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Meteorological and functional response partitioning to explain interannual variability of CO_2 exchange at an Irish Atlantic blanket bog

Philip McVeigh[a], Matteo Sottocornola[b,c,*], Nelius Foley[a], Paul Leahy[a,d], Gerard Kiely[a,d]

[a] Environmental Research Institute, University College Cork, Ireland
[b] Department of Chemical and Life Sciences, Waterford Institute of Technology, Waterford, Ireland
[c] Sustainable Agro-ecosystems and Bioresources Department, Research and Innovation Centre, Fondazione Edmund Mach, Italy
[d] Civil & Environmental Engineering Department, University College Cork, Ireland

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ABSTRACT

This study aims to develop models to describe CO_2 fluxes in terms of environmental and meteorological variables and their variation over an Atlantic blanket bog in Glencar, southwest Ireland. Ten full years (September 2002–August 2012) of data were included in the assessment of CO_2 flux and micrometeorological data. Models were based on non-gapfilled growing season data, using complete calendar years for annual models, and the entire time-series for weekly models, whilst taking interaction between variables into account for increased model accuracy. This was to determine which environmental variables were most influential in directly controlling CO_2 exchange on a long- and short-term basis. A homogeneity of slopes (HOS) model was used to determine if there was any ecosystem response to indirect effects (functional response) of environmental or meteorological interannual variation. This model uses multiple regression analysis to determine if the ecosystem response can be better predicted as a linear function of the variables using a single slope model for all years, or a separate slopes model for each year. The separate slopes model gave a different (and improved) outcome for both daytime and night-time CO_2 fluxes, and so functional responses were deemed to have occurred. The contribution to variation of day and night-time net ecosystem exchange (NEE_{day} and NEE_{night} respectively) was then separated into four components: indirect functional responses, direct interannual meteorological variability, direct week to week meteorological variability, and random error, which identified 13.8%, 36.6%, 28.2% and 21.4% respectively of the variation in NEE_{day}, as well as 23.4%, 24.4%, 22.2% and 30% respectively of the variation in NEE_{night}. Water table level (WTL) had the greatest influence upon functional variation of NEE at the Glencar blanket peatland, and comparisons of modelled NEE_{day} with leaf area index (LAI) measurements verified the estimate of functional contribution using the separate slopes model. The significance of interannual variation (IAV) and functional responses on NEE at Glencar suggests that it is a resilient ecosystem which might be able to adapt to environmental or climatic changes, although given current climate change predictions, it is likely to have a reduced carbon dioxide sink status in the future.

1. Introduction

Northern temperate peatlands are considered to be a major component of the global carbon cycle. Although accounting for only 3% of land cover, the importance of peatlands is due to the fact that they store vast quantities of carbon, amounting to 30% of the world's soil carbon stocks (Gorham, 1991). For thousands of years, northern peatlands have acted as sinks of atmospheric carbon (Frolking and Roulet, 2007). Pristine or almost intact peatlands are considered to currently act as net sinks, and are likely to continue doing so for decades to come (Limpens et al., 2008). This is despite some sites showing large interannual variability (IAV) and behaving as source of carbon in some years (Koehler et al., 2011; Moore et al., 1998; Roulet et al., 2007).

However, it is uncertain as to whether or not peatlands will continue to act as sinks in the long-term, given that they have the potential to become net sources of carbon in the form of methane (CH_4) and carbon dioxide (CO_2) fluxes to the atmosphere (Limpens et al., 2008), and of carbon exported in streams mainly as dissolved organic carbon (Dinsmore et al., 2010; Koehler et al., 2011). These feedbacks could occur through either climatic or land use changes. Climatic changes would be expected to change peatland hydrology and vegetation, whereas land use changes may perturb the hydrology or cause direct degradation (Strack et al., 2006; Weltzin et al., 2003). For future predictions, it is therefore important to

* Corresponding author at: Department of Chemical and Life Sciences, Waterford Institute of Technology, Waterford, Ireland. Tel.: +353 51302845.
E-mail address: msottocornola@wit.ie (M. Sottocornola).

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increase our understanding of the carbon dynamics of peatlands and of the various mechanisms that influence their carbon cycling (Limpens et al., 2008).

The Eddy-Covariance (EC) technique is regarded as the most appropriate method to estimate the long-term exchange of CO_2 between the biosphere and atmosphere at the ecosystem scale. Land-atmosphere exchange of CO_2 is the major carbon pathway within a peatland system, but despite its importance in the global carbon cycle, comparatively few EC CO_2 flux studies have been made over peatlands thus far. Of these, only a few sites have all-year round data sets spanning two years or more that have enabled longer term analysis (Aurela et al., 2009; Dinsmore et al., 2010; Lafleur et al., 2003; Nilsson et al., 2008; Olefeldt et al., 2012; Roulet et al., 2007; Sagerfors et al., 2008; Sottocornola and Kiely, 2010a; Worrall et al., 2009).

To better understand the impact of climate change upon ecosystems, interest has increasingly turned towards the drivers of IAV in net ecosystem CO_2 exchange (NEE). This is in an attempt to determine whether or not, and to what extent IAV is caused by direct annual variation in meteorological drivers, or indirectly by changes in ecosystem functioning such as subtle changes in vegetation or microbial community composition over time, known as functional responses (Hui et al., 2003). Previous studies that reported such effects on CO_2 NEE were conducted in forests using a physiological model (Richardson et al., 2007), and a step-wise linear regression model (Hui et al., 2003), or over grasslands using a look-up table based statistical approach (Marcolla et al., 2011). To the best of the authors' knowledge, the only other such work carried out over a peatland was that of Teklemariam et al. (2010), which was conducted at the Mer Bleue raised bog, Ontario, Canada.

In Ireland, blanket bogs comprise around 13% of total land area, yet they contain between 21% and 36% of the national soil carbon stock (Eaton et al., 2008; Xu et al., 2011). Similar to raised bogs, blanket bogs are largely ombrotrophic peatlands, receiving water and nutrients mainly from precipitation, even if minerotrophic areas also occur in extensive blanket bogs (Tallis, 1998). They are important not only for carbon storage, but also in terms of biodiversity. These ecosystems are normally located over relatively flat or gently sloping terrain (Tallis, 1998). They tend to form in temperate maritime climates with consistently high rainfall (>1200 mm per annum, >160 wet days a year, with a wet day receiving at least 1 mm of rain in a day) combined with low evaporation rates, resulting in a ground surface that may remain consistently waterlogged (Lindsay et al., 1988; Moore, 1993). Due to their proximity with the sea, these ecosystems also tend to have a high sea-origin ion concentration (Proctor, 1992; Sottocornola et al., 2009; Tallis, 1998).

Blanket bog surfaces are typically a mosaic of various undulating microforms, which differ in terms of WTL, plant composition and chemical characteristics (Sottocornola et al., 2009). Different vegetation communities support different CO_2 exchange dynamics, and therefore blanket bogs are likely to have different functional responses to other types of ecosystems that have been studied for such effects.

A study completed by Yurova et al. (2007) at a mire in Sweden implied that CO_2 uptake was controlled by interactions between WTL and air temperature. It was noted that higher air temperatures (>15 °C) and a WTL that was neither too low nor too high would result in conditions that were optimal for high NEE. In another study by Lindroth et al. (2007) at four mires at different latitudes in Sweden and Finland, findings were similar, in that WTL and temperature explained most of the variance in NEE. In addition to this, cooler temperatures and longer daylight hours at northerly locations were found to be beneficial for higher NEE during summer.

Previous studies at an Atlantic blanket bog in Glencar, South West Ireland, by Sottocornola and Kiely (2005, 2010a) and Koehler et al. (2011) demonstrated that it is a small sink for direct CO_2 NEE. It was found to have annual carbon and NEE balances similar to boreal raised bogs, but with lower Gross Ecosystem Production (GEP) and Ecosystem Respiration (ER). At the same location, Laine et al. (2009) reported that high water level conditions favoured communities acting as net sources of CO_2 and the wetter the conditions, the lower the ecosystem CO_2 sink.

The current investigation is a continuation of these studies at Glencar involving an extended data set from the same measurement location. Ten years of EC CO_2 flux data were analysed on a seasonal and annual basis to identify the main environmental and/or meteorological drivers responsible for carbon sequestration or emission. The statistical approach developed by Hui et al. (2003) was applied to model the CO_2 exchange, and to look for evidence of any indirect functional contribution to the variance in NEE.

2. Methods

2.1. Site description

The measurement site is an Atlantic Blanket Bog situated near Glencar, County Kerry, South West Ireland (Killorglin-Glencar, IE-Kil in the European Fluxes Database Cluster; Latitude: 51°55′ N, Longitude: 9°55′ W), approximately 150 m above sea level on sandstone bedrock. In the centre of the bog, the upper acrotelm peat layer is mainly sedge peat with a bulk density of 0.05 g cm^{-3} and a porosity of 95%, with peat depths ranging between 2 and 5 m (Lewis et al., 2012). A stream draining the bog with a catchment area of about 74 ha lies to the south, 85% of which is relatively intact blanket bog and 15% of which is on a hill slope that consists of alternating grazed patches of grassland and drained peaty soils (Koehler et al., 2011).

The bog is spatially heterogeneous, consisting of an assortment of microforms that differ in relative elevation, plant composition and water table level (Sottocornola et al., 2009). These were grouped into four categories based on relative elevation: hummocks, high lawns, low lawns and hollows (Laine et al., 2006; Sottocornola et al., 2009). The difference in height between the highest and lowest microforms is typically 20–40 cm. Hollows are 50–300 cm oblong depressions covered by standing water for most of the year. The division of microforms within the EC footprint was estimated as: 6% hummocks, 62% high lawns, 21% low lawns and 11% hollows (Laine et al., 2006).

Vascular plants account for 30% of land coverage during summer (Sottocornola et al., 2009). Of these, the species most commonly encountered are *Molinia caerulea* (L.) Moench (purple moor grass), *Calluna vulgaris* (L.) Hull (common heather), *Erica tetralix* L. (cross-leaved heath), *Narthecium ossifragum* (L.) Huds. (bog asphodel), *Rhynchospora alba* (L.) Vahl. (white beak-sedge), *Eriophorum angustifolium* Honck. (common cotton grass), *Schoenus nigricans* L. (black-top sedge) and *Menyanthes trifoliata* L. (buckbean). Bryophytes are not so widespread, accounting for about 25% of surface cover. The principal species here are *Racomitrium lanuginosum* (Hedw.) Brid. (woolly hair-moss) and bog mosses (*Sphagnum* spp.), both occurring in similar quantities (Sottocornola et al., 2009).

2.2. Instrumentation

Meteorological and environmental parameters were recorded at various levels either above or below ground. Micro-meteorological measurements were all made at a height of 3 m. All instruments were located at a 3 m tower, details of which are outlined in Sottocornola and Kiely (2010a).

The principal meteorological and environmental parameters measured were: net solar radiation (Rn), air and 5 cm depth soil temperatures (T_a and $T_{soil\_5\,cm}$ respectively), relative humidity (Rh), precipitation, water table level (WTL), atmospheric pressure (P_a) and soil heat flux (G). These variables were recorded every minute and then averaged to give 30-min means using a CR23X data logger (Campbell Scientific, UK). Wind speed (WS) and direction (WD) were computed using a sonic anemometer (see below). Also measured at different intervals was the one-sided leaf area index (LAI) using a PAR/LAI Ceptometer (LP-80 AccuPAR, Decagon Devices, Inc., USA).

The micro-meteorological parameters that were measured using a 3-D sonic anemometer included u, v, w (horizontal, lateral and vertical wind speeds respectively) and the speed of sound, in addition to CO_2 and H_2O mass densities from an open path infra red gas analyser (LI7500 IRGA, Li-COR, USA). These variables were recorded at 10 Hz, and the use of a running mean gave 30-min block averaged fluxes. The logging of EC data was with a CR23X until September 2009, after which a CR1000 data logger (both made by Campbell Scientific, UK) has been used continuously.

The 3 m measurement tower was centrally located on the bog with an uninterrupted fetch of at least 300 m radius, which was relatively flat in all directions. A footprint analysis following Hsieh et al. (2000) found that the footprint extended to around 300 m from the tower during unstable daytime conditions, and 750 m during stable night-time conditions.

2.3. Data processing

All data collected was added to a single file that included an entry for every half hour since the beginning of measurements. If no data was available, these entries were left empty and flagged for later gap filling. Data processing and filtering techniques used for the data from this site were very similar to those used previously, details of which can be found in Sottocornola and Kiely (2010a,b) and Koehler et al. (2011). Any variation on these approaches is described in this section. Filtering was mostly a result of the poor performance of the LI-7500 and sonic anemometer during precipitation events, or signal noise originating from very weak signals. The data is now published on the European Fluxes Database Cluster site under the site name of Killorglin-Glencar, IE-Kil (www.europe-fluxdata.eu).

The simplified model developed by Hsieh et al. (2000) was used to estimate the fetch length requirement (x_f) for reaching the 90% constant flux layer during neutral, stable and unstable conditions. Fluxes were discarded if x_f was more than 300 m away, which accounted for the removal of <1% of data based on the findings of Hsieh et al. (2000). Co-ordinate rotations are subject to larger errors as the rotational angle increases, especially when wind speeds are low and turbulence is high, therefore fluxes associated with unrealistic rotated u values were removed. This only accounted for the removal of <0.1% of data when wind speeds were practically zero, typically at night-time.

As a final step, sensible (H) and latent (LE) heat fluxes were filtered based on a fixed linear fit with net radiation (R_n), from which a fixed cut-off value above and below the line of fit was predetermined. Cut-off values were 75 W m^{-2} for upper and lower H as well as upper LE, whereas the lower cut-off for LE was 60 W m^{-2}. Removal of H and LE in this way provided an unbiased approach for data removal throughout all the seasons, and most removal occurred during periods when R_n, and hence energy transfer, was ≈0. In both cases, this method accounted for less than 4% of overall filtering. The amount of good H values remaining after filtering ranged between 58% (2011) and 80% (2004), whereas for LE it was between 53% (2009) and 78% (2004).

Similar filters were used for CO_2 flux data using a predetermined fixed fit. For daytime fluxes, an exponential fit with Q_{PAR} was used, whereas a linear fit with $T_{soil\_5\,cm}$ was used for night-time data. Alternatively, incoming solar radiation or T_a could have been used to give a nearly identical outcome.

Daytime data were filtered in two stages: first using non density corrected CO_2 fluxes to account for poor measurements, and then using density corrected fluxes to account for poor corrections, which were mostly over corrections (Webb et al., 1980). For non-corrected data, the upper cut-off was 7 μmol m^{-2} s^{-1} and the lower was 5 μmol m^{-2} s^{-1}. For corrected fluxes, upper and lower cut-offs ranged from 1.5 μmol m^{-2} s^{-1} to 4.5 μmol m^{-2} s^{-1} depending on the season. Removal in this way mainly accounted for periods when incoming solar radiation was near zero, resulting in a noisy CO_2 flux signal that had to be filtered.

Night-time data were filtered using only an upper cut-off of 0.5 μmol m^{-2} s^{-1}. Spurious results occurred across the whole temperature range due to the limitations of the EC method to measure accurately at night (Aubinet, 2008). No u_* filter was applied because no clear correlation between flux magnitude and u_* was apparent. The amount of good daytime fluxes remaining after filtering ranged from 44% (2009) to 68% (2004), whereas it ranged from 21% (2009) to 35% (2007) for night-time data.

The gap filling techniques used for LE, H and night-time CO_2 fluxes were similar to those described in Sottocornola and Kiely (2010a, b). Daytime CO_2 fluxes were filled by relating the CO_2 flux to Q_{PAR} using the Misterlich formula, defined as:

$$F_{c(\mathrm{day})} = -24[1 - e^{(\alpha \cdot Q_{PAR}/-24)}] + \gamma, \tag{1}$$

where α is the ecosystem quantum yield and γ is the daily respiration. Gap filling for daytime CO_2 fluxes was performed using a moving window of 5 days on either side of each day. This approach helped to ensure smooth seasonal transitions and more accurate curve fitting. Gap filling for all other fluxes used a fixed window covering the entire period of measurements. The uncertainty of NEE was estimated following Aurela et al. (2002) and Sottocornola and Kiely (2010a).

The partitioning of net ecosystem CO_2 exchange along with the separate study of ecosystem respiration and gross ecosystem production are necessary in order to evaluate the sensitivity of ecosystems to climate change (Barr et al., 2007; Dunn et al., 2007). To calculate ER, the Lloyd and Taylor (1994) exponential regression was used to model the daytime ER by considering night-time NEE to be ecosystem respiration, and applying a night-time derived ER model to daytime, assuming that the temperature dependence is the same during day and night (Reichstein et al., 2005). To calculate GEP, the following equation was used:

$$\mathrm{GEP} = \mathrm{ER} - \mathrm{NEE} \tag{2}$$

The start and the end of the growing seasons were estimated as the first and last three consecutive days with a cumulative GEP > 3 gC-CO_2 m^{-2}.

3. CO_2 flux modelling

In order to determine which meteorological parameters control CO_2 fluxes, the totals or averages of seven preliminary variables were taken into consideration, including Q_{PAR}, WTL, Rh, T_a, $T_{soil\_5\,cm}$, Pa and WS, although Q_{PAR} was not included for night-time analysis (see Table 1). Weekly and annual totals of separate night-time and daytime NEE were used for modelling, which contained no gap filled data and covered only the period from May until September of each year. Weekly totals used the complete data set from

Table 1
Comparison of correlation coefficient analysis methods to find most suitable controls for MLR modelling. Method 1 considers variable interactions, whereas method 2 considers variables individually. Variables are listed according to their importance in controlling CO_2 fluxes for each method. The max r^2 values indicate the maximum correlation possible using all the listed variables together, n defines the number of observations used for the models. $T_{soil\_5\,cm}$ = soil temperature, T_a = air temperature, Q_{PAR} = photosynthetically active radiation, Rh = relative humidity, WS = wind speed, WTL = water table level, P_a = air pressure.

DAYTIME WEEKLY (Max r^2=0.81; n=216)

	Method 1		Method 2	
1	T_{soil_5cm}	0.66	T_{soil_5cm}	0.66
2	Q_{PAR}	0.78	T_a	0.66
3	Rh	0.81	Q_{PAR}	0.79
4	WS		WS	
5	T_a		P_a	
6	WTL		WTL	
7	P_a		Rh	

DAYTIME ANNUAL (Max r^2=1.00; n=9)

	Method 1		Method 2	
1	WTL	0.52	Q_{PAR}	0.73
2	T_{soil_5cm}	0.60	WTL	0.74
3	T_a	0.83	P_a	0.79
4	Rh	0.98	T_{soil_5cm}	0.81
5	WS	1.00	WS	0.83
6	Q_{PAR}		T_a	
7	P_a		Rh	

NIGHT-TIME WEEKLY (Max r^2=0.69; n=216)

	Method 1		Method 2	
1	WTL	0.45	T_{soil_5cm}	0.60
2	T_{soil_5cm}	0.67	T_a	0.60
3	WS	0.68	WTL	0.67
4	T_a	0.69	WS	
5	Rh		P_a	
6	P_a		Rh	

NIGHT-TIME ANNUAL (Max r^2=0.98; n=9)

	Method 1		Method 2	
1	WTL	0.89	WTL	0.89
2	T_a	0.95	T_a	0.95
3	WS	0.96	WS	0.96
4	T_{soil_5cm}	0.98	T_{soil_5cm}	0.98
5	Rh		P_a	
6	P_a		Rh	

September 2002 until September 2012, whereas annual totals used only the complete calendar years of 2003–2011.

3.1. Choosing modelling variables

Before deciding which variables to include in the model, a simple regression analysis was conducted to see whether or not a linear model would be sufficient to describe the variation of NEE against the various meteorological variables. After trying quadratic, cubic and exponential fits, only WTL was better described using a non-linear relationship, but not significantly so, and therefore linear equations were used for the homogeneity of slopes (HOS) analysis. Standardised precipitation frequency was also considered (as in Sottocornola and Kiely, 2010a), but it was not found to greatly enhance results when compared to WTL or actual precipitation.

Two different methods were compared to determine which meteorological variables were most relevant for modelling (see Table 1). Method 1 involved combining all the variables in a multiple linear regression (MLR) model and then eliminating the variables from the model one by one until a decrease in the r^2 value of more than 0.01 was detected. Thus, this approach removed the variables that were least important to achieving maximum correlation against the observed values. Method 2 was a simple correlation coefficient analysis (as in Sottocornola and Kiely, 2010a) between measured CO_2 fluxes and each of the meteorological variables on an individual basis; this was followed by adding each variable that had the greatest individual correlation to the MLR model until the r^2 value between the measured and modelled data improved by no more than 0.01. Method 1 was chosen for further analysis because it optimises modelling by taking any interaction or co-linearity between variables into consideration. The results of this analysis for daytime and night-time fluxes are shown in Table 1, which lists the variables numerically according to their importance towards achieving maximum correlation for each method.

For weekly daytime NEE, $T_{soil\_5\,cm}$, Q_{PAR} and Rh were the only three variables needed to achieve the maximum possible r^2 value of 0.81 using all the variables listed (see Table 1). For weekly night-time values, WTL, $T_{soil\_5\,cm}$, WS and T_a were all needed to give the maximum r^2 value of 0.69. Maximum r^2 values approached 1 on an annual basis for both day and night, but more variables were needed to achieve the maximum than for weekly totals. In the case of night-time annual values, both methods for determining which variables to use for modelling gave the same output.

Co-linearity was present to a varying degree between T_a and $T_{soil\_5\,cm}$ for all the models. The daytime weekly model exhibited the maximum co-linearity between these variables, with an r^2 value of 0.88. The inclusion of either variable would have produced similar models, however the use of method 1 determined that the inclusion of $T_{soil\_5\,cm}$ was more important to achieve maximum correlation. For the weekly night-time model, the r^2 value was 0.85 using either T_a or $T_{soil\_5\,cm}$. The inclusion of T_a in this case did not considerably improve correlation with the measured data (r^2 = 0.68 compared to 0.67), but was included in order to adhere to the selection criteria for maximum possible correlation. In the cases of annual daytime and night-time models, the r^2 values between T_a and T_{soil} were 0.61 and 0.55 respectively, and so co-linearity was not an issue (O'Brien, 2007). The exclusion of Q_{PAR} from the daytime annual MLR model was not due to co-linearity with any of the included variables (r^2 with T_{air} was 0.42), indicating that Q_{PAR} is not an important influence on long-term CO_2 exchange.

3.2. Homogeneity of slopes model

Once variables for modelling were identified using method 1, the multiple linear regression operator in Matlab (Mathworks Inc., USA) was utilised to determine the coefficients for each meteorological variable based on their combined influence over the period of measurements. These coefficients were multiplied by their corresponding variable and used as an input (X) to determine the modelled NEE values ($\hat{Y}$) in the relationship with the measured NEE values (Y). The homogeneity of slopes (HOS) model was used to detect the presence (if any) of functional responses in NEE. The HOS model is a multiple linear regression model, but considers the interaction of meteorological variables and the year:

$$\hat{Y}_{ij} = \sum_{k=1}^{n} m_k X_{ijk} + \sum_{k=1}^{n} m_{ik} X_{ijk} + c + e_{ij}, \tag{3}$$

where i is the ith year, j is the jth week, k is the kth meteorological variable, m is the gradient, c is the intercept and e_{ij} is the random error associated with the measured values of Y_{ij}. To find out if functional responses were present, a test of the null hypothesis (H_0: $m_{ik} = 0$) across all years as opposed to H_1 ($H_1: m_{ik} \neq 0$) for any of the years was conducted (Hui et al., 2003). If H_1 is tested first, the *single slope model* is attained from the HOS model, which is a simplified version of Eq. (3):

$$\hat{Y}_{ij} = \sum_{k=1}^{n} m_k X_{ijk} + c + e_{ij} \tag{4}$$

The null hypothesis (H_0) assumes that there is a functional response, and so the *separate slopes model* is the result:

$$\hat{Y}'_{ij} = \sum_{k=1}^{n} m_{ik} X_{ijk} + c + e_{ij} \tag{5}$$

These models do as their names suggest, and give a single slope across all years, or separate slopes for each year. If the slopes vary among years, functional responses must be occurring, where the difference between Eqs. (4) and (5) is caused by the functional response. The separate slopes model was only used with weekly NEE totals.

On detecting functional response, the observed NEE can be partitioned into four components, which can be statistically represented by partitioning the sum of squares (SS) of the total deviation (SS_T):

$$SS_T = SS_f + SS_e + SS_{im} + SS_{wm} \tag{6}$$

These components represent indirect functional response (SS_f), random error (SS_e), direct interannual meteorological variability (SS_{im}) and direct week to week meteorological variability (SS_{wm}).

$$SS_f = \sum_{i=1}^{y} \sum_{j=1}^{n} (\hat{Y}'_{ij} - \hat{Y}_{ij})^2 \tag{7}$$

$$SS_e = \sum_{i=1}^{y} \sum_{j=1}^{n} (Y - \hat{Y}_{ij})^2 \tag{8}$$

To estimate SS_{im} and SS_{wm}, the comparison of values in a given year with the values at a similar point in other years gives a measure of temporal variability within an ecosystem (Teal and Howes, 1996). Modelled values of NEE at a point in the annual cycle were compared with other years, which would indicate differences caused by meteorological variability (SS_{im}), whereas differences between mean values of weekly modelled NEE and the mean of all modelled NEE values would be due to week to week differences (SS_{wm}).

$$SS_{im} = \sum_{i=1}^{y} \sum_{j=1}^{n} (\hat{Y}_{ij} - \hat{Y}_j)^2 \tag{9}$$

$$SS_{wm} = \sum_{i=1}^{y} \sum_{j=1}^{n} (\bar{Y}_j - \bar{Y})^2, \tag{10}$$

where $\bar{Y}$ is the mean of all NEE estimates and $\bar{Y}_j$ is the estimated NEE across all years on the jth week. If a functional response is not detected from the HOS model then SS_f is not included in SS_T. The contribution of these components expressed as a percentage of the total was then derived.

4. Results

The ten complete years of measurements between September 2002 and August 2012 in Glencar were characterised by a wide range of environmental conditions (see Figs. 1 and 2, and Table 2). These years have seen some of the warmest months coupled with the wettest months and years, as well as some of the coldest winters on Met Eireann's national archives (http://www.met.ie/climate-ireland/rainfall.asp; http://www.met.ie/climate-ireland/surface-temperature.asp).

Summer 2006 experienced the highest average seasonal temperatures (16.4 °C), as well as the highest half hourly temperature recorded in Glencar (27.9 °C). During the winters of 2009/2010 and 2010/2011, temperatures across the British Isles dropped to record lows, with half hour average temperatures as low as −11.1 °C measured in Glencar during December 2010, in what was the second coldest Irish winter on record between 1961 and 2010 according to the Irish National Meteorological Service (Met Eireann) records. Monthly values of T_a at Glencar ranged from 3 °C (December 2010) to 16 °C (July 2006). Annual T_a values were lowest in 2010 at 9.8 °C

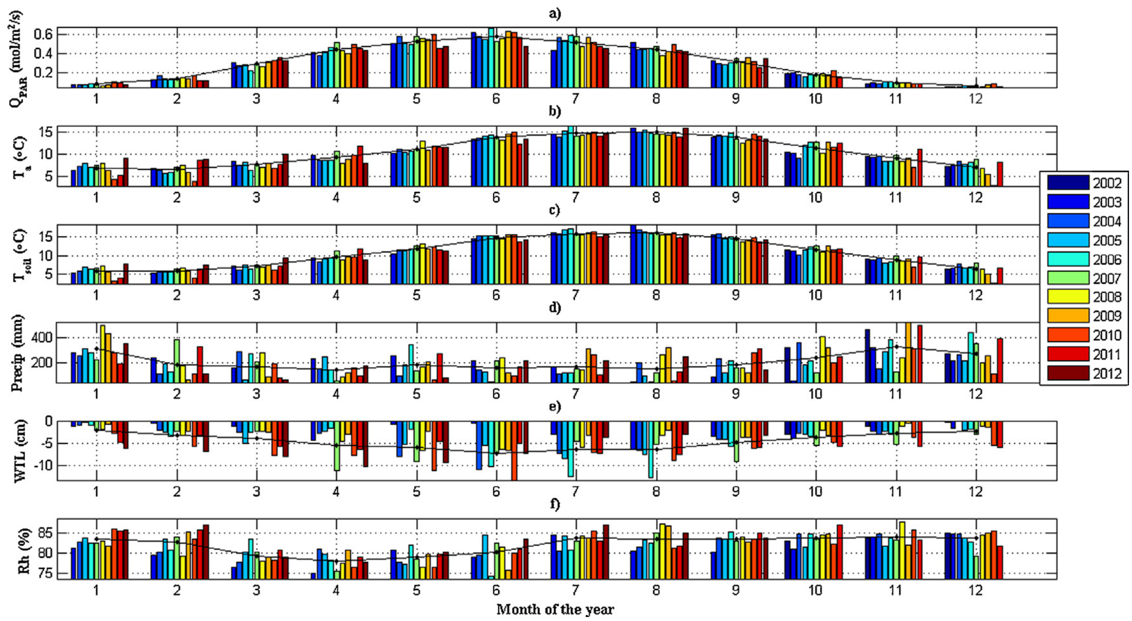

Fig. 1. Monthly values for meteorological variables across all years: (a) total Q_{PAR}, (b) average air temperature, (c) average soil temperature at 5 cm depth, (d) total precipitation, (e) average water table level, and (f) average relative humidity. The dots on the black lines represent the average for each month across all years.

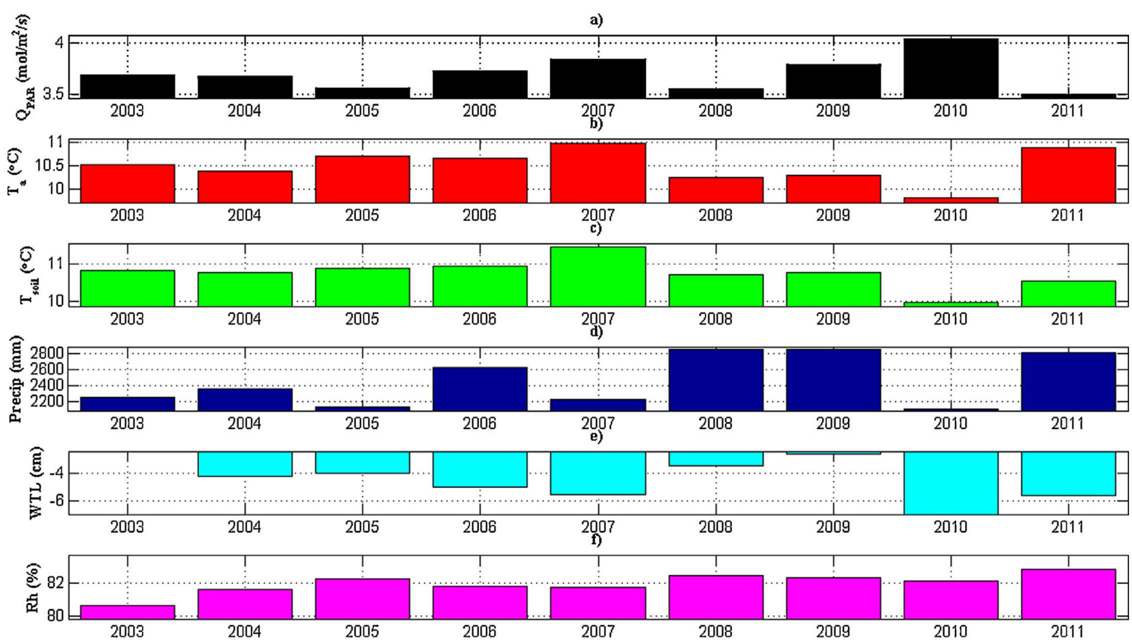

Fig. 2. Annual values for meteorological variables during each year of measurements: (a) total Q_{PAR}, (b) average air temperature, (c) average soil temperature at 5 cm depth, (d) total precipitation, (e) average water table level, and (f) average relative humidity.

Table 2
Annual sums or averages (see Section 4) for each year for various meteorological and CO_2 exchange variables. Q_{PAR} = photosynthetically active radiation, T_a = air temperature, $T_{soil\_5\,cm}$ = soil temperature at 5 cm depth, Precip = precipitation, WTL = water table level, Rh = relative humidity, NEE = net ecosystem CO_2 exchange, GEP = gross ecosystem production, ER = ecosystem respiration.

	2003	2004	2005	2006	2007	2008	2009	2010	2011
Q_{PAR} (μmol m^{-2} s^{-1})	3.68	3.67	3.55	3.73	3.84	3.54	3.79	4.04	3.49
T_a (°C)	10.51	10.38	10.70	10.66	10.97	10.25	10.30	9.82	10.88
$T_{soil\_5\,cm}$ (°C)	10.84	10.77	10.89	10.95	11.46	10.71	10.78	9.97	10.55
Precip (mm)	2254.2	2355.6	2134.9	2617.5	2229.9	2843.1	2854.4	2106.1	2810.5
WTL (cm)	−2.42	−4.20	−4.01	−4.99	−5.50	−3.50	−2.63	−7.01	−5.63
Rh (%)	80.65	81.62	82.25	81.82	81.73	82.41	82.32	82.08	82.84
NEE (gC-CO_2/m^2)	−67.9	−75.9	−79.2	−32.3	−32.1	−57.4	−59.3	−42.9	−54.2
ER (gC-CO_2/m^2)	236.0	233.6	234.7	236.5	244.8	227.4	231.3	220.8	223.1
GEP (gC-CO_2/m^2)	303.8	309.4	313.9	268.8	276.9	284.8	290.6	263.7	277.3

and highest in 2007 at 11 °C, with an overall annual average of 10.5 °C.

The three wettest years occurred during 2008, 2009 and 2011, after data from Glencar were last reported by Sottocornola and Kiely (2010a,b). Summers were generally drier than winters, although August 2008 had the greatest amount of rainfall recorded in a single half hour, amounting to nearly 14 mm. Seasonal precipitation variance was quite high, whereby monthly values ranged from 42 mm (August 2003) to 520 mm (November 2009), the latter of which resulted in widespread flooding nationwide. 2009 was the wettest year with 2854 mm of rainfall, whereas 2010 was the driest at 2106 mm, with an overall ten-year average of 2467 mm. 2009 was also the wettest year on record nationally for the period 1941–2010 according to Met Eireann records.

The WTL follows a similar seasonal and annual pattern to that of precipitation, whereby the WTL is generally higher (i.e., closer to the surface) in winter than summer. The IAV in WTL was relatively high, with one of the highest annual mean levels in 2009 (−2.6 cm) to the lowest in 2010 (−7.0 cm). Rh was typically lowest on average during the spring and early summer months, showing minimal IAV, being lowest during 2003 (81%), but highest in 2011 (83%). LE during 2011 and 2004 were the highest recorded over the ten years, averaging at 32.5 and 32.9 W m^{-2}, respectively. 2003 was the opposite having one of the highest WTL, yet one of the lowest Rh. Monthly WTL varied from −13 cm to 0 cm and monthly Rh from 74% to 88%.

Monthly and annual totals or averages of the seven meteorological variables considered the most important for long- and short-term CO_2 exchange control are displayed in Figs. 1 and 2, as well as Table 2. Totals (for Q_{PAR} and precipitation) and averages (all other meteorological variables) for each month of each year were calculated along with monthly averages across all years. Data from the complete years of 2003–2011 are presented as annual values in Fig. 2 and Table 2.

Cumulative values for NEE, GEP and ER indicate that on an annual basis the Glencar peatland acted as a net sink of direct CO_2 NEE throughout the entire period of measurements, ranging between −80 gC-CO_2 m^{-2} (grams of carbon as CO_2) in 2005 and −32 gC-CO_2 m^{-2} in 2007, with an overall annual average of -55.7 ± 18.9 gC-CO_2 m^{-2} (Fig. 3).

ER and GEP were highest during the summer months, with GEP displaying a larger seasonal variation (Fig. 4). Monthly ER values ranged between 6.7 gC-CO_2 m^{-2} (December 2010) to 38 gC-CO_2 m^{-2} (August 2003). Monthly GEP values ranged between 3.2 gC-CO_2 m^{-2} (December 2009) to 63.7 gC-CO_2 m^{-2} (July 2005). On an annual basis, ER was highest during 2007 and GEP during 2005 (Fig. 4). The start of the growing season varied between the 23rd April in 2004 and 27th May in 2010, while the end of the growing season ranged between the 15th September in 2011 and 5th October in 2005.

The outcome of modelling for NEE_{night} is shown in Fig. 5. Fig. 5a shows the weekly single slope and separate slopes models (from Eqs. (4) and (5) respectively), which were described using the following equations:

$$(\hat{Y}_{ij})_{nw} = 0.47(X) + 0.66 \tag{11}$$

$$(\hat{Y}'_{ij})_{nw} = 0.7(X) + 0.37, \tag{12}$$

where the variables used for X were T_a, $T_{soil\_5\,cm}$, WTL and wind speed (WS). Subscripts n and w denote night-time and weekly respectively. Fig. 5b shows the annual night-time model, which was described using the following equation:

$$\hat{Y}_{na} = 0.95(X) + 1.09, \tag{13}$$

where the variables used for X were T_a, $T_{soil\_5\,cm}$, WTL and WS. Subscript a denotes annual.

Table 3
Percentage of each component responsible for the variation in daytime NEE (net ecosystem CO_2 exchange) and night-time ER (ecosystem respiration). SS_f, SS_e, SS_{im} and SS_{wm} are the sum of squares of deviation that can be explained by the functional response, random error, direct interannual meteorological variability, and direct week to week meteorological variability, respectively.

	SS_f	SS_e	SS_{im}	SS_{wm}
Daytime NEE (%)	13.75	21.40	36.62	28.23
Night-time ER (%)	23.37	30.04	24.42	22.18

The outcome of modelling for NEE_{day} is shown in Fig. 6. Fig. 6a shows the weekly single slope and separate slopes models (from Eqs. (4) and (5) respectively), which were described using the following equations:

$$(\hat{Y}_{ij})_{dw} = 0.65(X) - 1.41 \tag{14}$$

$$(\hat{Y}'_{ij})_{dw} = 0.79(X) - 0.86, \tag{15}$$

where the variables used for X were Q_{PAR}, Rh and $T_{soil\_5\,cm}$. Subscripts d and w denote daytime and weekly respectively. Fig. 6b shows the annual daytime model, which was described using the following equation:

$$\hat{Y}_{da} = (X) - 0.32, \tag{16}$$

where the variables used for X were Rh, T_a, $T_{soil\_5\,cm}$, WTL and WS. Subscript a denotes annual.

The partitioning of the contribution of NEE_{day} and NEE_{night} into meteorological variation and functional response produced the following results (Table 3). The functional response contribution for NEE_{night} was higher than daytime, at over 23.4% compared to only 13.8% for NEE_{day}. The random error accounts for 30% of NEE_{night}, whereas random error was 21.4% for NEE_{day}. The direct interannual variations in meteorological drivers contributed to 36.6% of NEE_{day}, but only 24.4% of NEE_{night}. The week to week changes were lower than year to year at 28.2% for NEE_{day} and 22.2% for NEE_{night}, but still significant in both cases.

The leaf area index (LAI) data was measured at infrequent intervals over the Glencar bog between 2005 and 2008 to enable investigation of ecosystem functioning. Because data were quite sparse, a cubic polynomial was fitted to the data for the purposes of visualisation (thus, this curves are only indicative of the LAI development during the growing season). The LAI varies between 0.15 and 0.65 m^2 m^{-2} between day 120 and 300 of each year (Fig. 7a). The maximum LAI measured was 0.72 m^2 m^{-2} (2005) and the minimum was 0.18 m^2 m^{-2} (2008). To determine if there was any correspondence between LAI and NEE_{day}, the cumulative NEE_{day} curves during the growing season (May–September) for weekly averages both measured (non-gapfilled) and modelled (using separate slopes model) data are shown in Fig. 7b, which vary from −75 to −100 gC-CO_2 m^{-2}.

5. Discussion

From the meteorological data, precipitation had a high degree of IAV compared to the other variables, with, 2009 the wettest, and 2010 the driest year. The WTL followed a similar, but not identical pattern to precipitation, most likely due to the other factors that can affect it, such as ET (evapotranspiration) and surface runoff. Although precipitation levels were high during 2011, a low WTL during 2011 may have been a result of high T_a with corresponding high evapotranspiration.

The start of growing season occurred between the end of April (2004) and the end of May (2008, 2009 and 2010), while the end of the growing season occurred towards the end of September and the beginning of October for all years (not shown). This corresponds well with the ecosystem net CO_2 uptake period, highlighted by the

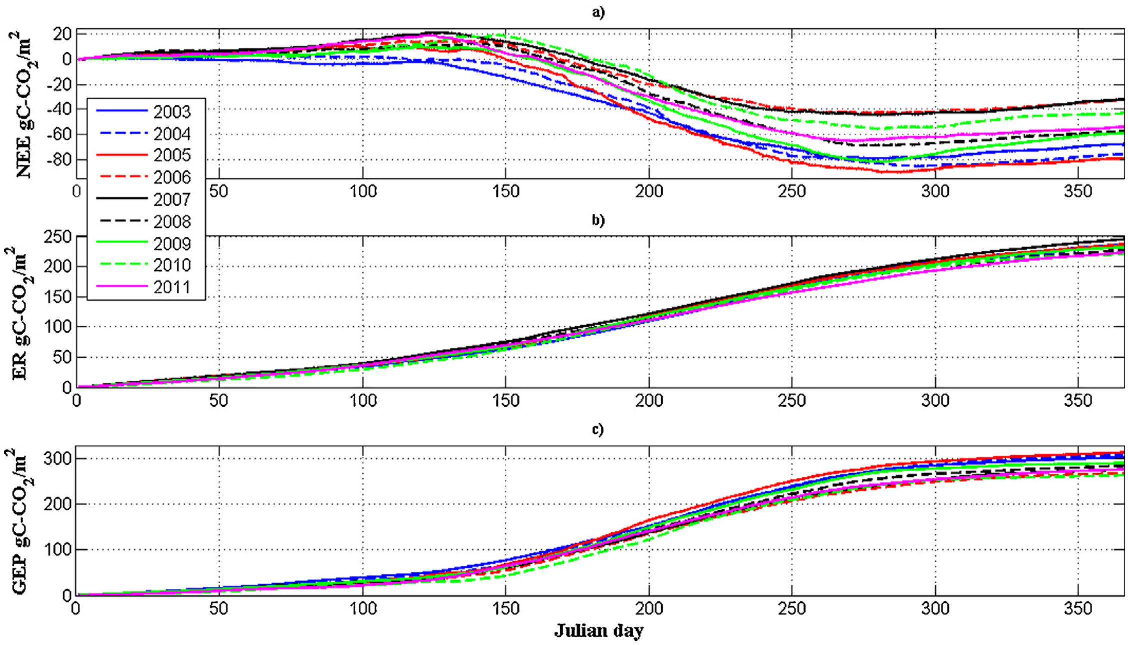

Fig. 3. Annual cumulative values for each CO_2 flux component. These curves represent consecutive half hour periods, whereby the values at the end of each curve are equivalent to the annual total values for each component: (a) NEE (net ecosystem exchange), (b) ER (ecosystem respiration), and (c) GEP (gross ecosystem production).

inflections in the NEE cumulative curves. The differences in annual NEE are mainly a result of how much growth occurs during the growing season period, which depends on how early it begins and how long it lasts (Fig. 3a).

The IAV of monthly NEE totals was greatest during May and July, whereas fluxes between November and February were less variable (Fig. 4). The lower water table years of 2006, 2007, 2010 and 2011 (see Fig. 2) coincided with the lowest uptake values (see Table 2), confirming that ground surface wetness has a significant influence upon the IAV of NEE (Sottocornola and Kiely, 2010a,b). This seems to be due to the correlation between WTL and both GEP and ER. Low WTL in 2006, 2007, 2010 and 2011 are associated with low GEP values, as found in other bog ecosystems with little shrub cover (Sulman et al., 2010), most likely due to the important role of the bryophytes in these ecosystems (Sottocornola and Kiely, 2010a,b; Wu et al., 2013). WTL also appears to have a strong negative correlation with NEE_{night}, and therefore ER (see Tables 1 and 2), as found in some other (Bubier et al., 2003b) but not all peatlands (Lafleur et al., 2005; Lund et al., 2010). The connection between WTL and ER is still largely unclear (Frolking et al., 2011), probably due to the dual nature of respiration, autotrophic and heterotrophic, which respond to different drivers (Yurova et al., 2007). The effect of WTL on NEE is not so obvious in the seasonal data, but it seems that the dry summer of 2006 and spring of 2007 might have affected uptake

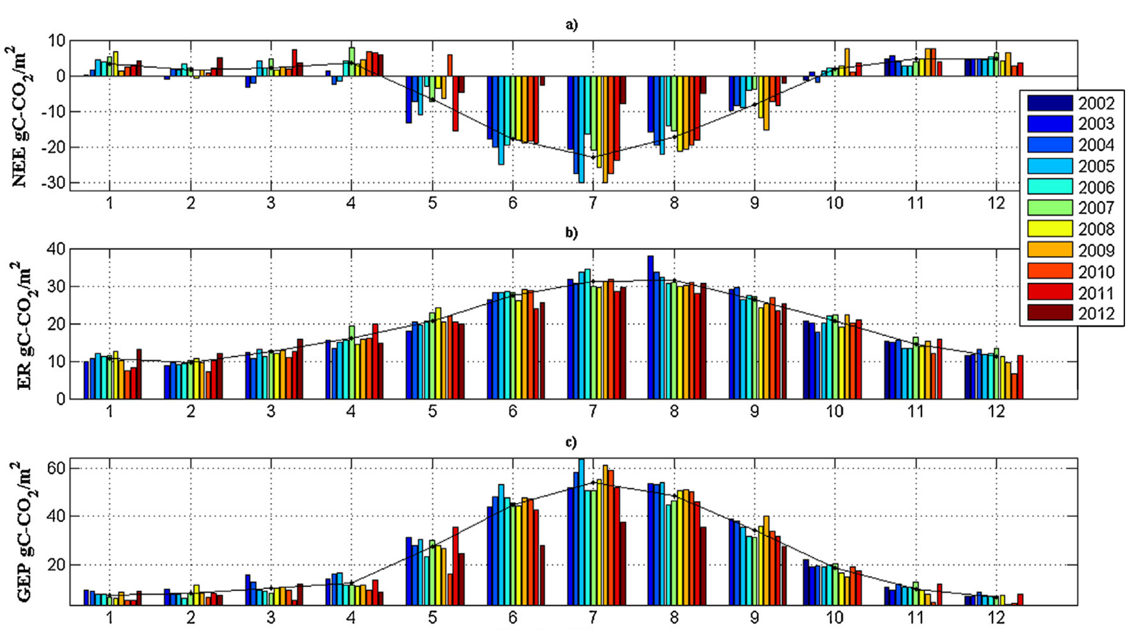

Fig. 4. Monthly sums of CO_2 flux components across all years: (a) NEE (net ecosystem exchange), (b) ER (ecosystem respiration), and (c) GEP (gross ecosystem production). The black dots joined by solid lines represent averages for each month across all years (2003–2011).

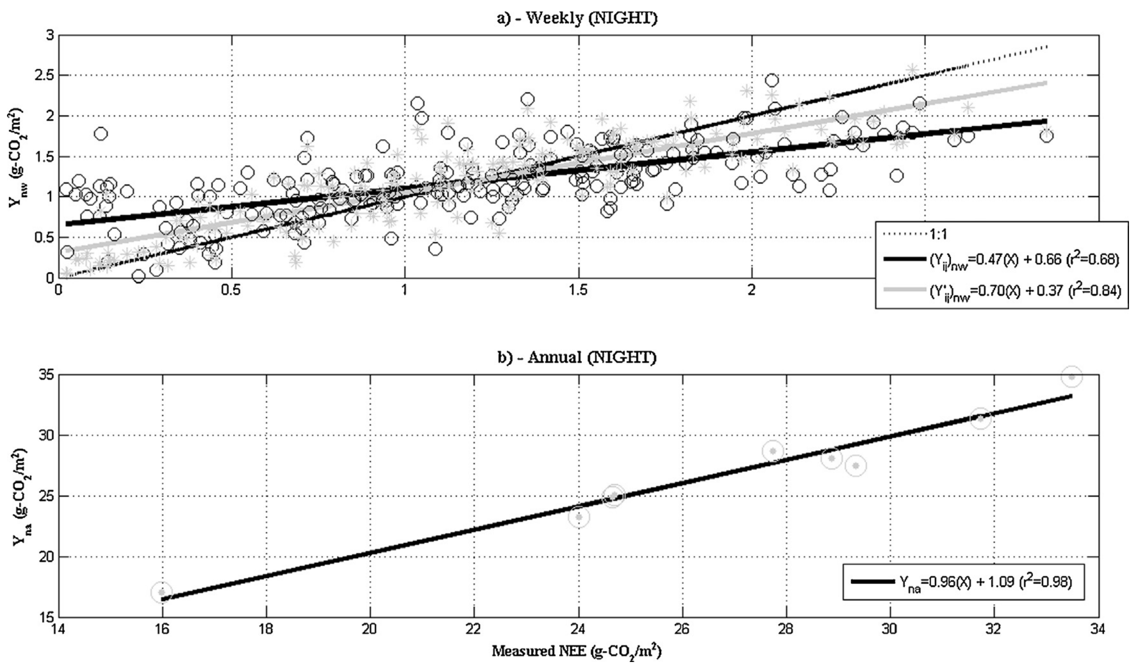

Fig. 5. Models for night-time ER (ecosystem respiration) for (a) weekly totals (n = 216) for separate slopes model (grey) and single slope model (black). The black solid line represents a theoretical 1:1 relationship. (b) annual totals (n = 9).

during the growing seasons of 2007 and 2008 (Figs. 1 and 4), indicating a possible lag effect of dry periods on NEE (van der Molen et al., 2011).

Net emission of CO_2 to the atmosphere (positive NEE values) across all years generally occurred between October and April. The peatland ecosystem behaved as a net sink during the growing season, and only during the very dry month of May 2010 did the bog act as a net source throughout all growing seasons. These observations are in keeping with the findings of Laine et al. (2009).

Over the 10 years of measurements, the average annual uptake of -55.7 ± 18.9 gC-CO_2 m^{-2} for NEE of atmospheric CO_2 at Glencar was similar to findings at other peatland sites. From two years of measurements, the Stordalen palsa mire (a nutrient poor permafrost peatland) in Sweden was found to be a net sink of carbon, with an average annual uptake of -46 gC-CO_2 m^{-2} per year (Olefeldt et al., 2012). Using two years of data, Nilsson et al. (2008) found that a boreal minerogenic oligotrophic mire in northern Sweden was also a net annual sink of -55 gC-CO_2 m^{-2}. At the

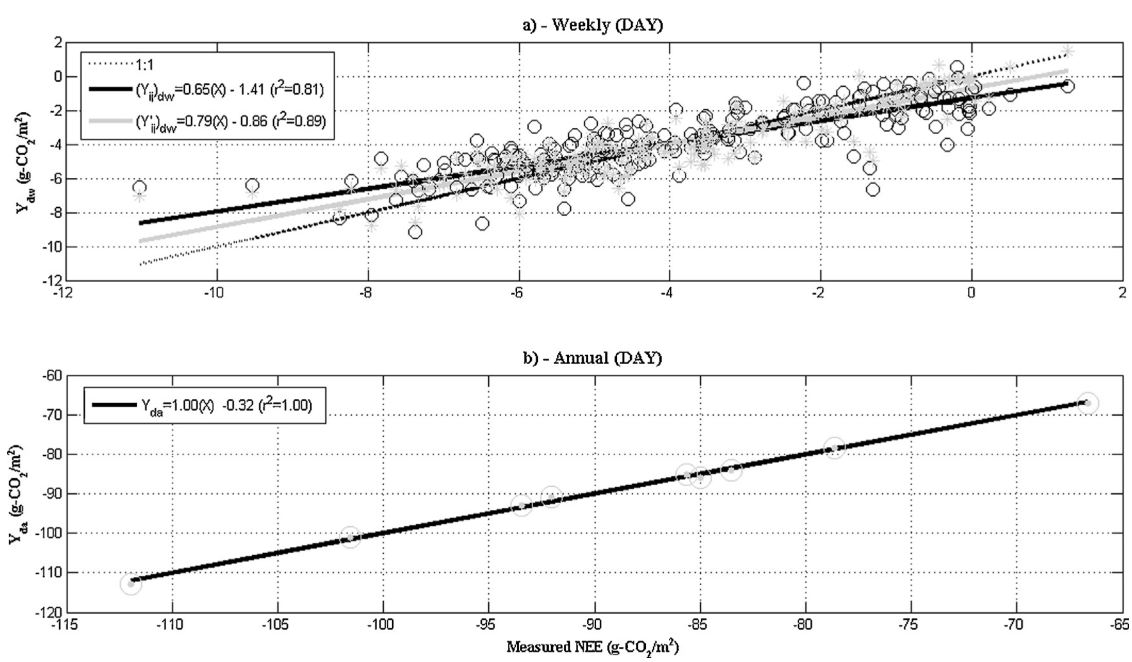

Fig. 6. Models for daytime NEE (net ecosystem exchange) for (a) weekly sums (n = 216) for separate slopes (grey) and single slope model (black). The black solid line represents a theoretical 1:1 relationship. (b) Annual totals (n = 9).

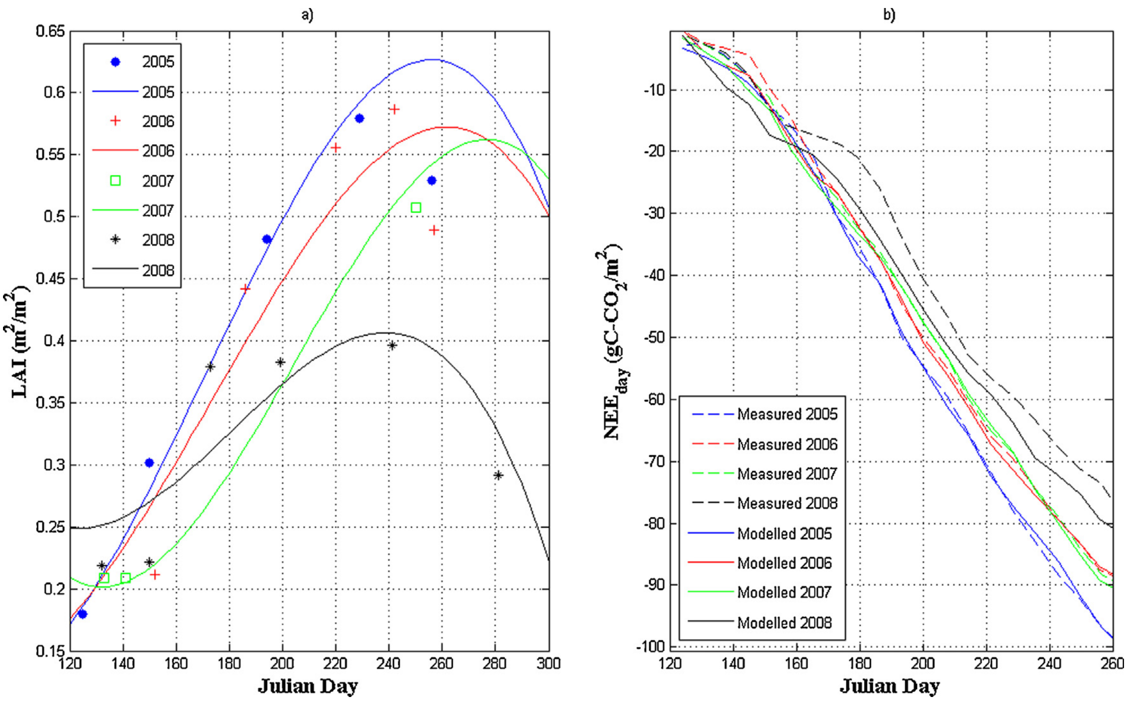

Fig. 7. (a) LAI (leaf area index) data measured in Glencar between Julian days 120 and 300 for 2005–2008, with a cumulative polynomial fit for each year. (b) Cumulative NEE_{day} values for real NEE_{day} data and the separate slopes modelled data. These curves represent consecutive weekly averages between 2005 and 2008, whereby the values at the end of each curve are equivalent to the total for the growing season (May–September).

same location, a separate study by Sagerfors et al. (2008) found the mire to be an annual net sink of −55 gC-CO_2 m^{-2} following three years of continuous EC measurements. The annual NEE average in a northern aapa mire at Kaamanen, Finland was reported to be of −22 gC-CO_2 m^{-2} over a 6-year period (Aurela et al., 2004). Auchencorth Moss, an ombrotrophic peatland with light grazing in southern Scotland, was also found to be a net sink after two years of measurements, with an average annual uptake of −69.5 gC-CO_2 m^{-2} (Dinsmore et al., 2010). Mean NEE values computed by Roulet et al. (2007) using a data set of six years showed that the Mer Bleue ombrotrophic raised bog in Ontario, Canada, was on average a net annual sink for NEE of −40.2 gC-CO_2 m^{-2}.

Using the 10 years of continuous flux and meteorological data available to us, it was possible to model NEE at the Glencar peatland to a reasonable degree of accuracy, with correlation coefficients as high as 1 (Fig. 6b). The use of method 1 correlation coefficient analysis to determine modelling variables proved to be effective in reducing the number of variables needed and to avoid co-linearity (Table 1). The key parameters that emerged for modelling were not surprising, seeing as soil (Lafleur et al., 2005; Lloyd and Taylor, 1994) and air (Lindroth et al., 2007; Lund et al., 2010) temperatures are linked to ER, a high WTL reduces ER (Bubier et al., 2003a; Laine et al., 2009), and Q_{PAR} (Lindroth et al., 2007) along with water vapour (Rh) are essential for photosynthesis. The inclusion of wind speed in all models to give increased accuracy in Table 1 implied a possible draining effect of CO_2 from the peat, similar to findings by Aurela et al. (2002) and Lai et al. (2012). To model day and night-time weekly CO_2 fluxes, the single slope (Eq. (4)) and separate slopes (Eq. (5)) models were both used. If there is a difference in their fits to the measured data, then functional responses can be said to have occurred.

The weekly single slope and separate slopes models for NEE_{night} clearly have a different fit (i.e., $m_{ik} \neq 0$, Fig. 5a, Eqs. (11) and (12)). The single slope model gave an r^2 value of 0.68, but the separate slopes model improved the fit, having an r^2 value of 0.84, therefore functional responses contributed to NEE_{night}. The fit on an annual timescale for NEE_{night} (Fig. 5b) is much better than for weekly totals, again suggesting that long-term changes and responses are important. WTL is the main control for NEE_{night} on an annual time-scale (Table 1), which confirms the correlation found between annual ER and WTL by Sottocornola and Kiely (2010a) at the same site, and is therefore likely to be the main functional control.

Findings were similar for NEE_{day} in that the fit of the single and separate slopes models were different (i.e., $m_{ik} \neq 0$, Fig. 6a, Eqs. (14) and (15)). Once again the separate slopes model improved r^2, giving a value of 0.89 compared to 0.81, and therefore functional responses must also have contributed to NEE_{day}. However, seeing as the fit is not as good an improvement compared to the night-time values, functional processes are likely to not be as significant. The fit on an annual basis is also better (Fig. 6b), again suggesting that long-term processes are influential. WTL appears to be the crucial functional variable on an annual time-scale also for NEE_{day} (Table 1).

Keeping random error in mind, the results indicate that direct interannual meteorological variability was the main contributor to variance for both day and night-time NEE (Table 3). IAV in NEE_{night} is explained almost equally by direct and indirect drivers, whilst IAV in NEE_{day} is three times more by direct than indirect. This higher functional contribution to NEE_{night} was expected from the greater improvement in correlation with measured data that the separate slopes model provided (Fig. 5a). Random error was high for NEE_{night} as expected due to the limitations of the EC technique to measure night fluxes accurately.

Besides indicating a different start of the growing season, the LAI curves from the Glencar bog in Fig. 7a give a quantitative representation of functional responses, such as a change in vascular plant cover from one year to the other. These responses are indicated by various features of the curves, such as the maximum values, or the integrated area underneath. A high LAI gradient early in the growing season should lead to higher productivity later on, and therefore give a higher total NEE overall, in which case 2005 would be expected to have the highest and 2008 the lowest. The cumulative curves for the measured data in Fig. 7b show that this was the case, and are in good agreement with those of the separate slopes model cumulative curves. This therefore verifies that the separate slopes model was able to account for functional responses in the community on an annual basis, yielding reliable predictions and estimates of functional contribution to variance in measured NEE at Glencar.

These values in Table 3 are relative, and so can be directly compared with similar figures from other sites. The functional contribution to variance is the average variance of the separate and single slope models from each other, the inter-annual and direct week to week meteorological variability contributions are the average variances of the single slope model from their respective means, whereas random error is the mean variance of the separate slopes model values from the measured values. Because the models were derived using meteorological variables, the direct contribution findings can be interpreted as variance in the relevant meteorological and environmental variables themselves.

Functional responses in the Mer Bleue raised bog in Ontario, Canada were found to comprise 5.3% and 3.4%, with interannual 17.4% and 6%, week to week changes 48.2% and 61.2% and random error 29.1% and 29.5% of NEE_{day} and NEE_{night} variation respectively (Teklemariam et al., 2010). The Glencar bog therefore has a larger contribution to variance from functional and interannual responses than the Mer Bleue bog, but has less from week to week responses. Week to week changes in the maritime temperate climate of Glencar are slight, and so it is not surprising that these changes are a less significant contributor to the variance of fluxes. Differently from Teklemariam et al. (2010), we believe that functional responses would be expected to be more influential in a younger, more patterned ecosystem, which would intensify with increased diversity. Almost intact ombrotrophic peatlands have been virtually undisturbed for thousands of years, with some studies arguing that they have developed self-regulating mechanisms, constraining their ecosystem processes and making them more resilient to long-term environmental changes (Belyea and Baird, 2006; Hilbert et al., 2000; Koehler et al., 2011). The disparity in behaviour between Glencar and Mer Bleue could be from differences in vascular vegetation (dominated by shrubs in Mer Bleue, and by grasses and sedges in Glencar), the younger age of Glencar or its possible past history of light sheep grazing, so that it may not have developed the same self-regulating mechanisms that Mer Bleue has, or may not have reached its equilibrium yet (Hilbert et al., 2000). As a consequence, Glencar's highly patterned vegetation may be more able to adapt throughout the year.

6. Conclusions

Over the course of this ten-year study, the Glencar bog behaved mainly as a net CO_2 sink during the growing season between 2003 and 2012 (no growing season data was available for 2002), and behaved as an annual net CO_2 sink when averaged across the entire duration of measurements. Qualitative and quantitative analysis found that water table level affected the functional variation of net ecosystem CO_2 exchange, in that lower WTL led to reduced uptake, and was similar to the findings of previous investigations carried out over the same ecosystem (Laine et al., 2009; Sottocornola and Kiely, 2010a). A possible lagging effect was also identified whereby dry Springs and Summers could affect NEE uptake in successive growing seasons. This seasonal and annual memory and its potential effects merit examination in a further study.

Accurate models for weekly and annual NEE_{day} and NEE_{night} were derived, making it possible to detect the presence of functional response, and will allow examination of past or future behaviour based on relatively basic data archives or forecasts. Highly accurate annual models suggested that interannual variation has a significant influence on changes in NEE, which was reinforced through partitioning of contribution to variability. The comparison of these contributions between Glencar and the Mer Bleue raised bog in Canada suggested that Glencar is more responsive to functional than direct interannual or week to week meteorological variability. These differences may have been due to the milder temperate maritime climate of Glencar, or to the fact that it is a younger ecosystem, causing it to have a more recent memory of disturbance and therefore enabling the ecosystem to adapt. This would indicate that Glencar could be more resilient to sudden changes.

The main effects of climate change in Glencar are expected to be WTL rise during winter as a result of increased rainfall, whereas decreased rainfall levels during summer may lead to a WTL fall. As drier conditions cause a reduction in CO_2 uptake at Glencar, in the predicted future drier summers, the annual NEE values are likely to decrease, because NEE is mainly dictated by ecosystem behaviour during the growing season. Our results, which consider only the CO_2 fluxes and not the entire net ecosystem carbon balance, therefore indicate that the Glencar blanket peatland is likely to have a reduced CO_2 sink status on the short-term if future climate change predictions are accurate, considering the sensitivity of the ecosystem to small water table variations. Conversely on the long-term, vegetation composition change, declining mineralisation rates and nutrient enrichment following a water table drop might shift the ecosystem to a new equilibrium (Frolking et al., 2011). Although ten years of data gives a good insight into the IAV of CO_2 fluxes in Glencar, a longer time frame of data is essential to assess these changes in more detail.

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