

Soil CO₂ efflux in a temperate deciduous forest: Environmental drivers and component contributions

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ABSTRACT

Soil CO₂ efflux is a large component of total respiration in many ecosystems. It is important to understand the environmental controls on soil CO₂ efflux, in order to evaluate potential responses of ecosystems to climate change. This study investigated the relationship between total soil CO₂ efflux and soil temperature, soil moisture and solar radiation on an interannual basis for a plot of temperate deciduous ancient semi-natural woodland at Wytham Woods in central southern England. We also aimed to quantify the contribution of soil organic matter decomposition (SOM), root-and-rhizosphere respiration, and mycorrhizal respiration components to total soil CO₂ efflux, and determine their environmental correlates. Total soil CO₂ efflux was measured regularly from April 2006 to December 2008 and found to average 4.1 Mg C ha⁻¹ yr⁻¹ in both 2007 and 2008. In addition, we applied a recently developed approach to partition the efflux into SOM, root-and-rhizosphere, and mycorrhizal components *in situ* using mesh bags. SOM decomposition, root-and-rhizosphere, and mycorrhizal respiration were estimated to contribute 70 ± 6%, 22 ± 6% and 8 ± 3% of total soil CO₂ efflux respectively, equating to 3.0 ± 0.3, 0.9 ± 0.2 and 0.3 ± 0.1 Mg C ha⁻¹ yr⁻¹. In order to avoid the effect of temporal correlation between variables caused by seasonality, we investigated interannual variability by examining the relationship between CO₂ flux anomalies and anomalies in environmental variables. Variation in soil temperature explained 50% of the interannual variance in soil CO₂ efflux, and soil moisture a further 18% of the residual variance. Solar radiation, as a proxy for plant photosynthesis, had no significant effect on total soil CO₂ efflux, but was positively correlated with root-and-rhizosphere respiration, and mycorrhizal respiration. The relationship between anomalies in soil CO₂ efflux and soil temperature was highly significant, with a sensitivity of 0.164 ± 0.023 μmol CO₂ m⁻² s⁻¹ °C⁻¹. For mean peak summer efflux rates (2.03 μmol CO₂ m⁻² s⁻¹), this is equivalent to 8% per °C, or a Q₁₀ temperature sensitivity of 2.2 ± 0.2. We demonstrate the utility of an anomaly analysis approach and conclude that soil temperature is the key driver of total soil CO₂ efflux primarily through its positive relationship with SOM-decomposition rate.

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1. Introduction

Soil carbon dioxide (CO₂) efflux is a major component of the forest carbon cycle, accounting for 30–80% of total respiration (Davidson et al., 2006). Predicted future increases in temperature and atmospheric CO₂ concentration, and changes in precipitation may result in a positive feedback with soil CO₂ release (Heath et al., 2005; Lloyd and Taylor, 1994). Plant metabolic activity increases in the

spring and summer, as temperature increases and daylight hours lengthen, and so can be a confounding factor in studies considering just soil factors as drivers of respiration. However, interannual variability in climate, as well as more short-term fluctuations in weather conditions, can be exploited to tease apart seasonal factors from direct environmental factors.

Total soil CO₂ efflux is a combination of plant-root, heterotrophic and mycorrhizal respiration (Kuzyakov, 2006) and the response of each to climate at different scales must be understood to model future total soil CO₂ efflux. In temperate woodlands, both root respiration and soil organic matter (SOM) decomposition show seasonal variation, with the greatest fluxes in the growing season (Savage and Davidson, 2001; Janssens and Pliegard, 2003). This seasonality results from the temperature dependence of soil heterotrophic activity (Lloyd and Taylor, 1994), and particularly in

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deciduous woodlands, from the plants' cycles of growth and dormancy (White et al., 1999). Recent studies have shown that photosynthate supply influences root (Tang et al., 2005; Hartley et al., 2006; Moyano et al., 2007) and mycorrhizal (Heinemeyer et al., 2006; Moyano et al., 2007) respiration rates. Mycorrhizal respiration has also been shown by Heinemeyer et al. (2007) to be sensitive to soil water, with mycorrhizal respiration rates decreasing during a period of drought.

The seasonality of each respiration component, and its contribution to the total flux, cannot easily be quantified without experimentation and previous studies have taken different approaches to this, in a variety of ecosystems, resulting in a range of respiration rate estimates (see Hanson et al., 2000; Subke et al., 2006 for reviews). Methods range from invasive, such as trenching to exclude roots from the system (Lee et al., 2003), to non(soil)-invasive, such as tree girdling to remove photosynthate input and reduce/prevent root respiration (Högberg et al., 2001; Bhupinderpal-Singh et al., 2003), or the addition of isotopically-labelled carbon in carbon dioxide enrichment studies (Andrews et al., 1999). Some methods are direct, such as the measurement of actual root respiration from excised roots (Burton et al., 2002), whilst others are indirect, for example the regression method of Rodeghiero & Cescatti (2005) which regresses total soil respiration against root biomass over a number of sample points. All have advantages and limitations, illustrated on Kuzyakov's (2006) ordination of disturbance against universality (the ability of the method to be applied to different ecosystems), with the best estimates being produced by methods directly measuring respiration in the field in a variety of ecosystems with the least disturbance to the natural system.

Johnson et al. (2001) presented a method of partitioning total soil CO₂ efflux into SOM decomposition, and root and mycorrhizal respiration using mesh of 35 µm and 1 µm gauge in windows of soil cores to exclude roots, and roots & mycorrhizal hyphae, respectively, from soil. This method was subsequently extended to the use of bags of these mesh gauges (Moyano et al., 2007), which then contain just soil and mycorrhizal hyphae, or just soil, from which CO₂ efflux measurements can be taken, alongside measurements of total soil CO₂ efflux. The contribution of each component can then be calculated by subtraction.

In this study, total soil CO₂ efflux was measured for three years in a British deciduous woodland. In the third year mesh bags were used to partition soil CO₂ efflux, for one growing season, alongside the continuing total soil CO₂ efflux measurements. The aims of this study were to:

1. Calculate the amount of carbon released annually, in a deciduous woodland, through total soil CO₂ efflux.
2. Utilise the interannual variability of environmental conditions to explore and quantify the sensitivity of total soil CO₂ efflux to soil temperature, soil moisture and solar radiation.
3. Calculate the percentage of total soil CO₂ efflux contributed by a) roots and their rhizosphere, b) mycorrhizas, c) SOM decomposition.
4. Determine whether these relative contributions remain constant over the year, or vary with temperature, soil water content and time of year/growing season.

2. Methods

2.1. Site description

All measurements were conducted in a 1 ha plot of Wytham Woods, Oxfordshire, UK (1°19'W 51°46'N; UK National Grid: SP 46 08) (Kirby and Thomas, 2000). The 1 ha study plot is divided

into 25 subplots, 20 m by 20 m, as a basis for measurement replication.

The site is ancient semi-natural woodland, UK National Vegetation Classification community W8 *Fraxinus excelsior*–*Acer campestre*–*Mercurialis perennis* woodland (Hall et al., 2004). The majority of trees in the study plot are sycamore *Acer pseudoplatanus* L. and ash *F. excelsior* L., the remainder being pedunculate oak *Quercus robur* L., hawthorn *Crataegus monogyna* L., hazel *Corylus avellana* L., blackthorn *Prunus spinosa* L. and field maple *A. campestre* L. The ground vegetation is predominantly dogs' mercury *M. perennis* L. with stinging nettle *Urtica dioica* L. and pendulous sedge *Carex pendula* Huds. Bluebells *Hyacinthoides non-scripta* L. Chourad ex Rothm. are active in spring.

The soil is mostly heavy clay of stagni-vertic cambisol type, with areas of areni-haplic luvisols and calcareous cambisols (FAO/UNESCO classification from Beard, 1993). Meteorological data have been recorded at a grassland site at Wytham, less than 1 km from the plot, since 1992 as part of the UK Environmental Change Network (ECN) monitoring programme (Morecroft et al., 1998). For the period 1993–2008 mean annual precipitation was 725.8 mm, mean annual temperature was 10.1 °C, mean air temperature of the warmest month (from hourly mean temperatures) was 16.7 °C for both July and August, and mean coolest month temperature (from hourly mean temperatures) was 4.4 °C (December). Total solar radiation, measured at this station, is used here as an indicator of potential photosynthesis during the growing season.

This work is part of a larger study of the carbon cycle at this site, with measurements of wood and leaf productivity, leaf decomposition, and measurements of ecosystem-atmosphere CO₂ exchange using eddy-covariance equipment, made over a three-year period.

2.2. Total soil CO₂ efflux

Sampling points for the measurement of total soil CO₂ efflux were installed in autumn 2005, one in each of the 25 subplots (approximately in the centre of each subplot). 'Soil collars' made from 110 mm diameter soil pipe (Flowline, Marley, Maidstone, UK), cut into 100 mm lengths and inserted 50 mm into the soil provide a fixed point for CO₂ efflux measurements and minimise disturbance-induced CO₂ efflux during measurements.

Soil CO₂ efflux measurements were made using a portable infra-red gas analysis system and soil CO₂ efflux chamber (PP Systems, Hitchin, UK) modified with a custom-made adaptor to fit the collars. Each measurement lasted 124 s; one was carried out per subplot, per session, except in the four corners where three were taken to check for measurement consistency. For each corner, the mean of these replicates was used as the value from that collar. These values were then used with each of the other individual measurements to generate the plot mean CO₂ efflux rate, used in the subsequent analysis. Surface litter was removed prior to efflux measurements as the amount of litter varied seasonally over the year.

Measurements were taken at approximately weekly intervals between 3rd April and 30th November 2006, 13th Feb to 23rd November 2007, and every two weeks between 1st April and 14th December 2008. The two-weekly measurements in 2008 were made on weeks between two-weekly partitioned CO₂ efflux measurements. Mean soil temperature over 0–150 mm depth (Digital Waterproof Thermometer, Barnstead International, Dubuque, USA) and volumetric soil water content over 0–200 mm depth (Hydrosense meter, Campbell Scientific, Australia) were measured within 500 mm of the soil collars during soil CO₂ efflux measurements.

2.3. Partitioned CO₂ efflux

We estimated root-and-rhizosphere respiration, mycorrhizal respiration and SOM decomposition using micromesh bags (Plastok Ltd, Birkenhead, UK) to enclose a core of soil *in situ*, from which CO₂ efflux measurements were repeatedly taken throughout the 2008 growing season. This method has been successfully used by Moyano et al. (2007, 2008) and Heinemeyer et al. (2007). Two mesh sizes were used; 36 μm to exclude roots but allow the growth of mycorrhizal hyphae (Smith and Read, 1997) and 1 μm to exclude both roots and hyphae. Both mesh sizes allow the passage of water.

Mesh bags 160 mm in diameter by 300 mm length were installed in Jan 2008, to allow the soil within them to settle before the growing season brought an increase of soil respiratory activity. One bag of each mesh size (36 μm and 1 μm) was installed within 3 m of the existing collars for total soil CO₂ efflux measurement. These bags are closed at the bottom but open at the top; this top opening being about 20 mm larger all round than the 110 mm soil pipe i.e. 150 mm approx open diameter. Collars were installed in the centre of each bag. The open top allows fallen leaves to lie on the soil and decompose as on unpartitioned soil, and migration into the partitioned soil by some soil fauna. For each bag, soil was dug from holes matching bag dimensions, large roots were removed, a bag was fitted into the hole and refilled with the removed soil. Care was taken to maintain the distinct soil horizons and minimise disturbance. The large roots were removed as their decomposition could otherwise have lead to unnaturally high CO₂ efflux rates. Using these bags, three 'partitions' of soil CO₂ efflux are produced:

1. The natural, control partition, producing total soil CO₂ efflux.

$$\begin{aligned} \text{Total soil CO}_2 \text{ efflux (R}_T\text{)} \\ = \text{SOM (R}_{\text{SOM}}\text{)} + \text{mycorrhizal (R}_{\text{MYC}}\text{)} \\ + \text{root rhizosphere (R}_{\text{RRHIZ}}\text{)} \end{aligned} \quad (1)$$

2. A partition without roots and their rhizosphere.

$$\text{R}_{\text{P1}} = \text{R}_{\text{SOM}} + \text{R}_{\text{MYC}} \quad (2)$$

3. A partition containing SOM and its associated soil biota.

$$\text{R}_{\text{P2}} = \text{R}_{\text{SOM}} \quad (3)$$

From these partitions, the relative contributions of the root-and-rhizosphere, mycorrhizal, and SOM-decomposition components of soil CO₂ efflux can be determined as follows:

$$\text{R}_{\text{RRHIZ}} = \text{R}_T - \text{R}_{\text{P1}} \quad (4)$$

$$\text{R}_{\text{MYC}} = \text{R}_{\text{P1}} - \text{R}_{\text{P2}} \quad (5)$$

$$\text{R}_{\text{SOM}} = \text{R}_{\text{P2}} \quad (6)$$

Nine of the 25 subplots were chosen for partitioning, representing variation within the plot. A *t*-test paired by month showed the mean total CO₂ efflux rates of this subset of nine plots do not differ significantly from the mean rates of all 25 subplots, over the three years of measurements (*p* = 0.38).

CO₂ efflux measurements were made approximately every two weeks between 15th April 2008 and 26th November 2008. Mean soil temperature over 0–150 mm depth (Barnstead International, Dubuque, USA) and volumetric soil water content

over 0–200 mm depth (Hydrosense meter, Campbell Scientific, Australia) were measured in all 9 subplots at points equidistant from all 3 collars during partitioned soil CO₂ efflux measurements.

2.4. Data analysis

Total annual soil CO₂ efflux (F_{soil}) was estimated by taking the mean of each consecutive pair of measurements sessions (in μmol m⁻² s⁻¹), multiplying this by the time between those sessions (in seconds), summing these consecutive values over the year. The summed rate in μmol CO₂ m⁻² yr⁻¹ was then converted to Mg C ha⁻¹ yr⁻¹. This simple integration method can be visualised as the area under the graph of all 25 subplots' data in Fig. 1d, and assumes that the mean of two sessions' rates is a fair estimate of efflux rate for the whole time period between the two measurements.

The last measurement of 2007 was on 23rd November and the first of 2008 on 1st April. The mean of these sessions' CO₂ efflux rates may be an overestimate of winter CO₂ efflux, at 0.630 μmol m⁻² s⁻¹, compared to the winter 2007 rate of 0.510 μmol m⁻² s⁻¹. A *t*-test showed no significant difference between the spring CO₂ efflux rates of 2007 and 2008, so the winter 2007 estimate was also used for 2008.

To compare the total CO₂ respired from soil in each season, between years, January–March were classed as winter, April–June as spring, July–September as summer and October–December as autumn. These periods were chosen as corresponding to the phenological cycle, as the majority of trees in the site leaf out in early April and lose their leaves between October and December (data not shown).

Five-week running means were calculated from the 2006–2008 data for total soil CO₂ efflux, soil temperature, soil water content, total solar radiation (used as an indicator of tree photosynthetic activity), and rainfall. The deviations of each year's measurements from this mean annual cycle were then calculated for soil CO₂ efflux and each environmental factor. The implicit assumption here was that the mean annual cycle was driven by a combination of seasonal shifts in plant activity and environmental conditions that are difficult to tease apart from a simple time series, but that interannual variations may be more susceptible to analysis in terms of environmental conditions. Anomalies in soil CO₂ efflux were regressed against anomalies in environmental conditions to determine which environmental factors had the greatest influence.

To calculate the contribution of each component to the total C released, the annual total, as calculated above, was multiplied by the mean annual percentage contributions of each component to total soil CO₂ efflux.

The relationship between soil temperature, soil water content and plant activity and the respiration rate of each component over the whole season, was determined using linear regressions on session mean data for soil temperature and soil water, and total solar radiation for the preceding week, against component respiration rate.

Pearson correlations were carried out to determine which day's total solar radiation had the greatest effect on total soil CO₂ efflux and each efflux component. The correlation coefficients produced and their significance levels are presented in the results. As the day with the greatest effect varied between components, it was felt that the fairest method was to use the sum of all total solar radiation for the whole preceding week.

Statistical analyses were carried out in SPSS version 16.0 for Windows (SPSS Inc., 1989–2007).

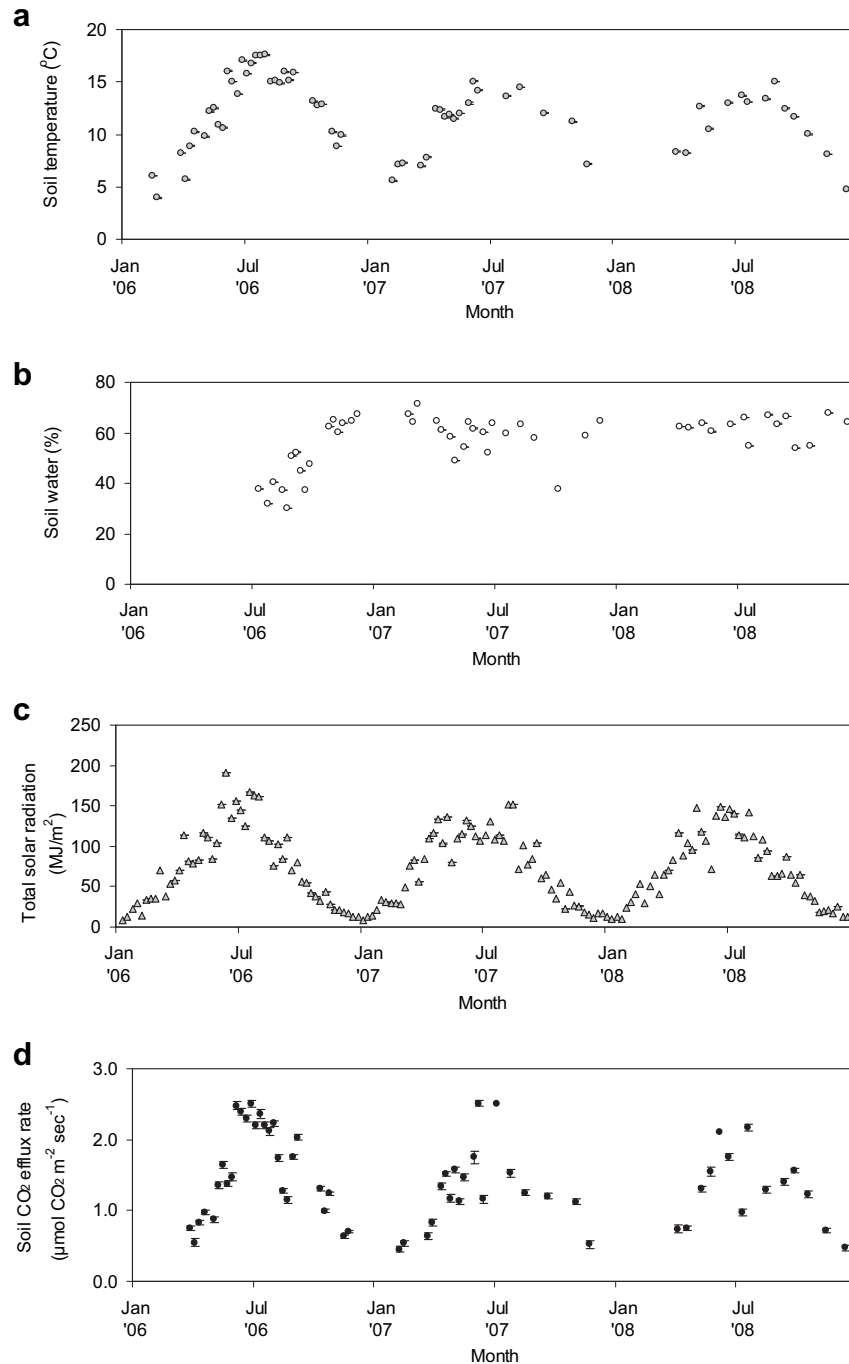


Fig. 1. a) Mean plot soil temperature and b) mean plot soil water content at each measurement session, c) weekly total solar radiation and d) plot mean soil CO₂ efflux rate at each measurement session, for 2006–2008. Error bars represent ± 1 standard error of the mean. X-axis labels indicate start of each month.

3. Results

3.1. Soil temperature, water content, rainfall and solar effects on total soil CO₂ efflux

Soil temperature, solar radiation and soil CO₂ efflux rate showed clear seasonal cycles (Fig. 1), increasing in spring to a summer peak, then decreasing to a winter minimum. The highest summer soil temperature, of 17.6 °C (mean of all 25 plots), occurred in 2006, the peaks in 2007 and 2008 were lower, 15.1 and 15.0 °C respectively; soil water content was also higher in these latter two summers than

2006. Table 1 presents the mean summer (June–September) precipitation and temperature for 2006, 2007, 2008 and the mean for 1993–2008. All three summers in the study period were wetter than the 1993–2008 mean, with 2008 being exceptionally wet (56% more summer rainfall than the long-term mean). Summer 2006 mean temperature was higher, but 2007 and 2008 were cooler, than the long-term mean (Table 1). This variability enabled exploration of the sensitivity of soil CO₂ efflux to temperature and moisture, but did not encompass summer drought conditions.

Rainfall and soil water content fluctuated, with a less clear seasonal pattern than temperature. Following the low 30% soil

water content of summer 2006, water content increased during the autumn to a peak of 71.3% in the spring of 2007, then fluctuated between 45 and 75% for the rest of 2007 and 2008, which were both characterised by cool, wet summers.

Smoothed annual cycles were derived using data for the period 2006–2008 and five-week running means for total soil respiration, soil temperature, soil water content and total solar radiation (Fig. 2). The differences between the raw data from each year and

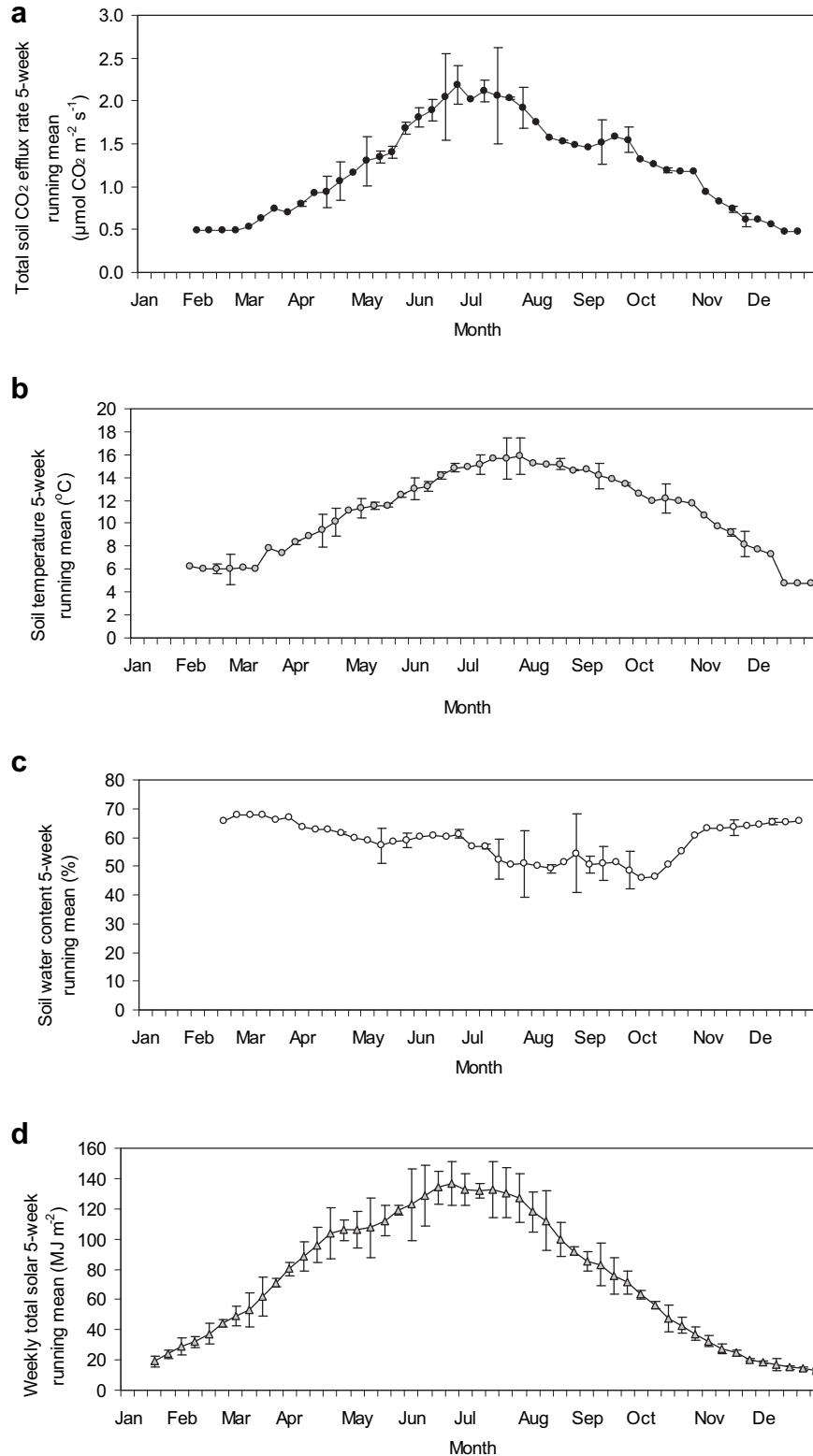


Fig. 2. Annual 5-week running means for the period 2006–2008 for a) total soil respiration; b) soil temperature; c) soil water content; d) total solar radiation, respectively. Error bars represent ±1 standard error of the mean.

Table 1

Mean summer air temperature and precipitation measured at Wytham meteorological station for 2006–2008, and the mean for the years 1993–2008. Summer is classed as July–September inclusive. Means calculated from monthly mean air temperature and monthly total precipitation.

	Mean monthly summer air temperature (°C)	Mean monthly summer precipitation (mm)	Total summer precipitation (mm)
Mean 1993–2008	15.8 ± 0.3	60.3 ± 5.3	180.9 ± 13.3
2006	17.8	82.2	246.6
2007	14.8	63.0	189.0
2008	14.9	93.8	281.4

these mean series (termed anomalies) were used for subsequent analyses. Individual linear regressions were carried out between the anomalies from the annual mean series for each of the factors soil temperature, soil water content and solar radiation (as an indicator of tree photosynthetic activity), against the anomalies from the seasonal mean total soil CO₂ efflux rate. Significant effects on total soil CO₂ efflux rate were shown for soil temperature and total solar radiation ($p < 0.001$, and $p < 0.01$, respectively, Table 2).

As soil temperature was found to be the principal factor affecting soil CO₂ efflux (explaining 50% of the interannual variance), further linear regressions were carried out using the residuals from the linear regression between total CO₂ efflux and soil temperature as the dependent factor, and soil water and total solar radiation again as independent factors. Soil moisture has a significant effect on the residual variation (explaining 18% of the residual variance; Table 3), whilst total solar radiation appears to have no significant effect. This suggests that the significant effect of total solar radiation in the initial regressions was a result of its strong correlation with soil temperature.

Similar regression analyses were then carried out in the same way for the soil CO₂ efflux data separated into spring, summer and autumn anomalies (there were insufficient winter data). Soil temperature explained 68% of the spring and 48% of summer variation in soil CO₂ efflux (Table 4). The sensitivity of soil CO₂ efflux to temperature did not differ significantly between spring and summer (0.207 ± 0.030 and $0.173 \pm 0.045 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} \text{ } ^\circ\text{C}^{-1}$, respectively), suggesting a common mechanism of temperature influence throughout these two seasons.

Regression analyses on the residuals from the soil temperature versus CO₂ efflux regressions, against soil water and total solar radiation, for both spring and summer showed that soil moisture was a significant secondary factor in the control of summer soil CO₂ efflux, accounting for 5% of residual variation (Table 5), although over the course of the study summer water stress was limited.

For June and July, the months of peak mean efflux (mean of all June and July measurements over the three years, $2.03 \pm 0.11 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, F_s), the change in CO₂ respired per 1 °C increase/decrease in soil temperature, ΔF , was $0.164 \pm 0.023 \text{ Mg C ha}^{-1} \text{ } ^\circ\text{C}^{-1}$ or $8.0 \pm 1.2\% \text{ } ^\circ\text{C}^{-1}$. If this percentage sensitivity is maintained over a wider temperature range (assuming respiration

Table 2

Output of individual linear regressions for anomalies in total soil efflux against anomalies in soil temperature, total solar radiation and soil. ***Denotes statistical significance at the $p < 0.001$ level.

	r^2	Intercept	Intercept error (±)	Slope	Slope error (±)	Slope sig.
Soil temperature	0.50	-0.017	0.032	0.164	0.023	0.00***
Total solar	0.17	-0.017	0.039	0.009	0.002	0.00***
Soil moisture	0.00	-0.016	0.066	-0.002	0.008	0.84

Table 3

Output of individual linear regressions of the residuals from the total soil CO₂ efflux versus soil temperature regression against total solar radiation and soil moisture. *Denotes statistical significance at the $p < 0.05$ level.

	r^2	Intercept	Intercept error (±)	Slope	Slope error (±)	Slope sig.
Total solar	0.04	0.145	0.110	0.010	0.007	0.15
Soil moisture	0.18	0.149	0.152	0.043	0.019	0.04*

rate has an exponential relationship to soil temperature), this is equivalent to a Q₁₀ of 2.2 ± 0.2 . For a theoretical 1 °C warming/cooling over the summer period July–September the amount of soil carbon released/retained (ΔF_{summer} , Mg C ha^{-1}) would be $\pm 0.165 \text{ Mg C ha}^{-1}$.

3.2. Annual C release through total soil CO₂ efflux

Total soil CO₂ efflux was estimated to be 4.12 ± 0.01 and $4.11 \pm 0.01 \text{ Mg C ha}^{-1}$, respectively, in 2007 and 2008. CO₂ efflux measurements began in April 2006, preventing an annual total being calculated for this year, however measurements then continued throughout the spring, summer and winter, enabling comparisons of these seasons' total effluxes with 2007 and 2008 data (Fig. 3).

3.3. Component contributions to total soil CO₂ efflux

The partitioning bags were installed in January. Initially, there was a disturbance effect, as would be expected, with the CO₂ efflux rates from the bags being greater than that from the undisturbed collars. By 19th June this disturbance effect appeared to be over as the expected hierarchy of respiration was established ($R_{\text{SOM}} > R_{\text{RRHIZ}} > R_{\text{MYC}}$) and continued throughout the growing season (Fig. 4b).

Analysis of Variance (ANOVA) and Least Significant Difference (LSD) tests were carried out on the CO₂ efflux data of the 11 weeks from 19th June 2008 to 26th November 2008 (weeks 5–15) to determine whether these differences in respiration contribution between components were significant. R_{SOM} was significantly higher than R_{MYC} in all 11 weeks, but significantly higher than R_{RRHIZ} in only six; four of which were the last of the season. Whilst R_{RRHIZ} was higher than R_{MYC} throughout the summer and early autumn (all weeks except 14 and 15), this difference was not significant in 8 of the 11 weeks.

Using the mean contributions averaged over all reliable measurements from 19th June to 26th November the overall contributions of each partition to total soil CO₂ efflux in 2008 can be estimated as 0.9 ± 0.2 , 0.3 ± 0.1 and $2.9 \pm 0.3 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ for R_{RRHIZ} , R_{MYC} and R_{SOM} respectively.

Table 4

Output of individual linear regressions for total soil efflux anomalies from mean against each environmental factor's anomalies from mean, for each of the seasons spring, summer, and autumn, separately. * and ** Denote statistical significance at the $p < 0.05$ and $p < 0.01$ levels, respectively. Spring, summer and autumn, are taken to be Apr–May–Jun, Jul–Aug–Sep, and Oct–Nov–Dec, respectively.

		r^2	Intercept	Intercept error (±)	Slope	Slope error (±)	Slope sig.
Spring	Soil temp.	0.68	-0.051	0.042	0.207	0.030	0.00**
	Total solar	0.16	-0.045	0.063	0.007	0.003	0.03*
	Soil moisture	0.00	-0.039	0.122	0.005	0.035	0.88
Summer	Soil temp.	0.48	0.004	0.069	0.173	0.045	0.00**
	Total solar	0.25	0.002	0.078	0.010	0.004	0.02*
	Soil moisture	0.01	0.011	0.119	-0.003	0.010	0.80
Autumn	Soil temp.	0.15	0.005	0.036	0.032	0.027	0.26
	Total solar	0.10	0.005	0.037	0.006	0.006	0.39
	Soil moisture	0.44	0.001	0.045	0.021	0.014	0.22

Table 5

Output of individual linear regressions of total solar radiation and soil moisture on the residuals from the total soil CO₂ efflux versus soil temperature regression, for spring and summer separately. *Denotes statistical significance at the $p < 0.05$ level.

		r^2	Intercept	Intercept error (\pm)	Slope	Slope error (\pm)	Slope sig.
Spring	Total solar	0.02	0.037	0.036	0.001	0.002	0.51
	Soil moisture	0.00	0.038	0.059	-0.001	0.017	0.94
Summer	Total solar	0.00	0.048	0.056	0.000	0.003	0.96
	Soil moisture	0.49	0.051	0.055	0.013	0.005	0.02*

3.4. Soil temperature, water content, rainfall and solar effects on component activity

All three components showed a positive relationship with soil temperature, that with R_{RRHIZ} was statistically significant ($p = 0.002$). Mycorrhizal respiration rate also showed a positive relationship with soil water content, but R_{SOM} and R_{RRHIZ} decreased with increasing soil water. All three components were positively related to total solar radiation, the relationships with R_{SOM} and R_{RRHIZ} were statistically significant ($p > 0.01$ for both).

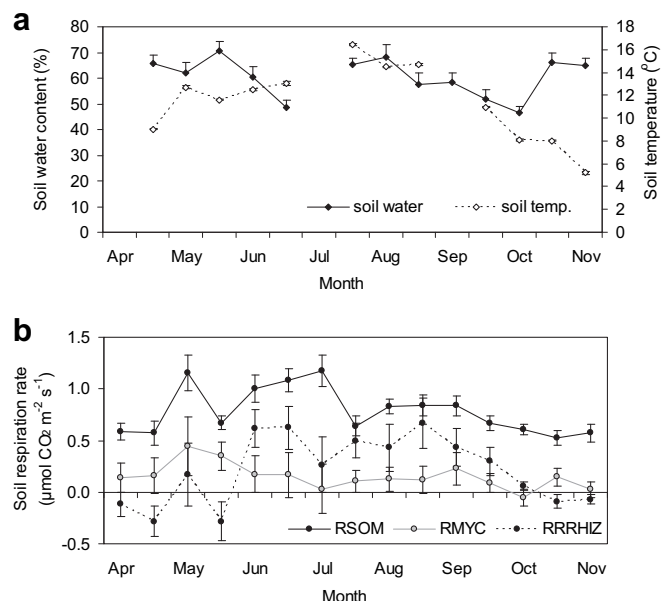
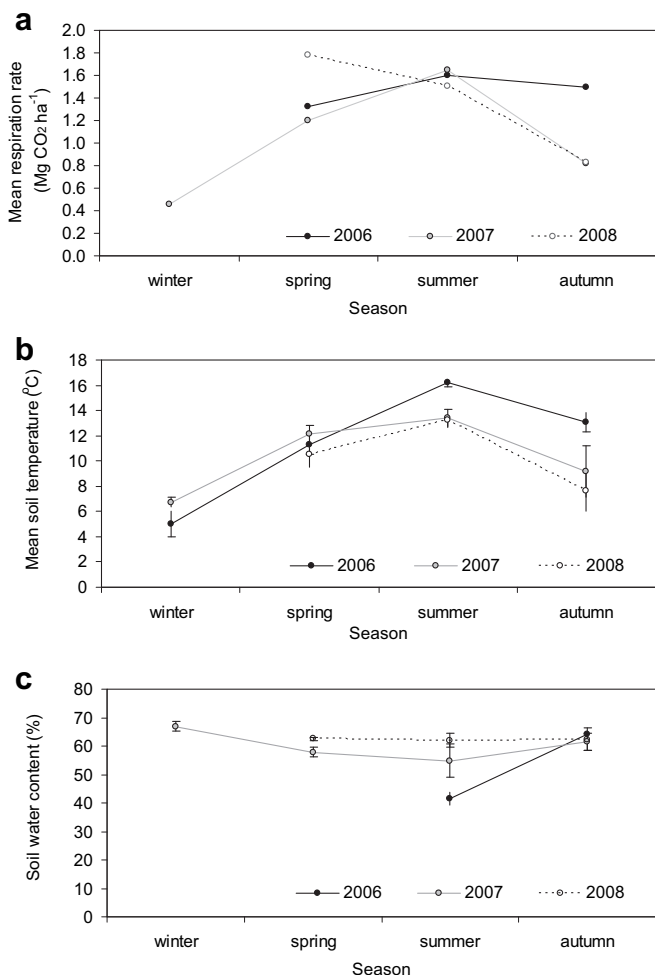


Fig. 4. Chart of **a)** mean soil temperature (grey) and mean soil water content (black), **b)** mean CO₂ efflux rate for SOM decomposition (black), mycorrhizal (white) and root (grey) components over the course of the partitioning experiment. Partitioned respiration results first considered reliable in week 5. Error bars represent ± 1 standard error of the mean.

The lag between solar radiation and respiration rate that generated maximal correlation differed between components. Total solar radiation 5, 1 and 4 days previous to measurement had the greatest correlation coefficient for R_{SOM} , R_{MYC} and R_{RRHIZ} respectively. As explained above, the correlation of R_T with same-day total solar radiation is likely to be an artefact caused by correlation with soil temperature. The lagged correlations may be indicative of a modest effect of solar radiation on root respiration rates, presumably through the supply and allocation of photosynthate.

4. Discussion

4.1. Annual C release through total soil CO₂ efflux

Total annual C efflux from the soil at this site was 4.1 Mg C ha⁻¹ yr⁻¹ for both full years studied. This is generally lower than, or towards the lower end of, annual total ranges found in similar ecosystems (Davidson et al., 1998; Epron et al., 1999; Borken et al., 2002; Mo et al., 2005), possibly due to the removal of leaf litter during soil CO₂ efflux measurements in this study. However soil efflux has been monitored at relatively few sites and more work is needed to identify general patterns relating to soil type, vegetation and management history.

4.2. Temperature sensitivity of total soil respiration

Interannual variability in total soil CO₂ efflux at this site has been shown to be most strongly affected by soil temperature and to a lesser extent by soil moisture. The positive relationship between temperature and soil CO₂ efflux was consistent in sensitivity over spring and summer, with increasing temperature increasing soil efflux rates. On an interannual timescale the sensitivity of soil CO₂ efflux at this site to soil temperature variation is $0.164 \pm 0.023 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} \text{ }^\circ\text{C}^{-1}$. This sensitivity is linear at the range of soil temperatures recorded during this study, but over an extended range equates to a Q_{10} of 2.2 ± 0.2 on an interannual

timescale. This compares well with the assumed Q_{10} of 2 used for soil CO_2 efflux in several ecosystem models (e.g. Friedlingstein et al., 2006), but to our knowledge this is the first study to exploit inter-annual variability in soil CO_2 efflux to test this assumption.

Whilst the effect of soil temperature can be hard to distinguish from the effect of tree activity and solar radiation within the annual growth cycle, analysing anomalies from interannual means allows relationships between environmental factors and soil CO_2 efflux to be investigated. Taking June and July, the months of peak mean efflux, as an example, a 1°C anomaly from mean soil temperature can result in an 8% anomaly from peak summer soil CO_2 efflux at this site. A summer period (July–September) during which the soil is warmer/cooler by 1°C results in the release/retention of $0.165 \text{ Mg C ha}^{-1}$ of soil carbon (unless a strong summer drought beyond the range of that observed in our measurement period causes a reduction in soil CO_2 efflux). The effect of soil moisture on the rate of soil CO_2 efflux becomes apparent in summer, with dry conditions depressing efflux. This study was carried out during a relatively wet period and larger effects may be found during drought conditions. Additionally, the warming-induced release of CO_2 from soil suggested by our temperature-sensitivity analysis may in reality decrease over the longer term, as interannual warming/cooling affects more labile pools than longer-term warming.

4.3. The mesh bag method for soil partitioning

The bag method for partitioning CO_2 efflux into SOM, mycorrhizal and root & rhizosphere components has been successfully applied for one growing season in this temperate deciduous wood. Six months were needed for soil CO_2 efflux rates within the bags to reach an apparent equilibrium, this may be because of the high clay content of the soil and/or because at this ancient woodland site has had very little previous soil disturbance (Morecroft et al., 2008). Once equilibrium had established, the hierarchy of component contribution was found to be $R_{\text{SOM}} > R_{\text{RRHIZ}} > R_{\text{MYC}}$; the same as found by Moyano et al. (2008).

The partition referred to here as SOM is as close an approximation to natural conditions as possible, with the exclusion of root and mycorrhizal presence. The respiration rates measured may however be an underestimate of the natural R_{SOM} , as the absence of roots leads to the absence of root exudates which are respired by soil microorganisms, and can elevate R_{SOM} by rhizosphere priming. Priming occurs when root exudates increase microbial activity, which in turn stimulates SOM breakdown (Kuzakov, 2002).

As mycorrhizal structures, the arbuscules, exist within roots, the R_{RRHIZ} component contains the respiration of roots, rhizosphere organisms and arbuscules. R_{MYC} is the respiration of only the mycorrhizal hyphae, the extraradical mycelium respiration referred to by Heinemeyer et al. (2007). As this is the situation in the field, we have not attempted to separate root and arbuscular respiration for the purposes of this study; this might be a topic for further work although it would be difficult to achieve in a field situation.

The observed differences in respiration rates and seasonality of respiration between partitions are taken as evidence that the bags are effectively partitioning total soil CO_2 efflux as intended. Johnson et al. (2002) found that ^{13}C taken up by plants in their pulse-labelling experiment was respired from soil into which only mycorrhizal mycelia, not roots, could gain access (within a $35 \mu\text{m}$ mesh), inferring that mycorrhizal mycelia had colonised the soil within the cores. Direct analysis of soil within bags for mycorrhizal and root presence and absence would add strength to any further studies using this method.

The absence of roots and their exudates and/or the disturbance and soil oxygenation caused by bag installation may also have

created changes in the bacterial communities within bags, with the result that they cannot be fairly compared. Soil bacterial analysis would therefore be an interesting aspect of any future work using the bag partitioning method. Additionally a control partition should be considered, using a bag with mesh large enough for roots and soil fauna to easily recolonise the soil. Disturbance would then be common across all partitions, allowing the three to be confidently compared.

4.4. Environmental factor effects on respiration components

Within an annual cycle, all three components showed a positive relationship with soil temperature and solar radiation, which is unsurprising as this tracks the seasonal cycle of biological activity. As partitioning of soil CO_2 efflux was carried out for only one year, it was not possible to separate the inherent seasonal cycle from direct effects of environmental variables. Hence the relationships observed do not indicate a causal relationship between environmental drivers and soil CO_2 efflux. Nevertheless, the analysis does provide an insight into the environmental correlates of seasonal variation of soil CO_2 efflux. R_{MYC} showed a positive relationship with soil water content, whilst R_{SOM} and R_{RRHIZ} decreased with increasing soil water, reinforcing the finding of Heinemeyer et al. (2007) that mycorrhizal respiration is more sensitive to drought than SOM respiration.

The one- and four-day lags between photosynthetic activity, and mycorrhizal and root respiration, respectively, at this site resemble the findings of Moyano et al. (2008) in a beech wood (*Fagus sylvatica*). Ekblad and Högborg (2001) also found a one- to four-day lag between canopy photosynthesis and root respiration in a mixed Boreal forest. As Moyano et al. (2008) used eddy-covariance derived GPP, this result suggests that for mycorrhizal and root respiration, the components most directly affected by photosynthesis, total solar radiation is an adequate proxy for plant activity. SOM respiration, however, appears to be most directly affected by total solar radiation through its effects on soil temperature. As SOM is the dominant respiration component in this system, accounting for 70% of total soil CO_2 efflux, its temperature-related response masked the plant activity-related response of the other two components in the analysis of the total soil CO_2 efflux relationship to total solar radiation.

Högborg et al. (2001), carried out a tree girdling experiment in a boreal pine forest and found SOM respiration to increase earlier in the summer than root and mycorrhizal respiration (which were measured together in that study), but both declined over a similar time in autumn. A similar early increase in R_{SOM} is seen here, but R_{RRHIZ} declines earlier in the autumn, and to a greater extent than R_{SOM} , possibly as a result of the autumn decline in plant activity. R_{MYC} also declines slightly in autumn, but shows a small increase around the end of October, similar to a peak observed by Heinemeyer et al. (2007) during fungal fruiting.

Whilst an increase in photosynthate supply increases respiration rate in the mycorrhizal and root-and-rhizosphere components of soil CO_2 efflux, it may also possibly result in increased tree growth and carbon storage in trunk and, over the shorter-term, in leaves.

5. Conclusions

In this study we have employed two recently developed approaches of general utility beyond this particular study: an interannual anomaly analysis to evaluate the sensitivity of soil CO_2 efflux to environmental drivers, and partitioning of the efflux into soil SOM decomposition and mycorrhizal and root respiration. We found that soil temperature has the greatest effect on interannual

variation of soil CO₂ efflux at this site, primarily through its influence on the rate of SOM decomposition. This effect is apparent on an interannual basis, separate from the seasonal cycle. Seasonal decreases in soil moisture were found to correlate with a decrease in mycorrhizal respiration rate, but an increase in SOM decomposition and root-and-rhizosphere respiration. As SOM decomposition and root-and-rhizosphere respiration contribute $70.3 \pm 6.2\%$ and $21.5 \pm 6.0\%$, respectively, to total soil respiration, we can expect increased summer CO₂ efflux rates during warm, dry summers which are expected to increase in frequency in this region over the 21st century.

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