

Growing season CO₂ fluxes from a drained peatland dominated by *Molinia caerulea*

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SUMMARY

- (1) *Molinia caerulea* occurs in peatland vegetation communities. However, under certain environmental and management conditions it may overwhelm the typical peatland vegetation, compromising ecosystem services including carbon dioxide (CO₂) sequestration and storage. Improved understanding of the effects of *M. caerulea* on CO₂ fluxes in peatland ecosystems will better inform landscape management.
- (2) Photosynthesis at a PPF of 600 μmol m⁻² s⁻¹ (P_{G600}), ecosystem respiration and partitioned (heterotrophic and autotrophic) below-ground respiration were calculated from closed-chamber measurements collected over the 2012–2014 growing seasons within two drained *M. caerulea* dominated peatland catchments in Exmoor National Park, southwest England.
- (3) All CO₂ fluxes peaked in mid-summer, in association with increased soil temperature and vegetation growth. During wetter periods, below-ground autotrophic respiration and P_{G600} significantly decreased (p=0.028 and p=0.002), conversely heterotrophic respiration increased insignificantly (p=0.081). An empirically derived net ecosystem exchange model estimated the growing season of 2012 to have been a smaller CO₂ sink in carbon equivalents (-126 ± 243 g m⁻²) than subsequent growing seasons (-146 ± 310 and -234 ± 325 g m⁻²) due to lower photosynthetic rates during a cool, wet summer (2012).
- (4) Management aimed at preserving the carbon store and increasing carbon sequestration through raising water tables may reduce photosynthesis and increase heterotrophic respiration unless the dominance of *M. caerulea* is reduced and *Sphagnum* spp. cover increased.

KEY WORDS: blanket bog, heterotrophic respiration, net ecosystem exchange, photosynthesis

INTRODUCTION

Natural peatlands are known to be significant stores of carbon (Gorham 1991, Yu *et al.* 2010, Page *et al.* 2011). In a functioning peatland, over time a small imbalance between primary productivity and decay leads to the gradual accumulation of carbon (Clymo 1984). Over recent decades, land management (Miller *et al.* 1984, Brys *et al.* 2005, Mälson *et al.* 2008) and increased nitrogen deposition (Heil & Diemont 1983, Hogg *et al.* 1995, Tomassen *et al.* 2003) have resulted in changes to the vegetation communities present in many peatlands towards communities dominated by *Molinia caerulea*. *M. caerulea*, a perennial tussock grass, is now widespread across northern Europe (Taylor *et al.* 2001). By 1988 it dominated approximately 10 % of upland British peatlands (Bunce & Barr 1988), and anecdotal evidence suggests this coverage has continued to increase. *M. caerulea* occurs in vegetation communities across a range of wet or

moist conditions (Rodwell 1991). However, under certain environmental and management conditions such as nutrient enrichment, overgrazing, burning and drainage (Berendse 1990, Brys *et al.* 2005) it may overwhelm other peatland vegetation leading to (very) low biodiversity, thereby compromising ecosystem function.

Although some graminoid species such as *Carex* spp. (sedges), *Phragmites* spp. (reeds) and *Scheuchzeria* spp. (rushes) regularly form peat, others that are also found living in peatlands (such as *M. caerulea*) may not, despite their significant annual biomass production (517 g m⁻², Gatis *et al.* 2019). At present there is only a limited understanding of the processes that drive growing season carbon dioxide (CO₂) fluxes in *M. caerulea* dominated ecosystems. This study aimed to understand and quantify the biotic and abiotic processes that drive seasonal and inter-annual variability in these ecosystems in order to improve the management of these landscapes, thereby protecting and enhancing ecosystem function.

We designed and implemented an experiment to test the hypothesis that in a *M. caerulea*-dominated, drained, shallow peatland, temporal variation in CO₂ fluxes will be driven primarily by vegetation phenology and temperature due to the deciduous nature of the vegetation. Furthermore, we tested the hypothesis that water table depth will have little effect on photosynthesis, ecosystem respiration and below-ground autotrophic respiration, as *M. caerulea* has evolved to live in environments with fluctuating water table depths (Taylor *et al.* 2001). In addition to needing new data to understand the large dynamic vegetation driven fluxes, partitioning below-ground heterotrophic respiration enables the decomposition of the longer-term peat store to be isolated. We hypothesised that below-ground heterotrophic respiration will decrease as water tables rise, due to oxygen limitation reducing aerobic respiration.

METHODS

Study sites

Two catchments (Figure 1) located in Exmoor National Park, southwest England, were selected as characteristic of drained *M. caerulea* dominated blanket bogs; Aclands (51° 7' 51.3" N, 3° 48' 44.4" W) and Spooners (51° 7' 21.9" N, 3° 44' 52.9" W). The effect of drainage on multiple ecosystem services has been extensively studied in these catchments (Grand-Clement *et al.* 2014, Gatis *et al.* 2015; Luscombe *et al.* 2015a, 2015b, 2017). Both catchments were initially drained by hand-dug ditches (up to 0.5 m wide and 0.5 m deep) from the 1830s (Hegarty & Toms 2009). Larger ditches (>1.5 m wide) were machine dug between the 1960s and 1980s (Mills *et al.* 2010). The catchments are currently used for low-intensity extensive grazing (cattle, sheep and ponies) in the summer. Within both catchments the peat is highly humified (H7–H9; von Post & Granlund 1926) *Sphagnum* peat of variable thickness, underlain by thin (~15 cm) silty clayey palaeosols (Carey *et al.* 2015) over the Morte Slaters Formation. The current vegetation is classified under the UK National Vegetation Classification scheme as Class M25: *M. caerulea* - *Potentilla erecta* mires (Rodwell 1991).

Three sites in each catchment (Figure 1c, d) were chosen to encompass the expected variation in altitude, aspect, slope, peat depth and ditch dimensions (Table 1). Three replicates were established at each site located along a transect perpendicular to the drainage ditch, giving a total of 18 sample locations. Data collected from these locations during 2012 were used with data from a further 18 locations to assess spatial patterns in

vegetation and CO₂ fluxes with respect to drainage ditches (Gatis *et al.* 2015). Here we analyse data from 2012 with additional data from 2013 and 2014 to assess temporal variations and estimate growing season NEE fluxes.

Net Ecosystem Exchange (NEE) measurements

A 55 × 55 × 25 cm Perspex chamber was rested on permanently installed 50 cm legs with a clear plastic skirt weighted down to the soil surface with a heavy chain following the method outlined in Street *et al.* (2007). Interlocking draught excluder tape ensured an airtight seal. Two fans continuously mixed the air inside the chamber.

Accumulated CO₂ was measured every ten seconds over two minutes with an EGM-4 infra-red gas analyser (PP Systems, Hitchin, UK) (350 ml min⁻¹ flow rate) concurrently with photosynthetic photon flux density (PPFD) at canopy height within the chamber (sensor from Skye Instruments, Llandrindod Wells, UK), soil temperature at 5 cm (thermometer from Electronic Soil Temperature Instruments, Worthing, UK) and the depth to the water table (manual measurement in dipwells, 40 mm diameter). Measured net CO₂ exchange in carbon equivalents (μg m⁻² s⁻¹) was calculated from the linear change in CO₂ concentration in the chamber, as this was found to be the most appropriate fit to the data collected. Fluxes were corrected for chamber volume, which was measured using a tape measure. The height of the chamber above the vegetation was measured in a grid of nine points. The width of each side was measured between the permanently installed legs, both along the ground and at the top of the legs. The resultant volume was added to the volume of the chamber. Temperature was not controlled over the duration of the test but the chamber was removed between measurements to restore ambient conditions. If, particularly at high PPFD values, the rate of CO₂ accumulation was observed to decrease with time towards the end of the measurements due to a stomatal response to high temperatures, the data were discarded. Seven measurements were collected at each location at 100, 100, ~60 ~40, ~10, 0 and 0 % light levels using a combination of shade cloths. The actual light level within the chamber varied for each measurement dependent on the shade cloth used and solar radiation levels (cloud cover/sun angle). However, as the PPFD sensor was inside the chamber and the aim was to achieve a range in PPFD values to model a hyperbolic light response curve this was considered acceptable provided the range of PPFD during the two-minute measurement was minimal (< 30 μmol m⁻² s⁻¹ for PPFD < 300 μmol m⁻² s⁻¹; < 10 % variation in PPFD for PPFD > 300 μmol m⁻² s⁻¹).

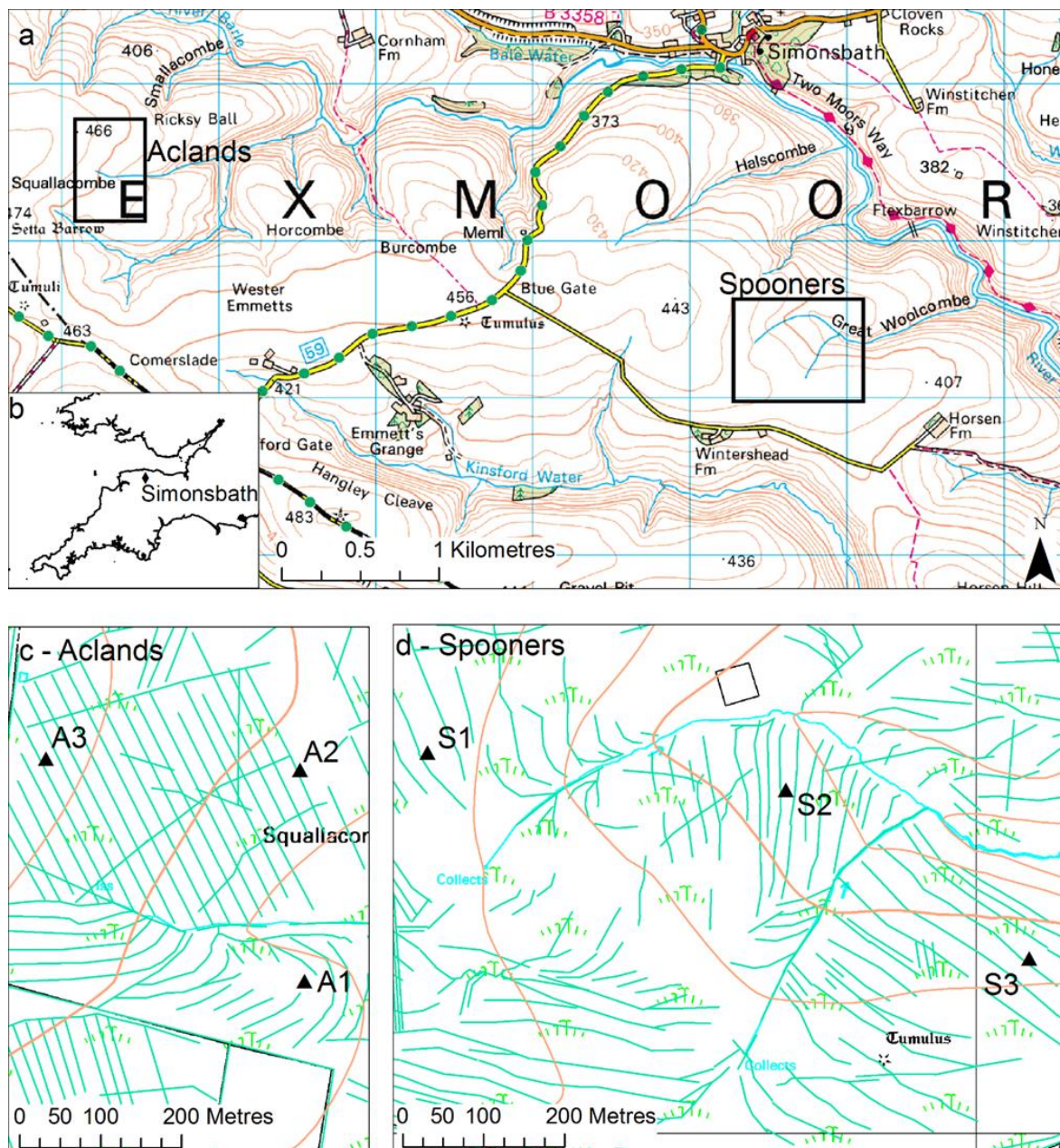


Figure 1. Top: the locations of Aclands and Spooners catchments within Exmoor (a), and of Exmoor within the southwest of England (b). Bottom: locations of study sites within Aclands (c) and Spooners (d) study catchments. Drainage ditches and natural streams are shown in light blue. Base maps: Ordnance Survey (2008, 2015).

Sampling was limited to the growing season due to the dominance and deciduous nature of *M. caerulea*. Samples were collected approximately monthly in both catchments over the 2012 (n=411) and 2014 (n=315) growing seasons (May to September). During 2013 (n=320) sampling was focused on Spooners as restoration was planned for Aclands. Monthly measurements (n=14) were collected over a measurement period of 2–4 days apart from one occasion when inclement weather resulted in a collection period of 13 days. Hyperbolic

light response curves were determined at each location for each month by solving Equation 1 using the GRG nonlinear method in the Solver tool of Microsoft Excel v15 (Microsoft Corporation, Seattle, WA).

$$NEE_{\text{measured}} = R_{\text{Eco}} - \frac{P_{\text{max}} \cdot \text{PPFD}}{k + \text{PPFD}} \quad [1]$$

where NEE is the measured net ecosystem exchange in carbon equivalents ($\mu\text{g m}^{-2} \text{s}^{-1}$; a positive value indicating CO₂ released to the atmosphere), P_{max} the

Table 1. Properties of the experimental sites at Aclands (A1–3) and Spooners (S1–3). Three replicates were located within each site. Peat depth (cm) measured from base of peat during dipwell installation. Ditch depth (cm) measured using a tape measure, from base of ditch to tussock shoulder. Ditch width (cm) and distance from ditch to adjacent down-gradient ditch (m) measured with a tape measure. Altitude (m), slope (°), orientation and direction of ditch (°) from LiDAR data.

Property	A1	A2	A3	S1	S2	S3
Mean peat depth and standard deviation (cm)	38 ± 4	43 ± 5	36 ± 7	23 ± 3	56 ± 4	29 ± 4
Mean <i>Molinia caerulea</i> cover and standard deviation (%)	90 ± 10	75 ± 25	80 ± 20	77 ± 12	85 ± 13	100 ± 0
Mean moss cover (%)	3 ± 4	1 ± 1	2 ± 1	1 ± 1	0 ± 0	0 ± 1
Non- <i>Molinia</i> cover (%)	6 ± 6	1 ± 1	8 ± 6	10 ± 3	11 ± 18	7 ± 11
Other species with > 5 % cover in one replicate	<i>Hypnum cupressiforme</i>		<i>Eriophorum vaginatum</i>	<i>Potentilla erecta</i> , <i>Eriophorum vaginatum</i>	<i>Narthecium ossifragum</i>	<i>Potentilla erecta</i>
Ditch depth (cm)	20	21	18	18	45	24
Ditch width (cm)	32	43	42	67	80	42
Distance from ditch to adjacent downslope ditch (m)	20.3	19.1	18.7	43.9	15.4	32.8
Altitude (m)	443	448	461	418	395	407
Slope (°)	2	5	3	4	5	5
Orientation	NE	SE	SE	ESE	NE	N
Direction of ditch (°)	10	150	151	150	0	300
Ditch direction with respect to slope	Down-slope	Down-slope	Down-slope	Cross-slope	Down-slope	Down-slope

rate of light saturated photosynthesis ($\mu\text{g C m}^{-2} \text{s}^{-1}$), k the half-saturation constant of photosynthesis ($\mu\text{mol m}^{-2} \text{s}^{-1}$), PPFD the incident PPFD ($\mu\text{mol m}^{-2} \text{s}^{-1}$) and R_{Eco} ecosystem respiration ($\mu\text{g C m}^{-2} \text{s}^{-1}$). R_{Eco} and gross photosynthesis at a PPFD of $600 \mu\text{mol m}^{-2} \text{s}^{-1}$ (P_{G600}) were modelled using the derived parameters P_{max} and k (Equation 1) for each month at PPFD=0 and $600 \mu\text{mol m}^{-2} \text{s}^{-1}$ to enable comparison between measurements taken under varied illumination conditions.

Soil CO₂ efflux measurements

Seventy-two polyvinyl chloride collars (diameter 16 cm, height 8 cm) were sealed to the peat in March 2012 using non-setting putty (Eco-Stick ‘Plumbers Mait’). At each location four collars were placed ~1 m apart in a square ~1 m downslope of the NEE sampling plot (Figure 2). All collars had above-ground vegetation removed by regular clipping (after collection of measurements) so the fluxes originated from below-ground only. In addition, 20 cm deep circular trenches (56 cm in diameter), were cut around two collars per location (total 36) to sever live roots and the whole area was maintained vegetation free, enabling measurement of the below-ground heterotrophic component. A 20 cm deep trench was considered sufficient because the majority of *M. caerulea* root biomass is near the surface (Taylor *et al.* 2001). Results from the two replicates of each treatment at each location were averaged to produce a value for total (clipped) below-ground and heterotrophic (trenched and clipped) below-ground respiration. Autotrophic respiration (including root respiration and microbial respiration of root exudates) was calculated from the difference between total below-ground and heterotrophic below-ground respiration.

The depth of the water table below the peat surface, soil temperature at 5 cm and 15 cm and CO₂ efflux were measured in a randomised pattern approximately every three weeks over the growing season across both catchments in 2012 ($n=588$) and 2014 ($n=504$) and at Spooners in 2013 only ($n=396$). CO₂ flux was measured over 2 minutes using an EGM-4 infra-red gas analyser and a CPY-4 canopy assimilation chamber (0.004 m^3) (PP Systems, Hitchin, UK). The level of detection was $0.09 \mu\text{mol m}^{-2} \text{s}^{-1}$. Measurements were excluded when the CO₂ flux varied between 10 and 120 seconds by $>0.47 \mu\text{mol m}^{-2} \text{s}^{-1}$. Flux estimates were volume corrected by measuring the vertical distance from the top of the collar to the ground in a grid of nine points using a tape measure. As below-ground respiration has been shown to be strongly controlled by soil temperature (Lloyd & Taylor 1994), which

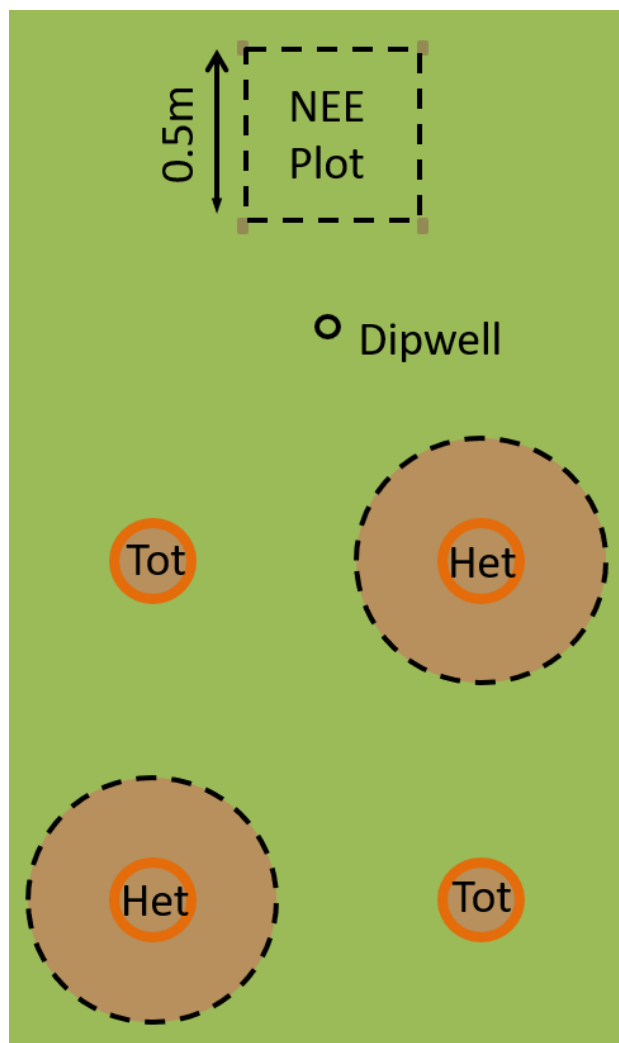


Figure 2. Schematic diagram of the equipment installed at each location showing the net ecosystem exchange plot and the pairs of plots to measure total (clipped) and heterotrophic (trenched and clipped) below-ground respiration.

can vary diurnally in drained peat soils, soil respiration fluxes were adjusted to 10°C (the annual average air temperature recorded at Aclands in 2012) to enable the effects of other variables to be analysed, following Equation 2:

$$r_{10} = R_T \cdot Q_{10}^{10-T/10} \quad [2]$$

where r_{10} is the respiration CO₂ flux at 10°C ($\mu\text{mol m}^{-2} \text{s}^{-1}$) for a measured respiration CO₂ flux (R_T) ($\mu\text{mol m}^{-2} \text{s}^{-1}$) at temperature T ($^\circ\text{C}$). The Q_{10} (increase in respiration flux for a 10°C increase in soil temperature) was determined for each sample location by regressing the soil temperature at 5 cm depth against the respiration rate.

Vegetation phenology proxy

MODerate resolution Imaging Spectroradiometer (MODIS) data were selected as a proxy for vegetation phenology as these remote sensing observations are non-destructive, less labour intensive than vegetative green area measurements (Wilson *et al.* 2007), and have been shown to capture up to 90 % of the daily variation in phenology in these *M. caerulea* dominated landscapes (Gatis *et al.* 2017). MODIS tile h17 v3 of 8-day 500 m MODIS9A1 surface reflectance product was downloaded from USGS Earth Explorer (<http://earthexplorer.usgs.gov>). The Normalised Difference Vegetation Index [NDVI=(Band 2–Band 1)/(Band 2+Band 1)] was derived from the red (Band 1) and near infra-red (Band 2) of the surface reflectance product.

Data were screened using MODIS data quality labels and poor quality data (cloudy, high aerosol concentrations or poor geometry) were given a weighting of 0 and all other data a weighting of 1. To minimise variation due to atmospheric conditions, illumination and observation geometry, a third order Fourier smoothing filter was applied. Points outside the 99 % confidence interval were excluded. All remaining points were then weighted equally and a Fourier third order series fitted to form a continuous daily time series (Gatis *et al.* 2017).

Statistical analysis

The temporal relationship between abiotic (water table depth, soil temperature, rainfall in the preceding 0, 7, 14 and 28 days, PPFD in the preceding hour and day) and biotic (NDVI and natural logarithm transformed NDVI) variables and CO₂ fluxes were tested using multiple linear regression analysis. In addition, Arrhenius (1898), Lloyd-Taylor (Lloyd & Taylor 1994) and exponential relationships between CO₂ fluxes (not temperature corrected) and soil temperature were tested. As temperature co-varied with NDVI, multiple stepwise linear regressions were carried out for P_{G600} and R_{Eco}. NDVI and soil temperature at 5 cm were natural logarithm transformed as they demonstrated exponential relationships with P_{G600} and R_{Eco}. Results were considered significant when $p < 0.050$. All statistical tests were carried out using SPSS 19.0 Statistical package (SPSS Inc., Chicago, Illinois, USA).

Net Ecosystem Exchange modelling

An empirically derived non-linear regression model (Equation 3) was parameterised using SPSS 19.0 (SPSS Inc., Chicago, Illinois, USA). All measurements collected (full dark, shaded and full light; $n = 1126$) were used to determine coefficients

which maximised the coefficient of determination (r^2) and minimised model root mean square error and model uncertainty. A model for both catchments combined was determined because greater variation was observed within than between catchments.

Soil temperature was measured every 15 minutes (Gemini Data Loggers, Chichester, UK) at Spooners Site 2 (Figure 1d). Instantaneous measurements collected concurrently with CO₂ fluxes strongly correlated with logged measurements ($r^2 = 0.87–0.99$, depending on the location). The logged data were averaged to create an hourly time series. A linear relationship ($r^2 = 0.87$) between full light PPFD measurements taken concurrently with the flux measurements ($n = 583$) and global irradiation measured at Liscombe Meteorological Station (15 km away) (UK Meteorological Office 2014) was established and used to derive an hourly time series of PPFD (and 95 % confidence interval) from hourly global irradiation measurements at Liscombe. Derivation of the daily NDVI time series is outlined above. Growing season estimates of NEE were calculated as cumulative sums of the hourly modelled NEE values. The growing season was defined as the period from the first three consecutive days with daily mean soil temperature > 10 °C until the first three consecutive days with daily soil temperature < 10 °C as this is the temperature above which root initiation and subsequent leaf growth occurs (Taylor *et al.* 2001). Confidence intervals (95 %) were determined from the root mean square error of modelled values compared to measured values.

RESULTS

Growing season variability

In June and July 2012 rainfall was notably higher (> 220 mm) and mean PPFD notably lower (< 690 $\mu\text{mol m}^{-2} \text{s}^{-1}$) than in both 2013 and 2014 (Figure 3b, e). In July 2012 mean monthly soil temperature (11.8 °C) was also lower than in the other years. Soil temperature and PPFD were more consistent between years for the other months (Figure 3a, b). Water tables were generally lower in 2014 and higher in 2012, reaching a summer low in July 2014 (depth 29.2 cm) and a summer high in July 2012 (depth 13.5 cm) (Figure 3d). During the 2012 and 2013 growing seasons, NDVI showed a rapid increase between June and July with a peak in August (Figure 3c). In 2014 this green-up occurred earlier (between May and June) and the seasonal peak was also a month earlier.

P_{G600}, R_{Eco} and below-ground respiration showed strong seasonal variation (Figures 4 and 5), reaching

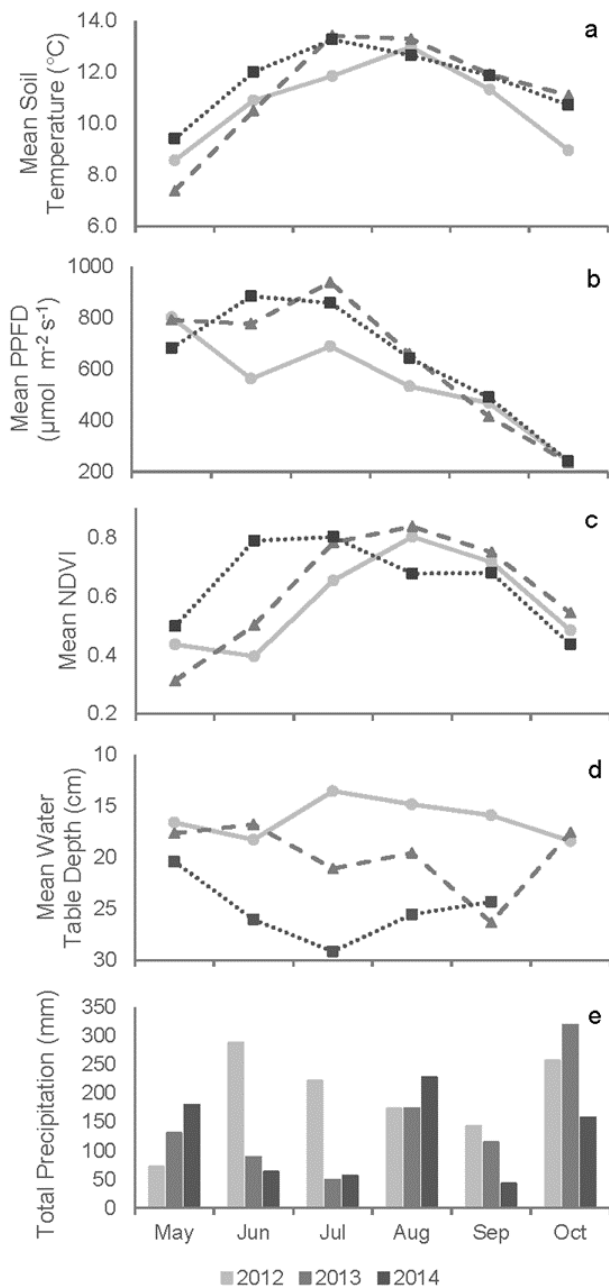


Figure 3. Environmental conditions at Spooners Site S2 in 2012–2014: (a) monthly mean soil temperature (°C); (b) photosynthetically photon flux density ($\mu\text{mol m}^{-2} \text{s}^{-1}$); (c) Normalised Difference Vegetation Index (NDVI); (d) water table depth (cm below surface); (e) precipitation (mm).

a mid-season peak in July–August. In May, prior to spring green-up, both photosynthesis and ecosystem respiration were low (<23 and $<14 \mu\text{g C m}^{-2} \text{s}^{-1}$). Although both heterotrophic and autotrophic respiration increased to a mid-season maximum, the proportional contribution of heterotrophic respiration decreased to a mid-season low in 2013 (44 %) and

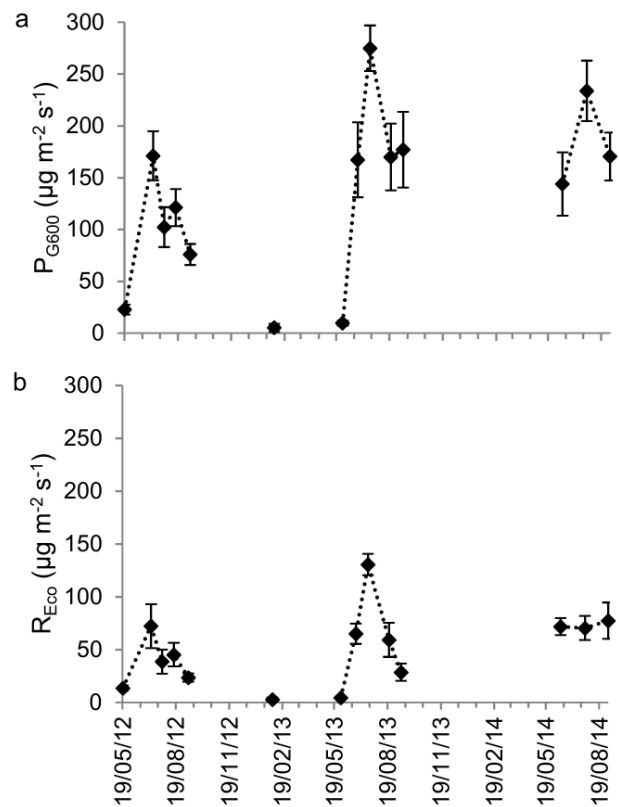


Figure 4. Temporal variation in (a) mean photosynthesis at PPFD of $600 \mu\text{mol m}^{-2} \text{s}^{-1}$ (P_{G600}) and (b) mean ecosystem respiration (R_{Eco}) in carbon equivalents ($\mu\text{g m}^{-2} \text{s}^{-1}$). Error bars are one standard error, $n=6$ in 2012 and 2014 (Aclands and Spooners) and $n=3$ in 2013 (Spooners only).

2014 (43 %) (Figure 5). Overall, the average contribution of heterotrophic respiration to total below-ground respiration was 59 %.

Inter-annual variations in growing conditions were reflected in the P_{G600} and R_{Eco} rates which were greatest in 2013 and least in 2012 (Figure 4). Total and autotrophic below-ground respiration were also generally greater at an equivalent time of the year in 2013 and 2014 than in 2012 (Figure 5). Heterotrophic below-ground respiration showed the least variation between years.

Drivers of temporal variation

Both photosynthesis and ecosystem respiration showed significant positive relationships with soil temperature ($r^2=0.74$, $p<0.001$; $r^2=0.72$, $p<0.001$) and NDVI ($r^2=0.71$, $p<0.001$; $r^2=0.61$, $p<0.001$) (Figure 6). Ecosystem respiration also showed a significant positive relationship with photosynthesis ($r^2=0.82$, $p<0.001$) suggesting relationships with soil temperature and NDVI may have been indirect, i.e. R_{Eco} responded to photosynthesis which was

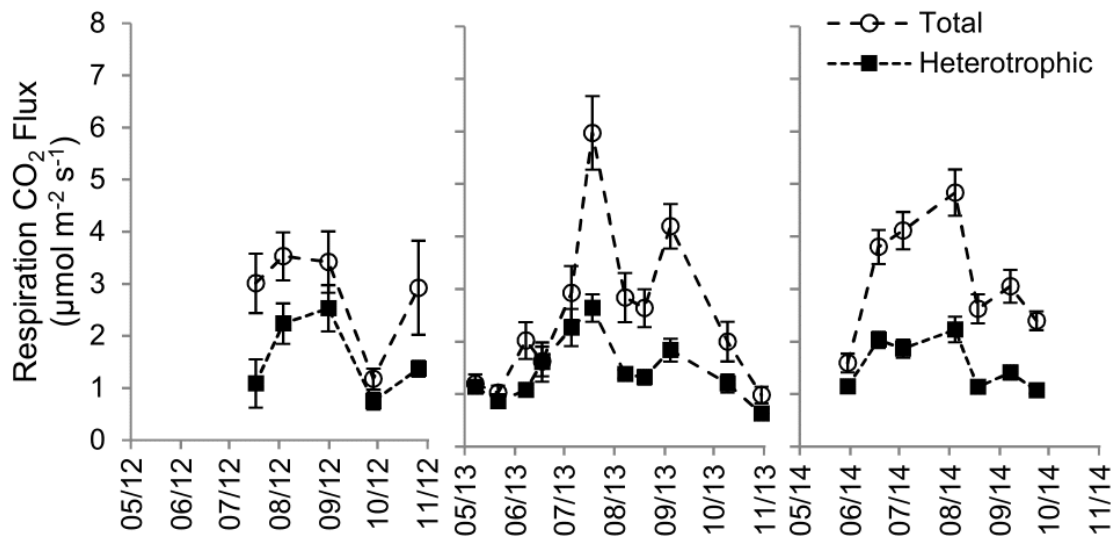


Figure 5. Seasonal variation in mean total below-ground and heterotrophic below-ground soil respiration CO₂ flux ($\mu\text{mol m}^{-2} \text{s}^{-1}$). Error bars are one standard error, $n = 18$ in 2012 and 2014 (Aclands and Spooners) and $n = 9$ in 2013 (Spooners only).

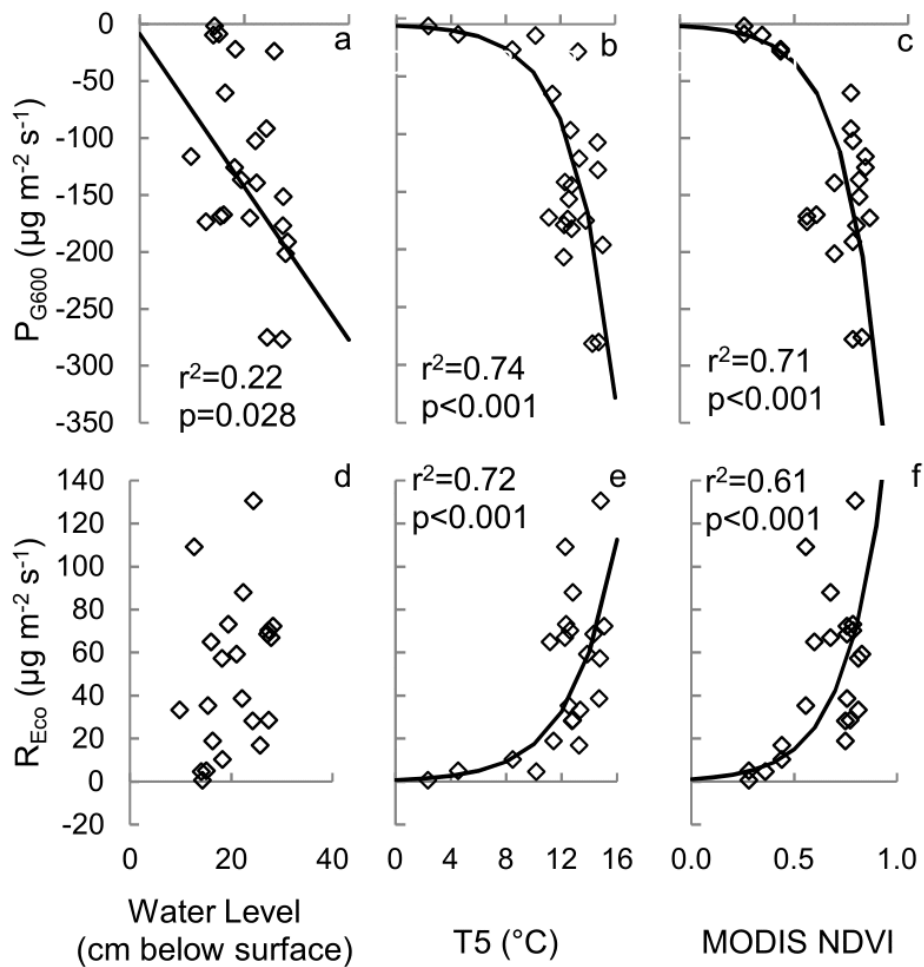


Figure 6. Relationship between photosynthesis at PPFD of $600 \mu\text{mol m}^{-2} \text{s}^{-1}$ (P_{G600}) (a, b & c) or ecosystem respiration (R_{Eco}) (d, e & f) in carbon equivalents ($\mu\text{g m}^{-2} \text{s}^{-1}$) with water table depth (cm below ground surface) (a & d), soil temperature at a depth of 5 cm ($^{\circ}\text{C}$) (b & e) and normalised difference vegetation index (NDVI) (c & f). A positive flux is CO₂ released to the atmosphere.

dependent on soil temperature and the controls on NDVI (greenness, biomass, leaf area etc.) rather than R_{Eco} changing directly with soil temperature or NDVI. R_{Eco} showed no relationship with water table depth (WTD) (Figure 6d) but P_{G600} (Figure 6a) had a weak but significant ($r^2=0.22$, $p=0.028$) linear relationship; P_{G600} increased when the water table fell. However, including WTD with NDVI in a multiple regression model did not result in a significant relationship for either P_{G600} or R_{Eco}.

Of the variables tested, soil temperature explained the most temporal variance in total (77 %), heterotrophic (59 %) and autotrophic (58 %) below-ground respiration (Table 2). Although a Lloyd-Taylor relationship best represented the ecosystem respiration component of the NEE model (Equation 3), below-ground respiration was better explained by an exponential function. Total and autotrophic (root derived) below-ground respiration increased exponentially with NDVI (Table 2). Once corrected to 10 °C, these relationships became non-significant; NDVI strongly co-varied with temperature, correcting to 10 °C removed any apparent relationships.

Total and autotrophic below-ground respiration, both as measured and corrected to 10 °C, showed significant but weak positive relationships with water table depth; respiration increased when water tables fell (Figure 7). The relationships were slightly more

significant when the effect of temperature was accounted for (Figure 7d, f). Heterotrophic respiration at 10 °C showed a weak non-significant decrease when water tables fell (Figure 7e).

Modelled Net Ecosystem Exchange

The NEE model based on empirical parameters (Table 3) explained 64 % of the variability in CO₂ fluxes observed. The model consisted of two components; the first was based on a Lloyd-Taylor response to soil temperature, the second was a hyperbolic light response curve. Both components were regulated by vegetation phenology (NDVI).

$$NEE_{modelled} = \frac{P_1 \cdot NDVI \cdot PPFD}{k_1 + PPFD} + a \cdot NDVI \cdot \exp \left[E_0 \cdot \left(\frac{1}{T_{Ref} - T_0} - \frac{1}{T_S - T_0} \right) \right] \quad [3]$$

where PPFD is the incident PPFD ($\mu\text{mol m}^{-2} \text{s}^{-1}$), NDVI the normalised difference vegetation index, T_S is the soil temperature (K), T_{Ref} the reference temperature set at 283.15 K (10 °C), T₀ the temperature at which respiration reaches zero (227.13 K) (Lloyd & Taylor 1994) and P₁ ($\mu\text{mol m}^{-2} \text{s}^{-1} \text{K}^{-1}$), k₁ ($\mu\text{mol m}^{-2} \text{s}^{-1}$), a and E₀ ($\mu\text{mol K m}^{-2} \text{s}^{-1}$) empirically derived coefficients.

Table 2. Relationships between below-ground respiration and temporal variables. Regression coefficient (r²) and significance (p) of exponential (E) or linear (L) relationships between total below-ground, heterotrophic below-ground and autotrophic below-ground respiration as measured and corrected to 10 °C and soil temperature at 5 cm (°C) (T5), water table depth (cm below surface) (WTD) and normalised difference vegetation index (NDVI). + indicates a positive relationship, – a negative relationship.

Below-ground Respiration Source	Variable	As measured			At 10 °C				
		r ²	p		r ²	p			
Total	T5	E	0.77	<0.001	+				
	WTD	L	0.17	0.017	+	L	0.22	0.005	+
	NDVI	E	0.47	<0.001	+				
Heterotrophic	T5	E	0.59	<0.001	+				
	WTD	E	0.02	0.459	+	L	0.09	0.081	-
	NDVI	E	0.33	<0.001	+				
Autotrophic	T5	E	0.58	<0.001	+				
	WTD	L	0.23	0.005	+	L	0.25	0.002	+
	NDVI	E	0.37	<0.001	+				

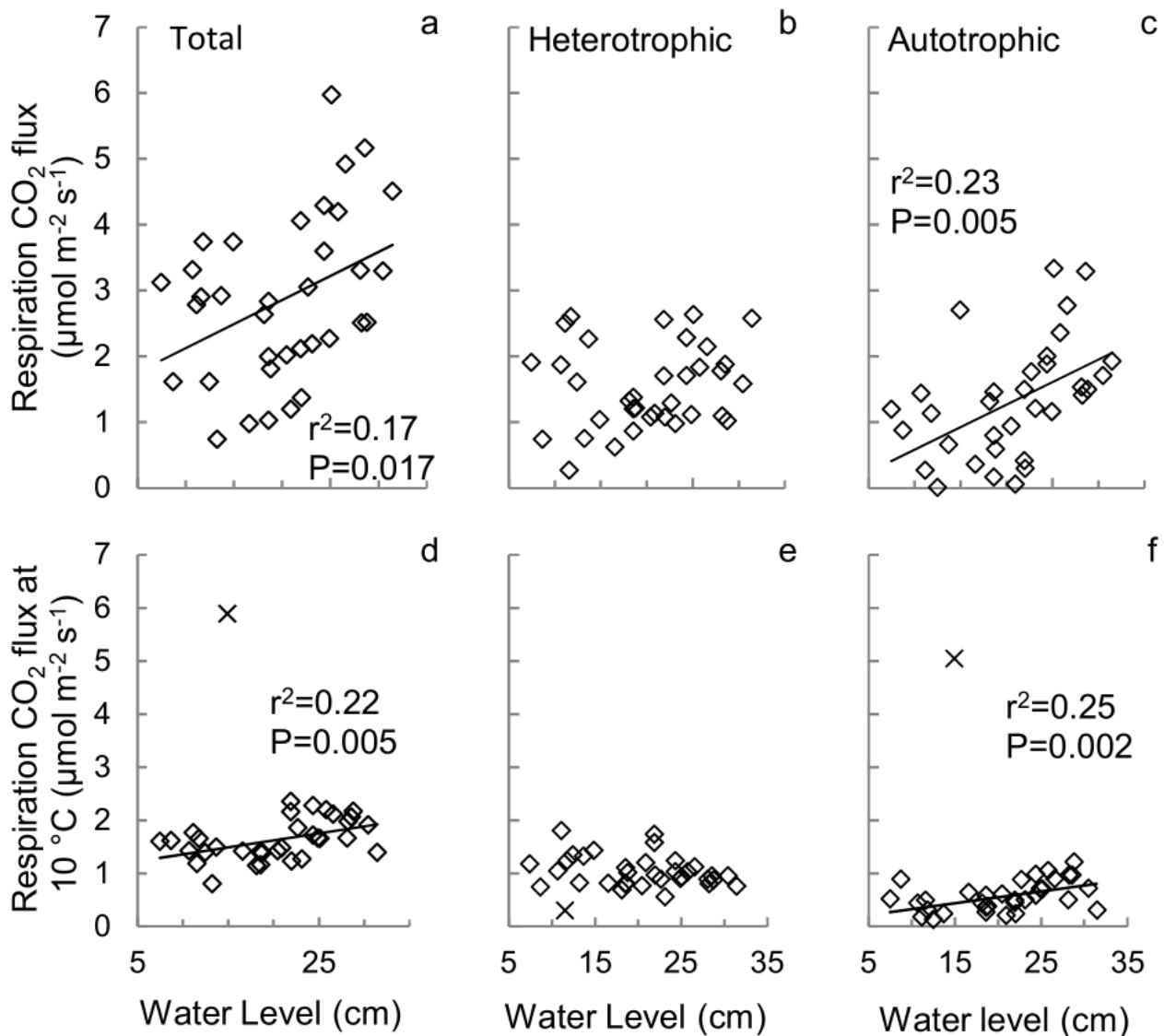


Figure 7. Relationship between below-ground respiration CO₂ flux (μmol m⁻² s⁻¹) as measured (a, b, c) and corrected to 10 °C (d, e, f) and water table depth (cm below ground surface) with total below-ground (a, d), heterotrophic below-ground (b, e) and autotrophic below-ground (c, f) respiration. Outliers (x) excluded from analysis.

Table 3. Net ecosystem exchange model (Equation 3) coefficients and standard errors ($r^2 = 0.64$).

Parameter	Coefficient Estimate	Standard Error
a	75.9	7.0
E ₀	-36.9	64.4
P ₁	-252.3	16.4
k ₁	159.6	4.8

Although an exponential function was found to best explain the relationship between temperature and ecosystem respiration (Figure 6e), when using the whole dataset to model NEE, the Lloyd-Taylor function, which allows for variation in temperature sensitivity, was found to produce lower parameter errors and consequently lower model uncertainty. Despite average P_{G600} varying with water table depth (Figure 6a), a water table depth term was not included in the NEE model (Equation 3) as it dramatically increased parameter uncertainty and reduced the coefficient of determination. Measured NEE shows a good agreement with modelled NEE (Figure 8a) but there is some scatter. Comparing residuals to modelled NEE (Figure 8b) suggests the model is

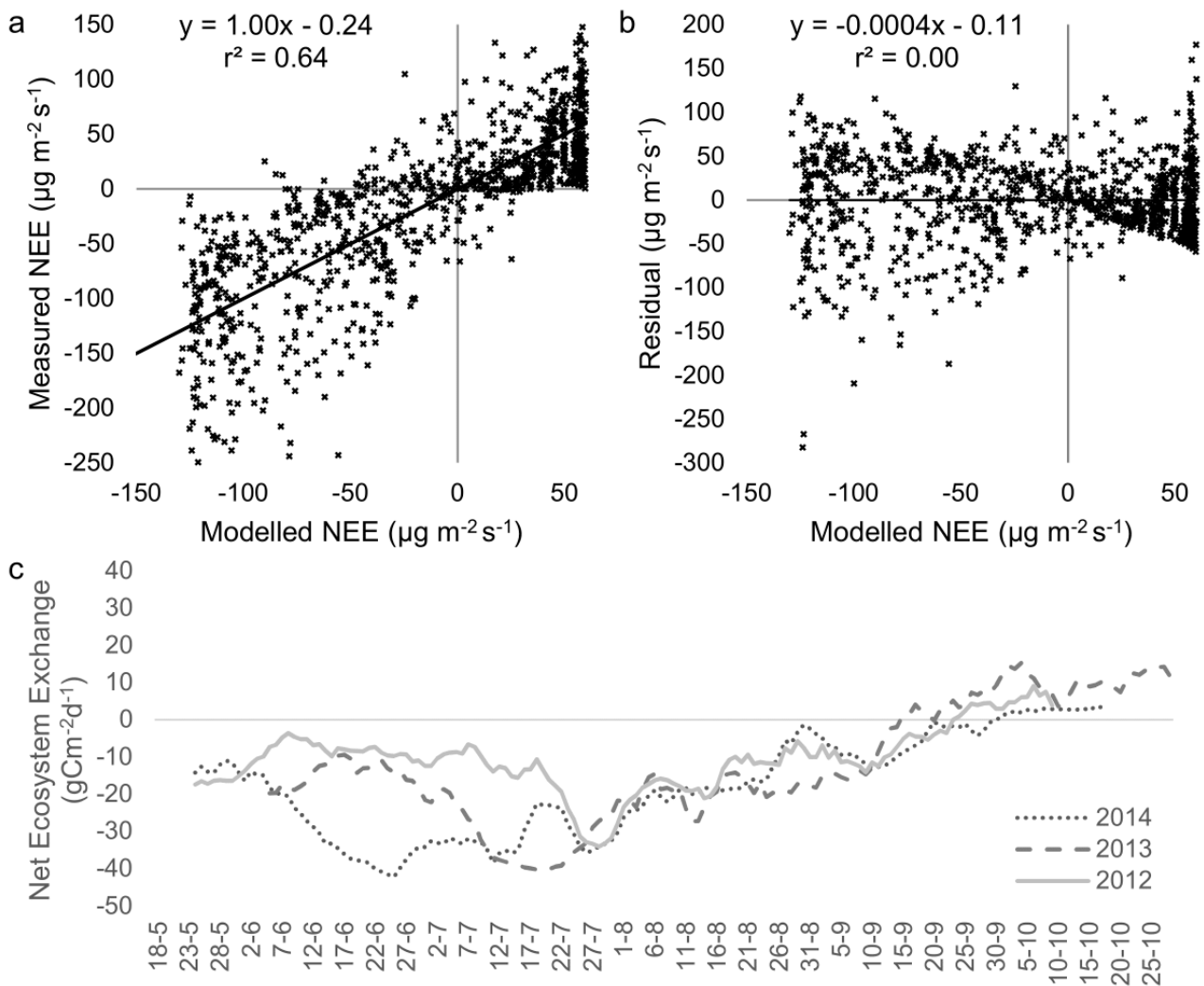


Figure 8. (a) Measured net ecosystem exchange (NEE) in carbon equivalents (µg m⁻² s⁻¹) against modelled NEE in carbon equivalents (µg m⁻² s⁻¹) using Equation 3. (b) Model residuals in carbon equivalents (µg m⁻² s⁻¹) against modelled NEE in carbon equivalents (µg m⁻² s⁻¹). (c) Weekly average NEE in carbon equivalents for the 2012, 2013 and 2014 growing seasons (g m⁻² d⁻¹).

unbiased with greater uncertainty during periods of greater flux.

This model suggests that the ecosystem is most likely to be a small CO₂ sink over the growing season, with 2014 a greater sink than 2013 and 2012 (Table 4). However, the confidence intervals range from a source of 164 g m⁻² to a sink of -538 g m⁻² so the direction of CO₂ flux (in carbon equivalents) is uncertain.

The 2014 growing season was modelled as the largest sink (Table 4), probably driven by the earlier increase in above-ground biomass (evidenced by an earlier time-series peak in NDVI) coincident with high PPFD (Figure 8c, Figure 3b, c). This was also the longest (146 days) and driest growing season (Figure 3d). In contrast, 2012 was the shortest growing season (132 days) with the lowest PPFD and

Table 4. Modelled growing season net ecosystem exchange (NEE; carbon equivalents) and 95 % confidence intervals (CI). Units: g m⁻².

Growing season dates		NEE	CI
start	finish		
24/05/2012	03/10/2012	-126	-357–117
05/06/2013	28/10/2013	-146	-433–164
18/05/2014	11/10/2014	-234	-358–91

NDVI, especially early in the season, resulting in lower modelled NEE rates until mid-July (Figure 8). The modelled NEE became more similar between years from August onwards with the ecosystem becoming a CO₂ source from mid-September (Figure 8).

DISCUSSION

Photosynthesis decreases under wetter conditions

We originally hypothesised that water table depth would have a limited effect on photosynthesis because *M. caerulea* has adapted to grow in areas of fluctuating water table (Taylor *et al.* 2001). However, both P_{G600} and autotrophic respiration increased as the water table fell (Figure 6a and Figure 7c, f). Similarly, Urbanová *et al.* (2013) found that photosynthesis increased during a drought year, attributing this result to the competitive advantage of shrubs over sedges. As the plots in our study have no sedges and few non-*Molinia* species present (9 ± 3 %) it is unlikely that a competitive advantage between species caused the increase we observed during drier periods. Despite their adaptation to wet environments (Taylor *et al.* 2001), it may be that drier conditions promote increased root growth (Gore & Urquhart 1966) and photosynthesis (Ballantyne *et al.* 2014). Alternatively it may be that because photosynthesis is dependent on temperature (Figure 6b) which covaries with water table depth ($r=0.45$, $p=0.029$), with warmer and drier conditions frequently coinciding, an indirect relationship may have occurred.

The proportion of soil respiration from autotrophic sources varied seasonally (Figure 5). However, the average (59 %) was similar to values observed for heather dominated peatlands (52 %) (Heinemeyer *et al.* 2011) but higher than values reported for a grass-dominated peatland site (35–45 %) (Silvola *et al.* 1996a) where the autotrophic contribution is likely to have been underestimated due to the inserted collars severing roots near the surface.

Heterotrophic respiration and water table depths

Unlike the previous work of Silvola *et al.* (1996b), who found water table depth to be the strongest control on below-ground respiration, there were no significant relationships between heterotrophic respiration (Figure 7b) and water table depths found in our study on Exmoor. Silvola *et al.* (1996b) showed that, as water table depth increased, there was an increase in oxygenation enabling rapid aerobic respiration to occur. On the other hand, it has also

been argued that as peat becomes older and more recalcitrant with depth, lowered water tables expose material with lower decomposition potential and therefore only a small (Updegraff *et al.* 1995) or no (Mäkiranta *et al.* 2008) increase in respiration can occur. It may be that, as the ditches on Exmoor are up to 150 years old and the peat humified (H7–H9; von Post & Granlund 1926), most of the labile organic matter may have already degraded. Although potentially vulnerable to priming (Freeman *et al.* 2004, Fontaine *et al.* 2007), humified peat will decompose slowly resulting in lower heterotrophic respiration rates and a limited effect of lowered water tables (Figure 7b). In the study of Silvola *et al.* (1996b), there may have been more labile organic matter remaining at depth as their sites had been drained for only 30 years.

Our work showed that, when water tables were higher, heterotrophic respiration at 10 °C increased insignificantly ($r^2=0.09$, $p=0.081$) (Figure 7e, Table 2) suggesting a possible second source of organic matter whose respiration was temperature controlled but moisture limited. It is proposed that this may be the near surface organic matter (predominately deciduous *M. caerulea* leaves) which would be susceptible to drying out between rainfall events. A source of readily decomposable organic matter controlled by near surface wetness would make detecting changes in the flux of peat carbon release difficult. Thus, experiments that exclude the litter layer and/or the top few centimetres of peat may be necessary to explore how water table fluctuations control decomposition of the main peat store.

Drained *Molinia caerulea* peatlands; small growing season sinks

P_{G600}, R_{Eco} and below-ground respiration showed strong seasonal variation (Figures 4 and 5), demonstrating their dependence on the phenology of *M. caerulea*. In the current study, 71 % of the variation in photosynthesis (Figure 8) was explained by NDVI, with photosynthetic activity showing seasonal correlation with vegetation phenology (Figure 3). MODIS NDVI has been found to explain up to 71 % of the variation in gross primary productivity in northern peatlands (Kross *et al.* 2013) and alpine grasslands (Rossini *et al.* 2012). It has been suggested that NDVI is best used as a measure of potential photosynthetic activity (Gamon *et al.* 1995) with actual photosynthetic activity often being limited by local variations in, for example, water availability, temperature or leaf shading. In this study, NDVI was used as a measure of potential photosynthetic activity moderated by hourly variation in PPFD and soil temperature in the NEE

model (Equation 3). The controls on NDVI (greenness, biomass, leaf area etc.) also limited maximum photosynthesis during spring green-up and autumn senescence, when PPFD and temperature could both be high (Figure 3) but photosynthetic biomass was diminished either because leaf growth was not complete or because the leaves had started to discolour and die off from the tips (Jefferies 1915).

There is considerable uncertainty (36 % of variability unaccounted for) in the model. Much of this may have occurred because the model is derived from 18 locations which show independent spatial and temporal variation in response to environmental factors - corroborated by the work of Laine *et al.* (2009) who found model performance to decrease as the number of independent plots increased. Some of the spatial variation across sites on Exmoor may have been accounted for if a spatially and temporally distributed plot scale measure of vegetation such as leaf area index or vegetation green index (Wilson *et al.* 2007) was included within the NEE model. However, these data are notoriously difficult to quantify due to spatial and temporal variability (Bréda 2003). Consequently, these data were not collected so MODIS NDVI, with a spatial resolution of 500 m, was used as proxy for vegetation phenology; and the lack of fine scale vegetation data (e.g. leaf area index) may explain some of the uncertainty in the model.

Mean modelled growing season NEE in carbon equivalents (-11, -12, -18 $\mu\text{g m}^{-2} \text{s}^{-1}$ for 2012, 2013 and 2014) were similar to fluxes reported for an upland drained *M. caerulea* dominated peatland (-17 and -25 $\mu\text{g m}^{-2} \text{s}^{-1}$) (Urbanová *et al.* 2013). However, growing season NEE fluxes modelled (Figure 8) in this study (-46 to 27 $\mu\text{g m}^{-2} \text{s}^{-1}$) were smaller in mid-summer than fluxes observed for a drained *M. caerulea*-dominated lowland peat bog (-70 to 20 $\mu\text{g m}^{-2} \text{s}^{-1}$) (Nieveen *et al.* 1998) but similar in the spring and autumn. The study by Nieveen *et al.* (1998) found that, despite higher summer NEE rates, over a whole year the *M. caerulea* dominated ecosystem was a CO₂ source (3 $\mu\text{g m}^{-2} \text{s}^{-1}$). This study suggests that although *M. caerulea* produces large volumes of leaf litter each year, it is only a small growing-season CO₂ sink which is unlikely to enable annual carbon accumulation.

Land management implications

M. caerulea is encroaching on upland areas (Bunce & Barr 1988, Berendse 1990, Brys *et al.* 2005). As stated above, this study suggests that these *Molinia*-dominated areas are only weak carbon sinks over the growing season, particularly under dull, cool and wet conditions (Figure 8). In order to preserve the carbon

stored within upland peatlands this encroachment must be managed appropriately - and if informed by evidence such as that presented here, best practice might involve eradication of *M. caerulea* (through restoration) in upland peatlands. Although cool, wet conditions are not a direct analogue of wetter conditions due to peatland restoration, this study does raise some concerns about the potential effects of restoration. Unless environmental conditions can be generated which allow other species to outcompete *M. caerulea* then restoration may reduce photosynthesis (carbon input) without a concomitant reduction in respiration (a carbon output) (Figure 6).

Ditch-blocking in deeper peats has been shown to raise and sustain high water levels (Wilson *et al.* 2010, Holden *et al.* 2011) resulting in changes to vegetation (Haapalehto *et al.* 2011, Bellamy *et al.* 2012). However, in shallow peats, such as those found on Exmoor, the water-holding capacity of the peat may not be sufficient for restoration to perturb the existing ecosystem enough to bring about the required change in vegetation.

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AUTHOR CONTRIBUTIONS

NG, IPH, KA and REB conceived the idea; NG, ECG and DJL participated in the fieldwork; NG led the analysis and writing; and all authors contributed to the manuscript and revisions.

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