)	–	0.91	0.11
HL5	1.25 (0.11)	453.03 (77.30)	0.19 (0.05)	23.00 (0.89)	12.54 (1.94)	–	0.92	0.09
HL6	0.91 (0.11)	395.79 (72.81)	0.86 (0.16)	23.70 (1.99)	17.07 (3.99)	–	0.83	0.14
LL1	0.91 (0.11)	200.66 (74.34)	0.21 (0.06)	24.64 (1.43)	13.61 (3.02)	–	0.82	0.09
LL2	1.37 (0.13)	418.45 (98.17)	–	–	–	–	0.80	0.13
LL3	0.80 (0.09)	421.93 (80.63)	0.52 (0.09)	24.20 (0.62)	10.63 (1.16)	–	0.88	0.08
LL4	0.75 (0.10)	561.37 (131.97)	0.32 (0.07)	22.17 (1.40)	12.74 (1.85)	–	0.73	0.10
LL5	0.74 (0.08)	345.29 (84.42)	0.39 (0.08)	25.42 (1.12)	13.59 (2.03)	–	0.75	0.12
LL6	0.57 (0.07)	327.30 (113.10)	–	–	–	–	0.78	0.06
HO1	0.33 (0.11)	163.65 (64.61)	0.29 (0.12)	28.13 (1.16)	14.27 (1.70)	0.10 (0.01)	0.85	0.02
HO2	0.40 (0.16)	163.65 (–)	0.68 (0.34)	29.24 (1.66)	11.40 (1.83)	0.13 (0.02)	0.62	0.07
HO3	0.68 (0.18)	163.65 (–)	0.26 (0.09)	37.00 (4.51)	14.27 (3.56)	0.07 (0.02)	0.65	0.04

Standard errors of the parameter estimates are given in brackets.

Table 3. Estimated Parameter Values, Goodness of Fit (R^2) and Standard Error of the Estimates (SEE) for the Model of Ecosystem Respiration (R_E) of Sample Plots

	b_1 (g CO_2 m^{-2} h^{-1} VGA unit^{-1})	b_2 (g CO_2 m^{-2} h^{-1} VGA unit^{-1} cm^{-1})	b_3 (K)	b_4 (VGA unit, m^2 m^{-2})	R^2	SEE (g CO_2 m^{-2} h^{-1})
HU1	0.029 (0.013)	−0.002 (0.001)	239.32 (20.27)	2.045 (0.753)	0.74	0.08
HU2	0.029 (0.008)	−0.001 (0.000)	184.01 (20.81)	2.893 (0.864)	0.70	0.08
HU3	0.021 (0.015)	0.005 (0.002)	159.67 (30.48)	2.664 (1.134)	0.80	0.06
HU4	0.046 (0.015)	−0.003 (0.001)	216.40 (34.19)	1.426 (0.474)	0.69	0.06
HU5	0.007 (0.005)	−0.003 (0.001)	195.31 (28.10)	3.929 (1.416)	0.76	0.07
HU6	0.039 (0.008)	−0.004 (0.001)	177.98 (26.44)	1.277 (0.282)	0.85	0.05
HL1	0.025 (0.006)	−0.002 (0.001)	229.08 (29.04)	2.696 (0.791)	0.79	0.06
HL2	0.033 (0.005)	−0.004 (0.001)	174.08 (17.68)	1.672 (0.332)	0.82	0.06
HL3	0.028 (0.007)	−0.004 (0.001)	190.45 (28.31)	1.932 (0.546)	0.82	0.06
HL4	0.023 (0.006)	−0.001 (0.000)	241.57 (21.96)	2.993 (0.791)	0.80	0.06
HL5	0.081 (0.013)	−0.013 (0.003)	119.90 (32.99)	0.616 (0.141)	0.83	0.05
HL6	0.054 (0.012)	−0.003 (0.001)	169.03 (27.60)	2.260 (0.622)	0.78	0.06
LL1	0.081 (0.020)	−0.010 (0.004)	183.91 (47.55)	0.674 (0.196)	0.74	0.05
LL2	0.086 (0.016)	−0.014 (0.004)	101.45 (42.63)	0.618 (0.156)	0.80	0.06
LL3	0.048 (0.010)	−0.006 (0.002)	212.02 (36.53)	0.987 (0.248)	0.82	0.05
LL4	0.082 (0.015)	−0.006 (0.002)	169.09 (33.53)	0.491 (0.120)	0.70	0.07
LL5	0.053 (0.012)	−0.008 (0.002)	156.74 (30.53)	0.956 (0.245)	0.72	0.07
LL6	0.046 (0.011)	−0.014 (0.004)	146.69 (48.48)	0.461 (0.160)	0.82	0.03
HO1	0.037 (0.008)	−0.006 (0.002)	176.97 (44.05)		0.46	0.03
HO2	0.086 (0.012)	−0.015 (0.003)	140.94 (44.05)		0.71	0.03
HO3	0.066 (0.014)	−0.007 (0.002)	151.44 (63.84)		0.63	0.03

Standard errors of the parameter estimates are given in brackets.

We used the Michaelis–Menten relationship (Stryer 1988) to describe the light dependence of P_G (Figure 1A). Photosynthesis is related to the amount of photosynthesizing green leaf area, which has strong seasonal dynamics. Because the moss cover remained constant over the study period, VGA was used to describe seasonal changes in P_G within each sample plot. The sample plot wise parameterization took into account the differences in P_G related to differences in moss cover between the sample plots. The relationship between P_G and VGA was linear (Figure 1B). We applied parameter s to describe the contribution of mosses to the total green area. Moss cover in plots LL2 and LL6 was negligible and parameter s did not differ significantly from zero and was, therefore, excluded. Photosynthesis has a unimodal response to temperature that is, photosynthesis increases with increasing temperature until it becomes restricted at high temperatures. We related P_G to air temperature (T) by using a Gaussian response (Figure 1C). In the hollow plots (HO1–HO3), the WT had a small range around zero, but had a strong impact on photosynthetic rate, which we described using an exponential relationship.

The P_G model format was as follows:

$$P_G = P_{MAX}\left(\frac{PPFD}{k_{PPFD} + PPFD}\right)(s + VGA)$$
$$\exp\left(-0.5\left(\frac{T - T_{opt}}{T_{tol}}\right)^2\right)(\exp(-bWT)) \quad (1)$$

where PPFD is the photosynthetic photon flux density, VGA is the vascular green area, T is the air temperature and WT is the water level. P_{MAX}, k_{PPFD}, s, T_{opt}, T_{tol} and b are fitted parameters. Parameter k_{PPFD} denotes the level of PPFD at which half of the maximum photosynthesis is reached; T_{opt} denotes the optimum air temperature for P_G; T_{tol} denotes the temperature tolerance. The P_G model parameter values for each plot are given in Table 2.

Ecosystem respiration (R_E) consists of soil and plant respiration, both of which are affected by temperature and WT (Silvola and others 1996; Tuittila and others 2004). We related R_E to air temperature (T) using an exponential relationship described by Lloyd and Taylor (1994) (Figure 1F). In our study, the WT fluctuation remained modest and we observed a linear relationship between R_E and WT (Figure 1D). Along with temperature, the seasonality in the flux rate was described by VGA. Respiration increased linearly with increasing VGA
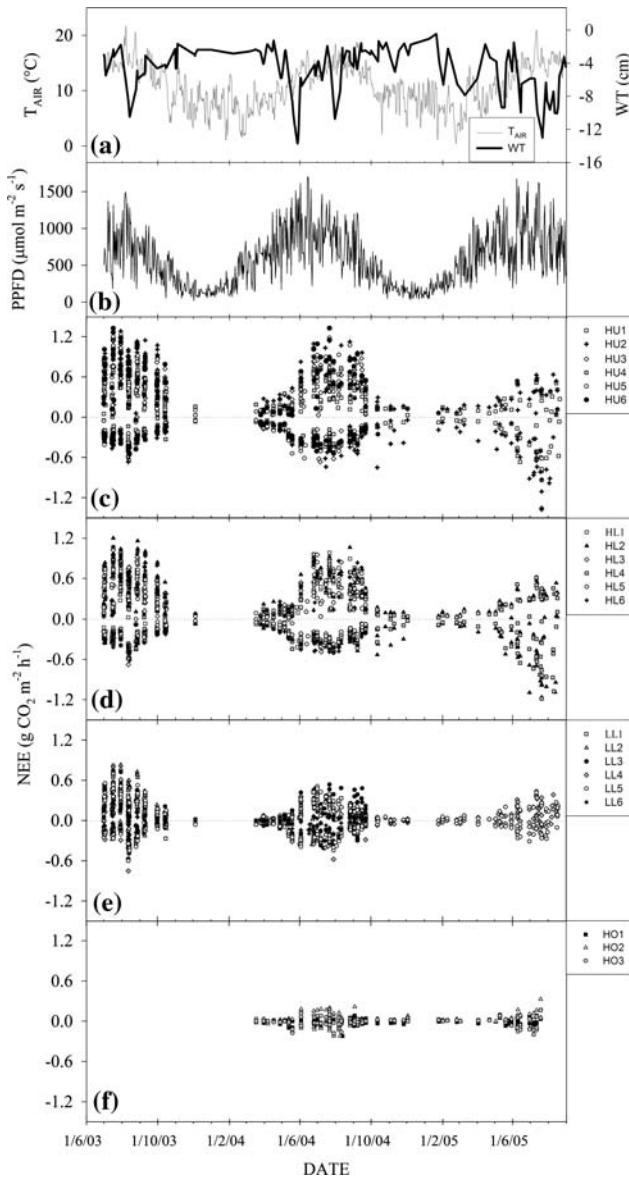
Figure 2. Daily average (**A**) air temperature (T_{AIR}) and average water level (WT) of the sample plots and (**B**) photosynthetic photon flux density (PPFD) during daylight hours. Measured net CO_2 exchange (light and dark measurements) in sample plots (**C**) HU1–HU6, (**D**) HL1–HL6, (**E**) LL1–LL6 and (**F**) HO1–HO3. Daily variation in fluxes is mainly due to variation between sample plots and differences in light levels between measurements.

(Figure 1E). For R_E in HO1–HO3, the effect of VGA was not significant and it was not used in the model. The R_E model format was:

$$R_E = (b_1 + b_2 WT)\left[\exp\left(b_3\left(\frac{1}{T_{ref} - T_0} - \frac{1}{T - T_0}\right)\right)\right]$$
$$(b_4 + VGA)$$

(2)

where T_{ref} was set at 283.15 K and T_0 at 227.13 K according to Lloyd and Taylor (1994). T_0 is the temperature minimum at which respiration reaches zero. The air temperature (T) is given in Kelvin and b_1, b_2, b_3 and b_4 are fitted parameters. According to Lloyd and Taylor (1994) parameter b_2 is the activation energy divided by the gas constant.

The R_E model parameters for each sample plot are given in Table 3.

SPSS 12.0.1 for Windows statistical package (SPSS, Inc.) was used in modelling P_G and R_E fluxes using non-linear regression with the Levenberg–Marquardt method. We tested the sensitivity of the modelled annual P_G and R_E to model parameters by varying separately each model parameter by its standard error. Furthermore, we tested the sensitivity of P_G and R_E to the environmental inputs (PPFD, T_{AIR}, WT, VGA) by varying the environmental data by ±10%.

Equations (1 and 2) were individually parameterized and used to calculate the hourly P_G and R_E for each sample plot. P_G and R_E fluxes were reconstructed for the time period, 1 October 2003–
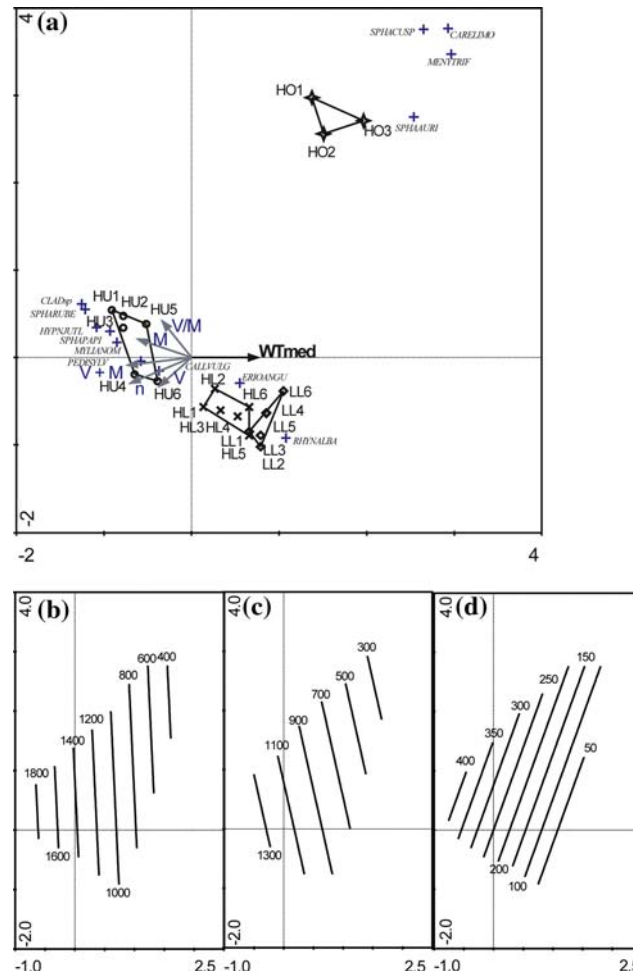
Figure 3. (**A**) Canonical correspondence analysis (CCA) of the interaction between species and median water level (WT med). Vascular green area (V), moss cover (M), V + M, V / M and number of species (*n*) were used as supplementary variables. The eigenvalue of axis 1 is 0.57. Species with 10% lower axis minimum fit are included in the figure. The second unconstrained axis that describes residual variation, which is unrelated to WT_{MED}, had a higher eigenvalue (0.75) than the first axis. CALLVULG *Calluna vulgaris*; CARELIMO *Carex limosa*; CLADsp *Cladonia* sp; ERIOANGU *Eriophorum angustifolium*; HYPNJUTL *Hypnum jutlandicum*; MENYTRIF *Menyanthes trifoliata*; MYLIANOM *Mylia anomala*; PEDISYLV *Pedicularis sylvaticum*; RHYNALBA *Rhynchospora alba*; SPHAAURI *Sphagnum auriculatum*; SPHACUSPI *Sphagnum cuspidatum*; SPHAPAPI *Sphagnum papillosum*; SPHARUBE *Sphagnum rubellum*. We plotted the isopleths of fluxes (P_G, R_E, NEE) in CCA space using the Loess Smoother to describe the correlation between seasonal gas exchange components: (**B**) gross photosynthesis (P_G), (**C**) ecosystem respiration (R_E) and (**D**) net ecosystem exchange (NEE).

30 September 2004 to obtain the annual fluxes using PPFD and air temperature data from an on-site weather station (Laine and others 2006). Daily WT was interpolated for each plot from WT measurements made during the chamber measurement campaigns. Daily VGA was estimated for each plot using the VGA models (Laine and others 2006). There were no measurements of WT or VGA of hollows from the period of 1 October 2003–5 April 2004. Therefore, the daily water level for the intervening period was estimated from LL values using the difference in the relative altitude between microforms LL and HO. To estimate the average

daily VGA of the HO for this period, the VGA models based on data from 2004 were used. The hourly NEE over the year were calculated as the difference between P_G and R_E.

RESULTS

Environmental Conditions

The seasonal dynamics in the average daily air temperature were noticeable but modest and during wintertime the daily air temperature often exceeded 10°C (Figure 2A). The average WT of the
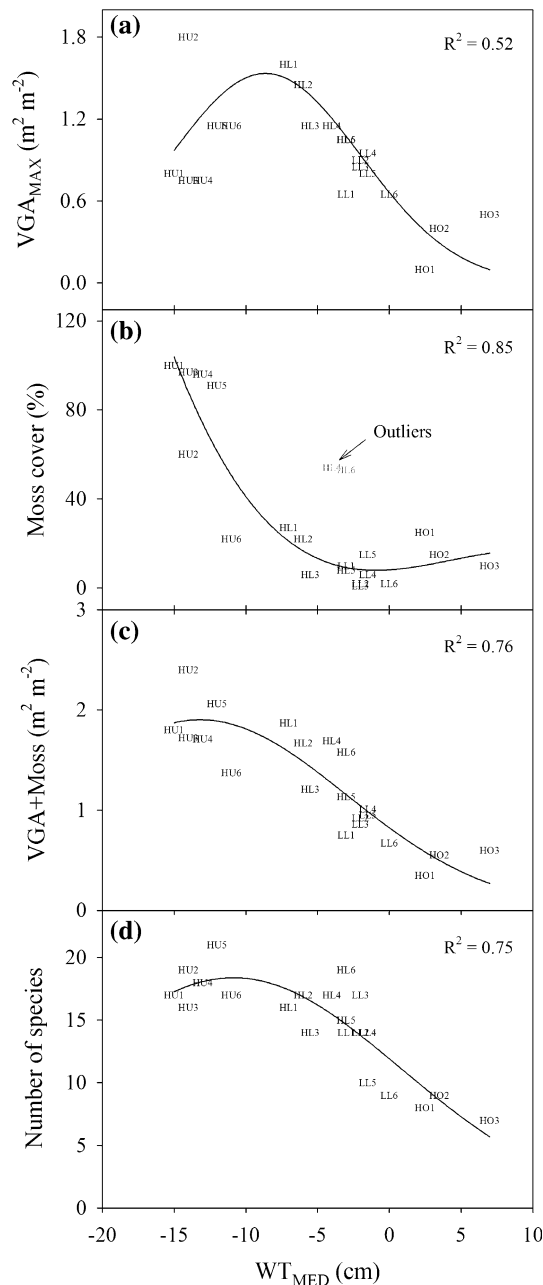
Figure 4. Correlation between median water level (WT$_{MED}$) and (**A**) maximum vascular green area (VGA$_{MAX}$), fitted with a unimodal Gaussian response model ($R^2 = 0.52$; SE $= 0.35$; $F = 9.6$; $P = 0.002$) and (**B**) moss cover, fitted with a cubic (third degree polynomial) model ($R^2 = 0.85$; SE $= 15.6$; $F = 27.5$; $P < 0.0001$) and (**C**) maximum vascular green area and moss area (VGA + Moss), fitted with a unimodal Gaussian model ($R^2 = 0.76$; SE $= 0.29$; $F = 28.2$; $P < 0.0001$) and (**D**) number of species, fitted with a Gaussian model ($R^2 = 0.75$; SE $= 2.1$; $F = 26.5$; $P < 0.0001$). In (**B**) sample plots HL4 and HL6 were excluded from the curve fitting as outliers.

sample plots remained within 5 cm of the surface during most of the study period (Figure 2A).

However, in all three summers the WT periodically lowered, particularly in the summer of 2005. Daytime daily average PPFD (Figure 2B) had stronger seasonal dynamics than air temperature or WT. The regularity of overcast days during all three growing seasons is pronounced. The environmental conditions at the study site during 2003 and 2004 are described in more detail by Sottocornola and Kiely (2005).

Moisture Gradient in Vegetation

Canonical Correspondence Analysis (CCA) for vegetation communities using WT parameters as explanatory variables indicated a strong correlation between WT parameters. After including a single WT parameter into the model, the partial effect of other parameters was very low and they did not improve the model. We selected the median water level (WT$_{MED}$) as a representative variable, which had a significant relationship with plant community data ($P = 0.002$) and explained 20.3% of the variation in species distribution.

The first axis separated sample plots forming a continuum from HU to HO (Figure 3A). Along this WT gradient there was a clear separation of species between HU and HO species (Figure 3A). At the dry end of the gradient the hummock forming mosses such as *Sphagnum rubellum* were associated together with lichens and a dwarf shrub *Calluna vulgaris*. A forb, *Menyanthes trifoliata* had its optimum at the wet end of the gradient together with hollow *Sphagna* (*Sphagnum cuspidatum, S. auriculatum*). Although *Rhynchosphora alba* was the only species having its optimum in lawns (Figure 3A), the highest VGA was associated with lawn communities (Figure 4A); the maximum vascular green area (VGA$_{MAX}$) followed the WT gradient being highest at the high lawn–hummock interface and the highest VGA$_{MAX}$ occurred at a WT 9 cm below the surface (Figure 4A). Unlike the vascular plants, mosses were most abundant in hummocks (Figure 4B), which had a WT$_{MED}$ below the optimal conditions for VGA (Figure 4A). None of the bryophytes had their optimum in the intermediate water level conditions (Figure 3). The combined leaf area of vascular plants and mosses was consequently the highest at WT 13 cm below the surface (Figure 4C). The CCA (Figure 3) showed negative correlation between WT and the combined leaf area of vascular plants and mosses. The species abundance was highest in the communities in the hummock–lawn interface and decreased with increasing moisture (Figure 4D). The second axis of CCA was related to internal variation within the
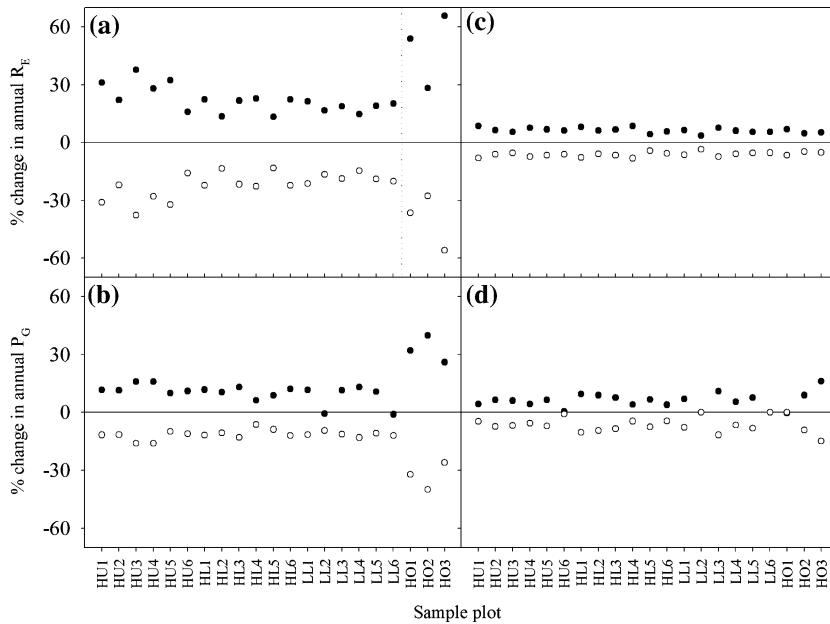
Figure 5. Sensitivity of the models to changes in model parameters or environmental parameters. In (**A**) and (**B**), the model parameter was varied by its standard error; (**A**) sensitivity of the modelled annual R_E to model parameter b_4, except for HO1, HO2 and HO3 to parameter b_1; (**B**) sensitivity of the modelled annual P_G to model parameter P_{MAX}. In (**C**) and (**D**), the model's environmental input T_{AIR} was varied by ± 10%; (**C**) sensitivity of the modelled annual R_E to T_{AIR}; and (**D**) sensitivity of the modelled annual P_G to T_{AIR}.

groups (Figure 3A). The internal variation is correlated with the moss / vascular plant ratio that is, the moss abundance in relation to vascular plant abundance in the sample plot.

Model Performance

On average, the regression models explained 82% of the variation in P_G (Table 2). The standard error of the estimates (SEE) varied from 0.02 to 0.2 g CO_2 m^{-2} h^{-1}. The models tended to slightly overestimate small and underestimate high fluxes. On average 75% of the variation in R_E was explained by the models (Table 3). The SEE of the R_E models varied from 0.03 to 0.08 g CO_2 m^{-2} h^{-1}. Similar to P_G models, the R_E models overestimate small and underestimate high fluxes.

We carried out a sensitivity analysis in which each model parameter (P_G and R_E) was varied separately by its standard error. The annual R_E estimates were generally most sensitive to changes in parameter b_4 (from the VGA sub-model), which caused on average a 22% change in annual R_E (Figure 5A) and least sensitive to changes in parameter b_3 (from the air temperature sub-model), which caused on average a 2% change in annual R_E. Due to the smaller data set, the parameters obtained for the hollow sample plots were less reliable, with an average change of 20% in annual R_E, which is higher than those for other sample plots (14% change). Hollows were most sensitive to parameter b_1 (Figure 5A). The annual P_G estimates were equally sensitive to all parameters, changing on average by 10% when parameters were chan-

ged by their SE. Again, the parameters for hollow sample plots were less reliable (causing a change of 22%) than for other sample plots (causing a change of 7%) (Figure 5B gives an example of parameter P_{MAX}).

We also carried out a sensitivity analysis in which the model's environmental inputs (PPFD, T_{AIR}, WT, VGA) were varied by ± 10%. The P_G and R_E models were rather robust with regard to variation in environmental inputs. The 10% increase or decrease in any of the environmental variables caused on average less than 10% change in the annual R_E and P_G estimates. In general R_E was most sensitive to change in T_{AIR} (Figure 5C), whereas in the HU and HO sample plots R_E was sensitive also to WT. In general P_G was most sensitive to T_{AIR} (Figure 5D) and VGA.

Controls of CO_2 Exchange along the Moisture Gradient

The measured CO_2 exchange, both in light and dark, followed the moisture gradient, being highest in HU (Figure 2C) and lowest in HO (Figure 2F). However, variation between the sample plots was large. We plotted the isopleths of gas exchange components (P_G, R_E, NEE) in CCA space using the Loess Smoother (CanoDraw for Windows 4.12 package) to describe the correlation between gas exchange components and the vegetation structure, described by the CCA axes 1 and 2 (Figure 3B, C, D). All flux components were strongly related with axis 1, increasing towards drier communities. Both P_G (Figure 3B) and R_E (Figure 3C) also in-
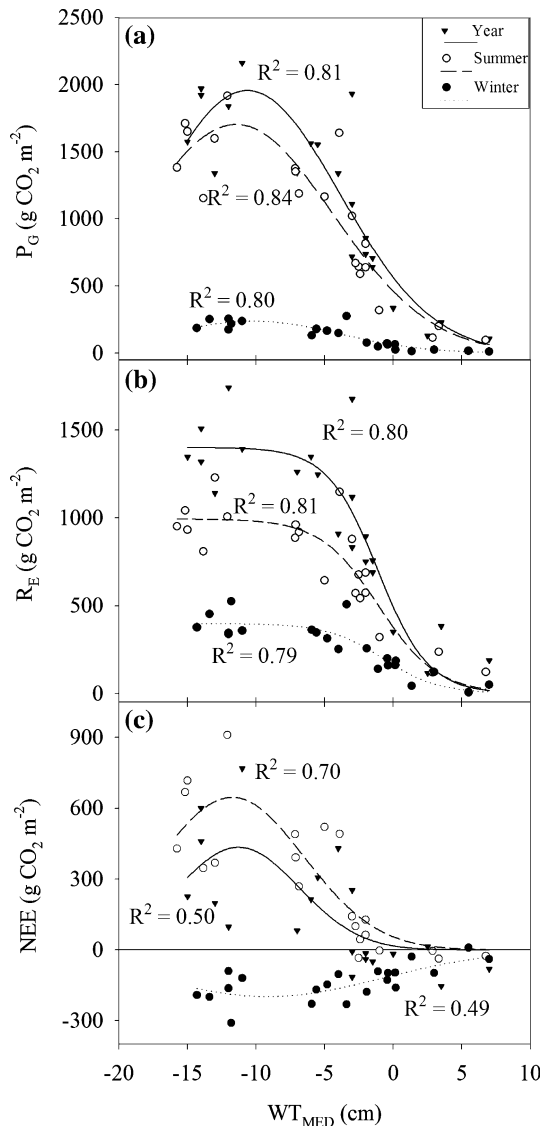
Figure 6. The relationship between sample plot's median water level (WT) and reconstructed annual, summer (April–October) and winter (November–March) (**A**) gross photosynthesis (P_G), fitted with a Gaussian response model, (**B**) ecosystem respiration (R_E), fitted with a sigmoidal curve and (**C**) net ecosystem exchange (NEE) fitted with a Gaussian model.

creased with the increasing vascular green area. Conversely, NEE was not directly linked to vascular green area (V) but increased towards the higher vascular plant–moss ratio (V/M) (Figure 3D).

The reconstructed annual P_G flux followed the WT gradient and the highest annual P_G was when the WT was at −11 cm (Figure 6A). The reconstructed annual R_E in the sample plots increased with deepening WT. The increase in R_E was most rapid between the WT range from 0 to 5 cm and slowed down at the driest end of the water level

gradient (Figure 6B). Similar to VGA_{MAX} and P_G, the reconstructed annual NEE (Figure 6C) was highest in the intermediate WT range at the high lawn–hummock interface. Compared to VGA_{MAX} and P_G, the correlation between WT and NEE was weaker and the flux rates stayed at the constant level when the WT was close to the soil surface. The photosynthesizing leaf area of vascular plants and mosses (VGA + Moss) had a linear relationship with annual P_G and annual R_E (Figure 7A, B). The correlation between NEE and VGA + Moss was weak (Figure 7C). The species diversity (amount of species in the sample plot) had a strong linear correlation with both annual P_G (Figure 7D) and annual R_E (Figure 7E), whereas the correlation with NEE was weaker (Figure 7F).

Temporal Variation in CO_2 Exchange Components along the Water Level Gradient

A strong seasonal variation was measured in all sample plots, with small fluxes and less spatial variation occurring during the winter periods (Figure 2C–F). The highest fluxes were measured in the second half of July in each of the three years. Fluxes were similar during the two summers of 2003 and 2004, although summertime NEE was higher in 2004. During the summer of 2005, the net CO_2 uptake was lower and the release higher in the sample plots HU1, HU2, HL2 and HL4 by comparison to the two previous summers (Figure 2C, D).

The water level affected P_G and R_E fluxes in a similar manner during the summer and winter. The highest P_G of 1917 g CO_2 m^{-2} was reached at a WT_{MED} of −11 cm in the summer. In winter, the highest P_G of 276 g CO_2 m^{-2} was reached at a WT_{MED} of −10 cm (Figure 6A). During the summer and winter, the WT_{MED} level at which the greatest change in R_E occurred was the same (−2 cm; Figure 6B). Conversely, the seasonal NEE, had a different relationship with the WT_{MED} during the summer and winter (Figure 6C). Similar to P_G, the highest summertime NEE was reached in those vegetation communities where the WT_{MED} was 12 cm below the soil surface. In winter the highest NEE was in the wet communities.

The reconstructed annual (October 2003–September 2004) P_G, R_E and NEE fluxes varied between the sample plots from 212 to 2160 g CO_2 m^{-2}, from 115 to 1742 g CO_2 m^{-2} and from −115 to 768 g CO_2 m^{-2}, respectively. The wintertime (November–March) respiration varied from 7 to 526 g CO_2 m^{-2}, which constituted 6–
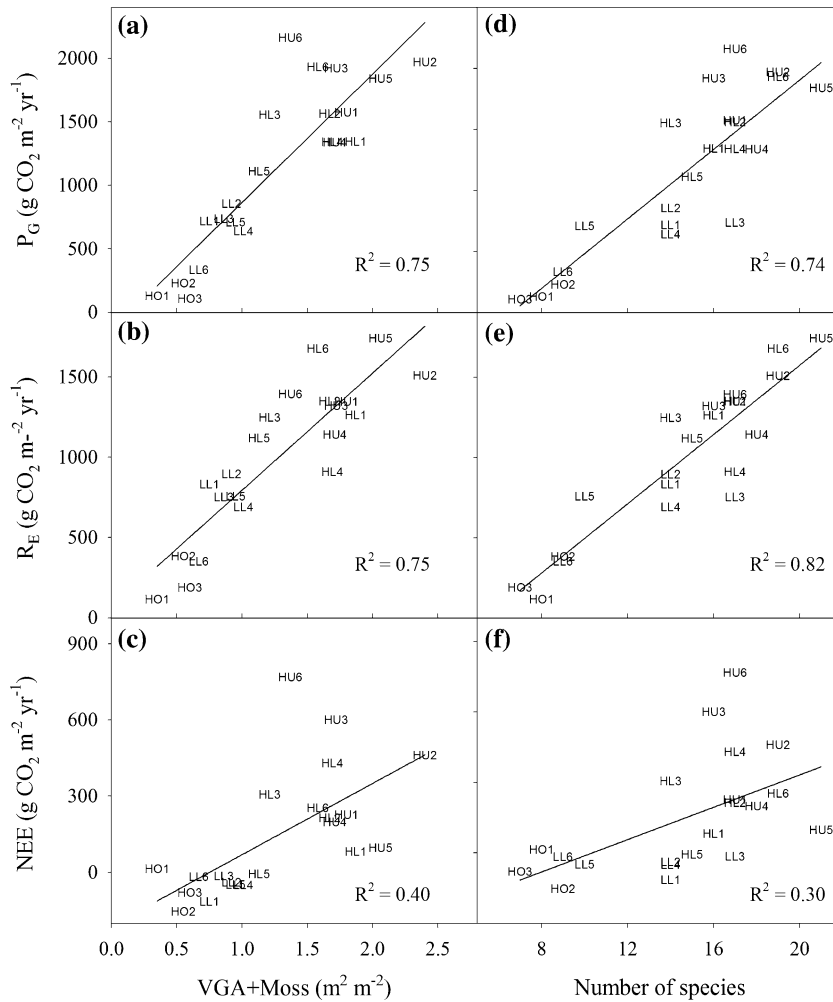
Figure 7. Relationship between sample plot's maximum vascular green area and moss area (VGA + Moss) and (**A**) annual gross photosynthesis (P_G) with a linear fit ($R^2 = 0.75$; SE = 332.5; $F = 58.2$; $P < 0.0001$), (**B**) annual ecosystem respiration (R_E) with a linear fit ($R^2 = 0.75$; SE = 238.16; $F = 59.25$; $P < 0.0001$) and (**C**) annual NEE with a linear fit ($R^2 = 0.40$; SE = 198.53; $F = 12.6$; $P < 0.002$). Relationship between number of species and (**D**) annual P_G with a linear fit ($R^2 = 0.74$; SE = 343.1; $F = 53.5$; $P < 0.0001$), (**E**) annual (R_E) with a linear fit ($R^2 = 0.82$; SE = 207.7; $F = 83.9$; $P < 0.0001$) and (**F**) annual NEE with a linear fit ($R^2 = 0.30$; SE = 214.1; $F = 8.03$; $P = 0.01$).

32% of the annual R_E. The wintertime P_G constituted only 3–14% of the annual flux.

DISCUSSION

Moisture Gradient in the Vegetation of a Lowland Blanket Bog

The vegetation of the study site resembles the typical blanket bog vegetation as described by Doyle and Moore (1980). It is characterized by a co-domination of *Schoenus nigricans* and *Molinia caerulea*, stunted Ericoid shrubs and generally poorly developed *Sphagnum* cover. In these generally wet conditions, even in hummock level, the shrub height varied from approximately 5–15 cm whereas, for example, in Canadian bogs the shrub heights are commonly higher (20–30 cm in Ontario) (Bubier and others 2005; Lafleur and others 2005a). A surface pattern composed of different vegetation communities ranging from dryer hummocks to wetter hollows and pools is a typical

feature of blanket bogs (Lindsay 1995). The sample plots of the current study formed a continuum along the consequent WT gradient in CCA analysis. The plant species, which had a distinct optimum along the WT gradient, were mostly hummock and hollow dwelling species, that is, species having their highest abundance at opposite ends of the gradient (Figure 3). The permanently inundated hollows that Doyle (1990) classified into a different plant physiological association than the common ombrotrophic bog vegetation, were separated from other communities. The lawn level vegetation was chiefly composed of vascular species, which have a broader distribution along the moisture gradient. Species such as, *M. caerulea*, *S. nigricans* and *Eriophorum angustifolium* occur in all vegetation associations typical of lowland blanket bogs (Doyle 1990) and occurred in all vegetation communities in the study site. The *Sphagnum* species that have distinct WT optima (Rydin and McDonald 1985) and therefore describe the moisture gradient better were practically missing from the lawn communi-

ties in our study site, whereas the hummock and hollow *Sphagnum* species represented opposite ends of the WT gradient. This is a typical feature of blanket bogs where *Sphagnum* cover is poorly developed except in hummocks and in some depressions (Doyle 1990).

In addition to species composition, the effect of WT on the quantity of vegetation was evident and conflicting at first sight. Although the optima of vascular plant species were at extreme ends of the WT gradient, the overlap of hummock and hollow species resulted in the highest vascular leaf area in the intermediate WT range, that is, in high lawn communities. In a much drier continental bog in Canada, the vascular plant biomass continued to increase even when the WT was −50 cm below the surface, largely due to the shrub growth (Bubier and others 2005). This is in contrast with blanket bogs where shrubs are often stunted (Doyle and Moore 1980) and the vegetation tends to be taller and denser in lawns than in wetter habitats (Doyle 1982). The contribution of *Sphagnum* to production is often low in blanket bogs compared to raised bogs (Forrest 1971). In the current study, the highest moss cover, ranging from 22 to 100%, was observed in hummocks. This is in contrast with raised bogs where the *Sphagnum* cover can be smaller in hummocks compared with the common occurrence of full cover in hollows (Vasander 1982; Madden and Doyle 1990); also in a dry bog in Canada the moss biomass decreased with increasing WT (Bubier and others 2005). In this study, the combined leaf area of vascular plants and mosses was highest in hummocks. Although there were no great differences in the species composition within different lawn communities, the amount of photosynthesizing surface area varied. VGA and moss cover were lower in low lawns than in high lawns. The species diversity had a similar relationship with WT as VGA, however the highest diversity was observed at deeper WT, which was likely due to higher moss species richness in hummocks than in high lawns. In other blanket bogs the lawn vegetation was found to be richest in species compared to other microforms, especially hollows and pools (Guinan and others 1998).

Factors Controlling the Spatial Variation in P_G and R_E

Similar to other studies (for example, Alm and others 1997; Bubier and others 1998; Waddington and Roulet 2000) we found a strong spatial variation in CO_2 exchange between the vegetation communities. The magnitude of uptake and release

varied between vegetation communities following the moisture gradient. The variability within each vegetation community group (HU, HL, LL, HO) suggests that vegetation forms a continuum of communities rather than clearly delineated groups. This is in line with Guinan and others (1998), who described a blanket bog as an ecosystem with a gradient of overlapping vegetation communities. In contrast to this study, Alm and others (1997) observed higher CO_2 fluxes from lawns compared to hummocks. Also we noticed a decline in P_G and NEE and saturation in R_E above a certain WT threshold but on average the fluxes were highest in hummocks. A reason for this may be that the height of the hummocks was, on average only 14 cm above the WT_{MED}. This is typical of bogs in oceanic conditions. Moreover, they were the only sample plots with abundant moss cover that continued to photosynthesize at times when vascular plants had senesced. The annual P_G, R_E and NEE were higher in hummocks and high lawns, and lower in hollows than those measured by Alm and others (1997) in boreal conditions.

In this study, the strongest controllers of spatial variation of CO_2 fluxes were WT and vegetation structure. High WT is crucial for peat accumulation and lowering WT may turn a peatland into a C source (for example, Alm and others 1999). WT controls the depth of the oxic peat layer where aerobic decomposition occurs (Clymo 1983) and the thinner this layer is, the lower is the decomposition rate (Moore and Dalva 1993; Silvola and others 1996). We observed a strong correlation between the median sample plot WT and the reconstructed annual P_G, R_E and NEE, with all flux components being lowest at the wet end of the WT gradient. We observed the highest NEE at a WT depth of (−11 cm) which is similar to the WT depth at which Belyea and Clymo (2001) estimated the maximum rate of peat accumulation to occur in a raised bog in Scotland. The importance of the water level in determining the rate of R_E varies for different WT ranges and is higher in the intermediate WT ranges as was observed in this study. In agreement with the constant rate of R_E fluxes at the drier end of the WT gradient Lafleur and others (2005b) observed that in a dry bog (WT 30–70 cm below surface) the effect of WT on R_E is small.

The vegetation structure in peatlands is controlled by ecohydrology (Laine and others 2002; Bubier and others 2005) and therefore the abundance of vascular plants and mosses is strongly affected by WT. The vegetation communities along the WT gradient have different levels of photosynthetic capacity and productivity (Wallén and

others 1988; Belyea and Clymo 2001). Therefore, the leaf area of vascular plants and mosses (VGA + Moss) affected all CO_2 flux components. An increase in the VGA + Moss accelerated both P_G and R_E; however, the correlation of fluxes with VGA + Moss was not as strong as with WT_{MED}. This is in accordance with Belyea and Clymo (1998) who found that the total net primary production increases with falling WT and increasing vascular species density until the mosses cannot transport water to their apices. Photosynthesis and respiration were highest in communities with the largest number of species (Figure 7D, E). This indicates that species diversity increases the productivity of the community.

Temporal Variation in CO_2 Exchange

The seasonal variation in CO_2 exchange, which we observed, is a well-reported phenomenon in boreal conditions (Lafleur and others 2001). In all three summers, the fluxes were highest during July and August when the peak biomass of most vascular species present in the study site is known to occur in Ireland (Doyle 1982; Madden and Doyle 1990). The slightly higher NEE in the summer of 2004 may be due to the somewhat higher PPFD and consequent higher VGA during the summer of 2004 compared to the summer of 2003. The temperature and WT were on average similar between the summers. The increased respiration rates in the summer of 2005 were possibly due to WT, which remained low for a considerable time period. However, the phenomenon was only observed in the hummock and high lawn sample plots.

The relationships of cumulative P_G and R_E with WT were similar during summer and winter. P_G had a stronger seasonality than R_E. The seasonal changes in P_G are mainly controlled by irradiation and photosynthesizing leaf area that have a distinctive seasonality compared to temperature, which controls R_E (Griffis and others 2000). Therefore, soil respiration continued throughout the winter when the deciduous plants had senesced and plant respiration ceased. The contribution of wintertime (November–March) respiration varied from 6 to 32% of annual respiration, which is in the same range as reported by Roehm and Roulet (2003) and Martikainen and others (1995) for boreal conditions. This does not suggest increased respiration rates in snow and soil frost-free conditions, as was observed by Wilson and others (2007) in a restored Irish peatland. The high WT likely reduced wintertime respiration. Some photosynthesis took place during winter, as was observed by

Sottocornola and Kiely (2005). The contribution of wintertime photosynthesis ranged from 3 to 14% of the annual flux, which is noticeably lower than the contribution of wintertime respiration. NEE showed a dissimilar pattern along the WT gradient between the seasons. The difference between summer and wintertime NEE was greatest in the drier half of the WT gradient (Figure 6C). The summertime NEE was highest at drier sample plots and in wintertime, the highest net loss of carbon (smallest NEE) was observed in the same communities with high R_E fluxes triggered by the thick aerobic peat layer. In wet communities the high WT retarded R_E fluxes and the wintertime CO_2 losses were consequently small.

The annual NEE was negative in low lawn and hollow communities and it varied from −115 to 768 g CO_2 m^{-2} between all vegetation communities. Although this is within the range of estimates from various peatland ecosystems, a higher NEE could be expected in a temperate maritime blanket bog with a longer growing season, a high WT and snow-free winters. Both P_G and R_E were lower when compared to a raised bog in Ontario, Canada (Lafleur and others 2003), where the WT was markedly lower (−27 to −70 cm). The low P_G suggests that the vegetation in the Irish blanket bog may be less productive than in Canadian bogs. The main differences in the vegetation composition are the scattered *Sphagnum* cover and the less vigorous shrub canopy in the blanket bog than those associated with lower WT of continental bogs. Another reason for the low productivity could be the regular cloudiness of the Irish climate that decreases the PPFD during the growing seasons and limits the rate of photosynthesis.

CONCLUSIONS

Our results highlight the strong spatial variation in carbon dynamics within a lowland blanket bog. This variation is largely controlled by WT and consequent differences in vegetation. The studied bog is wet compared to most of the previously studied bogs and therefore this study fills in some gaps in relations of C gas fluxes and WT. The NEE was largest in communities with WT approximately 10 cm below the soil surface; these communities have abundant cover of both vascular plants and mosses producing the highest alpha diversity. The annual NEE was negative in communities with water level close to or above the soil surface. Climate change is expected to affect the peatland C exchange via changing the WT rather than directly increasing temperature. This is

supported by our results. The sensitivity analysis we carried out indicates that a change in temperature has a smaller effect on respiration than on photosynthesis; all together the effect of temperature was only moderate. Our results indicate that a rising WT would increase the proportion of communities with negative annual NEE consequently decreasing the areal NEE. In contrast a considerable water level drawdown would increase the proportion of dry communities. Because the NEE starts to decrease in communities with water level greater than 10 cm below the soil surface, a decrease in areal NEE is expected. However, a small decrease in water level that would increase the proportion of high lawns and small hummocks could increase the areal NEE. More research is required to examine the effects of changing water level and temperature on C exchange of the vegetation communities.

ACKNOWLEDGEMENTS

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