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Exploring the “overflow tap” theory: linking forest soil CO_2 fluxes and individual mycorrhizosphere components to photosynthesis

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Abstract. Quantifying soil organic carbon stocks (SOC) and their dynamics accurately is crucial for better predictions of climate change feedbacks within the atmosphere-vegetation-soil system. However, the components, environmental responses and controls of the soil CO_2 efflux (R_s) are still unclear and limited by field data availability. The objectives of this study were (1) to quantify the contribution of the various R_s components, specifically its mycorrhizal component, (2) to determine their temporal variability, and (3) to establish their environmental responses and dependence on gross primary productivity (GPP). In a temperate deciduous oak forest in south east England hourly soil and ecosystem CO_2 fluxes over four years were measured using automated soil chambers and eddy covariance techniques. Mesh-bag and steel collar soil chamber treatments prevented root or both root and mycorrhizal hyphal in-growth, respectively, to allow separation of heterotrophic (R_h) and autotrophic (R_a) soil CO_2 fluxes and the R_a components, roots (R_r) and mycorrhizal hyphae (R_m).

Annual cumulative R_s values were very similar between years ($740 \pm 43\,\mathrm{g\ C\,m^{-2}\,yr^{-1}}$) with an average flux of $2.0 \pm 0.3\,\mu\mathrm{mol\ CO_2\,m^{-2}\,s^{-1}}$, but R_s components varied. On average, annual R_r, R_m and R_h fluxes contributed 38, 18 and 44 %, respectively, showing a large R_a contribution (56 %) with a considerable R_m component varying seasonally. Soil temperature largely explained the daily variation of R_s ($R^2 = 0.81$), mostly because of strong responses by R_h ($R^2 = 0.65$) and less so for R_r ($R^2 = 0.41$) and R_m ($R^2 = 0.18$). Time series analysis revealed strong daily periodicities for R_s and R_r, whilst R_m was dominated by seasonal (∼150 days), and R_h by annual periodicities. Wavelet coherence analysis revealed that R_r and R_m were related to short-term (daily) GPP changes, but for R_m there was a strong relationship with GPP over much longer (weekly to monthly) periods and notably during periods of low R_r. The need to include individual R_s components in C flux models is discussed, in particular, the need to represent the linkage between GPP and R_a components, in addition to temperature responses for each component. The potential consequences of these findings for understanding the limitations for long-term forest C sequestration are highlighted, as GPP via root-derived C including R_m seems to function as a C “overflow tap”, with implications on the turnover of SOC.

1 Introduction

Soils contain the largest terrestrial organic carbon (C) stock (Bolin et al., 2000), representing two-thirds or more of terrestrial C (Schimel et al., 1994; Tarnocai et al., 2009). Each year an amount equivalent to ∼10 % of the atmospheric CO_2 is respired from soils (Raich and Potter, 1995), and even small changes in soil CO_2 efflux (R_s) may have profound feedback implications on atmospheric CO_2 concentration (Schlesinger and Andrews, 2000), and thus global temperatures through the greenhouse effect (Kirschbaum, 2000; Sulzman et al., 2005). Quantifying soil organic carbon (SOC) dynamics accurately is therefore crucial for better predictions of climate change feedbacks within the atmosphere-vegetation-soil system (Cox et al., 2000; Smith and Fang, 2010). Our basic understanding of soil CO_2 efflux and its components (i.e. autotrophic, R_a, activities of roots and their associated mycorrhizal fungi, and heterotrophic, R_h, free-living microbes and soil animals), their controlling factors and environmental

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responses are still under debate and limited by available field methodologies (Kutsch et al., 2009; Kuzyakov, 2006a, b). Despite a wide network of field-based R_s measurements (Bond-Lamberty and Thomson, 2010) and analyses of its abiotic and biotic drivers, there is still considerable uncertainty regarding the response of the individual flux components to changes in climate. In particular, how R_s and its biological components will respond to rising temperatures in situ is still uncertain (e.g. Grace and Rayment, 2000) and might be overestimated globally (Mahecha et al., 2010). It is becoming clear that models have to treat R_s components independently, as R_h and R_a are influenced differently by changes in biotic and abiotic conditions, so that predictions based only on abiotic drivers (e.g. temperature and moisture) are not sufficient (Smith and Fang, 2010; Mahecha et al., 2010). Further, R_s shows linkages to gross primary productivity (GPP) through its R_a component, yet with time-lags, apparently due to changes in C allocation patterns between shoots, roots and mycorrhizas (Mencuccini and Hölttä, 2010; Vargas et al., 2010a), a process still to be understood and included in models (Kuzyakov and Gavrichkova, 2010). Recently, Heinemeyer et al. (2007) proposed that the mycorrhizal component (R_m) might function as an "overflow tap" in forest C allocation, allowing the plant to allocate C to the mycorrhizal partner under either C surplus or nutrient limiting conditions with consequent impacts on ecosystem C turnover and storage. However, this hypothesis was based on only a short-term seasonal flux separation, and only indirectly indicated the R_m dependence on assimilate supply. Crucially, the R_a components (i.e. roots and mycorrhizas) seem to respond differently to short-term temperature and moisture variations than R_h (Heinemeyer et al., 2006, 2007), thus impacting on the overall R_s temperature responses (Subke and Bahn, 2010). Long-term partitioning studies of R_s components into soil R_a and R_h and their temperature responses (Fitter et al., 2004; Kirschbaum, 2006; Heinemeyer et al., 2007) are increasingly becoming a research focus in order to better understand the measured R_s responses to key environmental factors and thus model forest C cycling (Hanson et al., 2000; Bond-Lamberty et al., 2004; Ekblad et al., 2005).

The desired separation of R_s components is challenging yet necessary to understand the link between the canopy and soil processes and currently no perfect method is available for accomplishing it (Kuzyakov, 2006b; Subke et al., 2006). Recently, a mesh-collar methodology was developed to separate seasonal R_r, R_m and R_h components and the results showed their different environmental responses (Heinemeyer et al., 2007). In the past R_r was considered the main R_a component, ignoring the central role of mycorrhizal mycelia in terrestrial C-dynamics and global environmental change (Fitter et al., 2004). Mycorrhizal fungal mycelia have a central role in C and nutrient translocation between roots and soil organisms (Coutry et al., 2010), influencing litter decomposition (Lindahl et al., 2007) and possibly SOC priming (Talbot et al., 2008) that could influence C fluxes at the ecosystem scale (Vargas et al., 2010b). For example, although there can be 8000 m of ectomycorrhizal (ECM) hyphae per metre of root (Leake et al., 2004) few studies have measured R_m in-situ (Heinemeyer et al., 2007; Moyano et al., 2008; Fenn et al., 2010) despite strong evidence of its key role in soil R_a (Söderström and Read, 1987; Rygiewicz and Andersen, 1994). Moreover, soil respiration collars are routinely inserted several centimeters into the soil, inevitably cutting through considerable amounts of roots (and mycorrhizal hyphae), causing a loss of a potentially large proportion of the autotrophic substrate supply for R_s, leading to altered R_h/R_s ratios and thus biased environmental flux correlations (Heinemeyer et al., 2011).

This study addressed four related research questions: (1) How much of the measured total R_s derives from heterotrophic R_h versus autotrophic R_a components (R_r and R_m) and how constant are the proportional contributions over temporal scales from hours to years? (2) Do these R_s components respond similarly to weather variability and key environmental factors? (3) To what extent do these component fluxes depend on GPP? (4) Is there continued evidence to support the concept of mycorrhizal activity to depend on a plant regulated "overflow tap" for labile C in plants (Heinemeyer et al., 2007)?

The study aims to provide fundamental insights into the linkage between canopy and soil carbon fluxes (i.e. temporal variations and correlations both in the time and frequency domains among GPP and R_s components). Specifically, it aims to provide additional data to evaluate the concept of a mycorrhizal "overflow tap" for labile C in plants, and to explore any plant regulation of this process.

2 Materials and methods

2.1 Site description

The study site was located within the Alice Holt research forest in SE England (51°10′ N; 0°51′ W; 80 m a.s.l.). The 30 yr (1961–1990) average mean annual air temperature was 9.4 °C and precipitation was 780 mm. The site lies within the Straits Enclosure, a ∼90 ha block of lowland woodland, comprising mainly deciduous oak (*Quercus robur* L.), ∼10 % ash (*Fraxinus excelsior* L.), a mixed understory of woody shrubs, dominated by hazel (*Corylus avellana* L.) and hawthorn (*Crataegus monogyna* L.). The maximum LAI was ∼5 and budburst occurred from March (understory) to May (trees). The average tree height was about 25 m with an age of 75–80 yr. The soil is a surface water gleysol (England and Wales soil classification: Wickham series) with a shallow O-horizon (∼3 cm) and a total depth of 80 cm to the C horizon of the Cretaceous clay, with a high water table. The $pH_{(H_2O)}$ is 4.6 and 4.8 in the organic and mineral horizons, respectively.

2.2 Soil respiration and soil environmental measurements

A multiplexed (custom-built gas handler unit; Electronics Workshop, Biology Department, University of York, UK) closed dynamic soil CO_2 flux system (Li-Cor 8100, chamber model: 8100-101; Li-Cor Biosciences, Lincoln, Nebraska, USA) was used for measuring R_s in the field. Up to 16 chambers can be sampled within a 10 m radius, individually closing, measuring and opening all chambers within an hourly cycle. As our research questions address the periodicity of fluxes and linkages to canopy assimilation over a wide range of temporal resolutions, rather than the spatially explicit characterisation of R_s, we used a continuous sampling method from fixed locations. R_s was calculated as the linear CO_2 increase (2 s measurements) during chamber closure time (less than 2 min), discarding a 45 s mixing period. Soil surface collars (3.5 cm × 20 cm diameter PVC drain pipe [Wolseley, UK]) were placed onto the soil surface and pressed into position by 25 cm long steel rods (2 mm diameter) attached to the collar rim. This provided an airtight collar seal, which was verified during routine maintenance checks, with no disturbance to shallow root and hyphal networks (Heinemeyer et al., 2011). The litter layer was first removed and combined from all collar positions. After mixing, an equal sub-sample (15 g fresh weight) was returned to each collar. Further equal litter additions were performed regularly (weekly to monthly according to season) from mixed equal area samples from on-site litter traps, which were air dried, weighed and returned the next week. To prevent litter loss, uncontrolled additions or disturbance, litter in soil collars was covered with a circle of coarse plastic mesh (2 cm grid). To prevent twigs and other falling debris obstructing chamber closure a coarse (2 cm grid), thin nylon mesh (1 × 1 m) was fixed at 1 m above each collar. Hourly soil temperature profiles at 0, 2, 10 and 20 cm depths ($n = 3$) and soil volumetric moisture content (at 2–7 cm depth; $n = 1$) were monitored centrally within the site (DL2e logger, ST4 temperature probes and ML2x Theta moisture probe, Delta-T Devices, Burwell, Cambridge, UK). This soil moisture probe was repositioned at about monthly intervals during the experiment. A similar hand-held moisture probe was periodically (about monthly) used to record soil volumetric moisture content (SMC) in all collars. In 2010 similar moisture probes (SM200, also Delta-T Devices) were installed inside treatment collars. Air temperatures inside each chamber were also recorded during each measurement.

2.3 Eddy covariance CO_2 flux measurements

Net ecosystem CO_2 exchange (NEE) was measured continuously with the eddy covariance (EC) methodology since 1999, after Moncrieff et al. (1997). Measurements and calculation procedures followed the "Euroflux" project, described by Aubinet et al. (2000). The equipment consisted of a sonic anemometer (Solent R2, Gill Instruments, Lymington, UK) and a closed path CO_2 and H_2O infrared gas analyser (IRGA; Li-7000, Li-Cor Biosciences, Lincoln, Nebraska, USA). Sample air was drawn from the top of a 28 m high instrument mast down a tube (6 mm ID Dekabon) and through two inline 1 µm PTFE Teflon filters (Gelman Acro 50, Pall Life Sciences, Ann Arbor, Michigan, USA) at a rate of $\sim$6 l min^{-1} by a pump (Capex V2 SE, Charles Austen Pumps, Byfleet, Surrey, UK). Calibration of the IRGA with certified reference gases was performed weekly. Raw data outputs from the anemometer and IRGA were logged (Edisol software: http://www.geos.ed.ac.uk/abs/research/micromet/edisol/) at a rate of 20 Hz. For this study, continuous 30 min data were available from January 2007 to December 2010. An automatic weather station recorded supplementary meteorological variables, including air temperature, at both mast height and at ground level.

In order to account for flux losses mainly caused by signal damping inside the tube, limited time response, and sensor separation (e.g. Leuning and Moncrieff, 1990; Massman, 1991; Aubinet et al., 2000), EC data were reprocessed using the EdiRe software (www.geos.ed.ac.uk/abs/research/micromet). NEE was calculated from corrected CO_2 fluxes, but no allowance was made for canopy CO_2 storage, which can be significant for short periods around dawn and dusk. To calculate hourly, daily and annual NEE, missing data were substituted based on the standard CarboEurope gap-filling procedure (http://www.bgc-jena.mpg.de/bgc-mdi/html/eddyproc/index.html; Reichstein et al., 2005). The on-line tool accounts for temporal auto-correlation of fluxes, replacing missing data with the average value under similar meteorological conditions within a 7-day window or longer if needed. The tool was also used to partition NEE flux data into GPP and total ecosystem respiration (R_{eco}). This uses night-time temperature regression models to estimate R_{eco} with linear interpolation between time periods (Reichstein et al., 2005), and GPP was calculated as the difference between NEE and R_{eco}. At the instrument mast site, the fetch over the woodland is up to 800 m in the direction of the prevailing south-westerly winds, but less in other directions. Typically >70 % of measured fluxes in near-neutral atmospheric stability conditions are estimated to occur completely within the woodland (within 350 m of the mast, calculated using the Kormann and Meixner model (2001) in EdiRe); if the wind is from the south-west, this percentage is typically >85 %.

2.4 Experimental design

On 22 March 2007 twelve soil collars were randomly installed within the enclosure around the EC instrument mast. During the first year (2007) collars were all surface collars (see Sect. 2.2) which did not cut roots or mycorrhizas. On 18 September 2007 four surface collars were left undisturbed and under the other two pairs of four collars was installed either a mesh-bag (diameter 25 cm × 45 cm deep with 42 µm pore size; Normesh Ltd., Oldham, UK) allowing in-growth by mycorrhizal hyphae but not roots, or a similar 1 µm mesh-bag to exclude both. The main fine rooting depth in this periodically waterlogged clay soil is down to about 40 cm (unpublished data), declining in an expected exponentially pattern similar to other sites (Heinemeyer et al., 2011). Therefore, more than 95 % of the fine root mass will be captured by this depth. To enable meaningful flux comparisons between treatments, we allocated the treatments on ranking the annual pre-treatment fluxes from the individual collar locations. The overall variation during the pre-treatment period was quite large (STDEV of $\pm 0.86\,\mu mol\,m^{-2}\,s^{-1}$) and no significant differences were detected between collar averages (ranging from 2.64 to $2.71\,\mu mol\,m^{-2}\,s^{-1}$ for the three pre-treatment averages with an SE of between 0.26 to $0.39\,\mu mol\,m^{-2}\,s^{-1}$). However, the 1 µm mesh-bags were replaced in March 2008 by open-ended steel collars (deep collar treatment; same dimensions), as it was evident from the considerable hyphal in-growth that this mesh did not exclude hyphae. For mesh-bag insertion soil was extracted with the steel collar in 5 cm horizon layers, and stored on individual trays. Larger roots were removed (to limit additional CO_2 from root decomposition) and soil was then back-filled in horizon order to packing density. Consequently, measured CO_2 fluxes were: (a) total R_s (RMS treatment; surface collars), (b) R_m and R_h (MS treatment; 42 µm mesh-bag), and (c) R_h only (S treatment; deep steel collar). In March 2008 a fourth treatment was added, whereby roots and mycorrhizas were cut repeatedly with a spade to a depth of 45 cm (monthly during the growing season, otherwise bi-monthly) around four additional soil surface collars at a 30 cm diameter (S_{cut}). This enabled comparison with the S treatment but without the permanent barrier of a steel collar. CO_2 fluxes from all 12 or 16 collar locations were monitored at hourly intervals until December 2010. Following Heinemeyer et al. (2007), the contribution of individual R_s components was calculated as:

1. $R_r = RMS_{resp} - MS_{resp}$
2. $R_m = MS_{resp} - S_{resp}$
3. $R_h = S_{resp}$
4. $R_a = R_m + R_r$

where RMS_{resp} is the mean rate of respiration of the RMS treatment, and MS_{resp} and S_{resp} are those for the MS and S treatments, respectively. As the MS, S and S_{cut} treatments tended to have higher volumetric soil moisture than the RMS treatment, because there was no root water uptake, removable plastic covers (45 × 45 cm clear tilted plastic sheets) were used to reduce rainfall input to MS, S and S_{cut} treatments. From March 2009 these were periodically (based on regular soil moisture readings and aimed at reducing any observed differences) placed at 1 m height together over the permanent protection meshes (see Sect. 2.2). The above-ground respiration rate (R_{ab}) was estimated as the difference between R_{eco} and R_s from the soil chambers; and net primary productivity (NPP) calculated as GPP $-(R_{ab}+R_a)$.

2.5 Temperature sensitivity

A Q_{10} function (Atkin et al., 2000) was applied to annual and seasonal periods using mean daily values of R_s and its components, whereby the slope of the $\log_{10}$ of soil CO_2 effluxes against soil or air temperature, β, is used to calculate the $Q_{10} = 10^{[10\times\beta]}$. The SE of β was used to calculate the uncertainty of Q_{10}.

2.6 Time series analysis

Wavelet analysis was used to study the temporal variation of the time series of each CO_2 flux component. This technique has been widely used for climatological applications (Daubechies, 1990; Torrence and Compo, 1998; Grinsted et al., 2004) and more recently for R_s analyses (Vargas et al., 2010a, 2011). Wavelet analysis has an advantage over the alternative Fourier analysis because the window size of the wavelet transform is not fixed giving a better resolution of the temporal variations. Here continuous wavelet transform (CWT) with the Morlet mother wavelet was used because of its ability to produce a smooth picture in the time-scale domain of non-stationary processes (e.g. R_s) and its suitability for visual interpretation (Torrence and Compo, 1998). Wavelet analysis was applied on the temperature de-trended time series of hourly GPP, R_{ab}, R_s, R_r, R_m, and R_h fluxes based on individual exponential temperature corrections (flux = $B_0 e^{(T\cdot B_1)}$) for each day according to Vargas et al. (2011). Therefore, B_0 and B_1 are constants for individual fluxes and vary for each day and temperature (T) was soil temperature at 2 cm depth, which showed maximum diurnal fluctuations and highest correlation with R_s. Removing the effect of temperature is important when studying the periodicity of fluxes in order to isolate the temporal variation of biological drivers (Vargas et al., 2010a). Temperature is auto-correlated with GPP and R_s (and its components) because the daily oscillations of all those variables respond to diurnal changes imposed by solar radiation (i.e. day versus night). Thus a conservative estimate of the influence of GPP on R_s and component fluxes was obtained by this de-trending method, which can be viewed as an analysis of residuals. Although different approaches can be applied, we kept consistency with a recently published protocol by Vargas et al. (2011).

Wavelet coherence analysis (WCA; see Grinsted et al., 2004) was used to determine the temporal correlation between the two de-trended time series and to quantify the phase difference or time-lag between them at specific periods (e.g. 1-day, 8-day). In the figures and tables we only provide information about variations between days (in terms of hourly data for the 1-day time period (i.e. intra daily variations) for clarity, although high temporal resolution fluxes (hourly) were used in the actual analysis. The statistical significance (5 % probability level) of common power between two time series (e.g. R_s and GPP) was assessed within the "cone of influence" of the WCA using Monte Carlo simulations of wavelet coherency (Grinsted et al., 2004). The cone of influence delimits the region in which the wavelet transform is not influenced by edge effects because of incomplete time-locality across frequencies (Torrence and Compo, 1998), and multiple studies have described in detail this technique for climatology applications (Grinsted et al., 2004; Torrence and Compo, 1998) and soil respiration research (Vargas et al., 2010a).

The phase relationships, or time-lag gives information on the synchronization between oscillations of the two time series (Govindan et al., 2005). The delay between two time series can provide information on the nature and origin of coupling between the processes, and causality under the assumption that the effect must follow the cause. The mean phase difference between hourly fluxes of R_s, R_r and R_m and GPP (as a surrogate for substrate supply) at the 1-day period was calculated from the WCA to explore the potential fast control of recent photosynthesis on soil CO_2 fluxes. Data analyses were performed using MATLAB R2007a (The MathWorks Inc.).

2.7 Statistical analysis

Statistical analyses were carried out using SPSS (Version 18, SPSS Science, Birmingham, UK) and Kolmogorov-Smirnov and Levene's tests were used to test for normality and homogeneity of variances. One-way ANOVAs with a post-hoc test (Tukey's) were used to determine significant differences between treatments for SMC and also annual R_s component differences. For the Q_{10} values the SE was derived from the slope of the individual $\log_{10}$ regressions. For regression analysis, the regression coefficients of determination (R^2) between flux and environmental variable are reported.

3 Results

3.1 Annual soil respiration patterns

The multiple soil chamber system provided near continuous hourly soil CO_2 efflux over four years. Over the first year (2007) daily R_s averages varied between 0.5 to 4.5 µmol m^{-2} s^{-1} (Fig. 1) and showed a general association with the seasonal pattern of temperature, although there were marked changes in the responsiveness during active canopy growth between budburst (spring) and leaf fall (autumn).

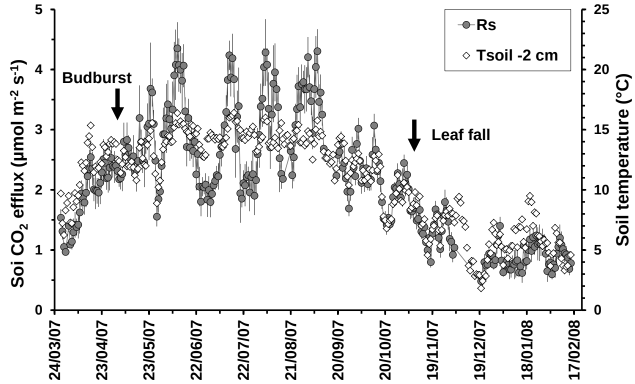

Fig. 1. Mean daily CO_2 efflux from soil respiration (R_s) measured from surface collars and soil temperature (T_{soil}) at 2 cm depth at the Straits Enclosure, Alice Holt forest from 24 March 2007 to 17 February 2008. Bars indicate ± s.d. ($n = 12$ until 18 September and thereafter $n = 4$), and arrows indicate the approximate onset of budburst (1 May) and leaf fall (1 November) of the oak canopy. Gaps were due to system power failure.

3.2 Environmental conditions and treatment effects on soil moisture

In general, the site temperature is relatively mild (1961–1990 mean annual air temperature is 9.6 °C), and monthly rainfall usually quite evenly distributed through the year (∼65 mm month^{-1}), although near-surface volumetric SMC can be less than 30 % in summer (Tables 1, 2 and Fig. 2). The first three years (2007–2009) of measurement showed annual air temperatures 0.6–1.0 °C warmer than the long-term average, and were much wetter, particularly 2007, but the final year (2010) was slightly colder than the long-term average (Table 1), with a pronounced summer dry period and cold winter (see Fig. 3a). Consequently, average annual near-surface SMC was high in the first two (∼50 % v/v) and lower (∼40 %) in the last two years with summer values reaching ∼20 % (Fig. 2).

Air temperatures in the treatment soil chambers closely matched those measured at the adjacent automatic weather station (Table 1). However, the root and hyphal exclusion treatments showed higher SMC than in the RMS collars during the manual measurements at all plots in 2008 (Table 2). Removable rain covers were deployed in 2009 and 2010 over the MS, S and S_{cut} collars at 1 m height (see Sect. 2.4) to adjust the SMC towards the drier RMS treatments. Although during mid-summer differences were significant (mostly between RMS and S treatments), the mean volumetric SMC difference was about less than 10 %, 15 % (Table 2) and 10 % (Fig. 2) in 2008, 2009 and 2010, respectively. In 2010 hourly soil moisture within individual treatments showed similar seasonal trends; although it was lower in the RMS treatment than others, there was good agreement between the central location and the RMS treatments and the effect of rain exclusion in the MS and S treatments was evident (Fig. 2).

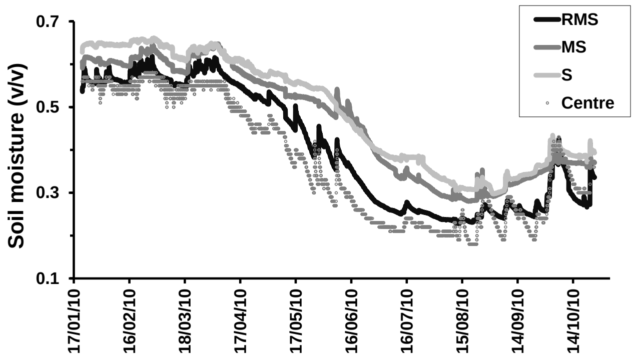

Fig. 2. Seasonal changes of soil volumetric moisture content (v/v) at the Straits Enclosure, Alice Holt forest in 2010 measured hourly at 6 cm depth for three replicated ($n = 4$) soil collar treatments (surface collar, RMS), mycorrhizal 41 µm mesh bag (MS) and steel collar (S) and in the undisturbed central area (Centre). The average SE was ~0.02 (v/v) for all treatments (not shown for clarity).

3.3 Separation of soil respiration components

The mesh collar insertion on 18 September 2007 and subsequent replacement with a steel collar for root and mycorrhizal exclusion, respectively, resulted in a disturbance period lasting around six months (evidently higher CO_2 flux rates initially, then subsequent reduction; data not shown). The CO_2 fluxes measured from the end of March 2008 onwards showed clear differences between treatments with daily CO_2 flux rates in the treatment order RMS > RM > S (data not shown). Example results for the derived daily component fluxes in 2010 are shown in Fig. 3c. Overall R_s showed large seasonal fluctuations which reflected different periods of high R_a and R_h activity. Generally R_h was higher than R_a in winter but sometimes lower during the growing season. Whereas R_a increased around budburst of the understory (March) and tree (May) canopy and declined in late summer, R_h was more sustained and less variable. Moreover, whereas in spring and summer R_r and R_m showed parallel patterns, in early autumn daily R_m tended to show higher increases coinciding with the emergence of ECM fruiting bodies around September to October (Fig. 3c). However, in autumn daily R_m also showed marked declines during periods of high or even increasing R_r. Fluxes from the S treatments (i.e. deep collar) compared well to those measured from repeatedly cut (S_{cut}) treatments (see Fig. 3c inset).

3.4 Interannual and seasonal forest and soil C flux components

The CO_2 flux components of the forest showed large interannual differences (Table 3) with a range in GPP of 33 % of the 4-yr mean (declining over the four years and in 2010 was 65 % smaller than in 2007) and for R_{eco} a range of 30 %. Overall, net C gain (represented by a negative NEE) during

Table 1. Monthly and annual average air temperature (T_{air}) from 2007 to 2010 measured at 1 m at the eddy covariance measurement site in the Straits Enclosure, Alice Holt forest, and inside the soil CO_2 flux chambers (T_{chamb}) together with precipitation sums (Precip), and soil volumetric moisture content (SMC; v/v) at 6 cm depth in the mineral layer. The long-term averages are provided for comparison; n.a. indicates data not available.

Month	T_{air} (°C)	T_{chamb} (°C)	Precip (mm)	SMC (%)
1	4.7	4.2	104	53
2	5.0	4.3	77	55
3	6.6	6.3	76	55
4	9.7	9.8	42	50
5	12.4	12.4	63	45
6	15.2	14.9	49	41
7	16.2	15.4	90	38
8	15.8	15.1	69	36
9	13.6	12.9	56	31
10	10.4	9.7	73	37
11	7.4	6.7	133	47
12	3.3	2.4	71	51
Year				
2007	10.6	10.2	995	50
2008	10.2	9.6	943	46
2009	10.2	9.6	938	43
2010	9.2	8.7	747	40
30-yr average (1961–1990)	9.6	n.a.	780	n.a.

the first two years was about twice as high than during the latter two (Table 3) which following a cold winter (Table 4). Annual above ground respiration (R_{ab}; see Sect. 2.4) varied considerably and annual NPP declined substantially over three years (Table 3). In the two years with similar GPP, 2008 and 2009, the ratios of R_{eco}/GPP and NPP/GPP (carbon use efficiency, CUE) were different reflecting the varying influences of the key environmental and biological drivers on the individual C flux components (Fig. 3a). In contrast, annual R_s (range of 9 %) and the ratio R_h/R_s changed little (~0.44) between the 3 yr (Table 3).

The four-year time-courses of daily GPP and R_s components are shown in Fig. 3b together with the key environmental drivers of air and soil surface temperature, precipitation and soil moisture (Fig. 3a). As expected for a deciduous temperate forest, average monthly GPP peaked in summer, with values ranging from 1.2 to 1.8 mol m^{-2} d^{-1} (Fig. 3b) and monthly values of ~400 g C m^{-2} (Table 4). Large variations in daily R_s in summer usually coincided with changes in GPP, particularly during summer (Fig. 3b). Importantly, in 2009 and 2010 the oak canopy experienced major defoliation by moth caterpillars in the spring (mostly *Tortrix viridana*,

Table 2. Volumetric SMC (% v/v) measured in each of the four soil collar treatments: surface collar (RMS), mycorrhizal mesh (MS), steel collar (S) and repeatedly cut (S_{cut}), during (A) 2008 and 2009 and (B) 2010 with monthly averages from continuous hourly monitoring. Each treatment was replicated ($n = 4$) and shown are mean ± s.d.; significant differences between treatments are indicated by different letters, based on a one-way ANOVA (n.s. = not significant; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$) and a Tukey's B post-hoc test.

(A) 2008	22-May				15-Jul				26-Nov			
Treatment	Mean		s.d.	(*)	Mean		s.d.	(n.s.)	Mean		s.d.	(*)
RMS	0.39	±	0.01	B	0.43	±	0.03		0.51	±	0.02	C
MS	0.41	±	0.05	B	0.48	±	0.05		0.59	±	0.08	AB
S	0.50	±	0.01	A	0.50	±	0.01		0.62	±	0.02	A
S_{Cut}	0.42	±	0.05	B	0.47	±	0.03		0.60	±	0.02	AB

2009	25-Feb				12-May				7-Jul				3-Nov			
Treatment	Mean		s.d.	(*)	Mean		s.d.	(**)	Mean		s.d.	(***)	Mean		s.d.	(n.s.)
RMS	0.57	±	0.02	C	0.50	±	0.04	B	0.37	±	0.05	B	0.45	±	0.11	
MS	0.57	±	0.05	C	0.57	±	0.05	A	0.54	±	0.06	A	0.58	±	0.10	
S	0.63	±	0.01	A	0.62	±	0.02	A	0.60	±	0.02	A	0.63	±	0.02	
S_{cut}	0.61	±	0.01	AB	0.59	±	0.04	A	0.58	±	0.03	A	0.53	±	0.12	

(B) 2010	January				February				March				April				May			
Treatment	Mean		s.d.	(*)	Mean		s.d.	(*)	Mean		s.d.	(**)	Mean		s.d.	(**)	Mean		s.d.	(***)
RMS	0.56	±	0.00	B	0.58	±	0.01	B	0.57	±	0.02	B	0.55	±	0.02	B	0.46	±	0.02	B
MS	0.61	±	0.05	AB	0.61	±	0.05	AB	0.61	±	0.03	AB	0.59	±	0.02	A	0.53	±	0.01	A
S	0.65	±	0.03	A	0.65	±	0.04	A	0.63	±	0.01	A	0.61	±	0.02	A	0.56	±	0.02	A

2010	June				July				August				September				October			
Treatment	Mean		s.d.	(***)	Mean		s.d.	(***)	Mean		s.d.	(***)	Mean		s.d.	(**)	Mean		s.d.	(*)
RMS	0.35	±	0.03	B	0.26	±	0.02	C	0.24	±	0.02	B	0.26	±	0.03	B	0.32	±	0.04	B
MS	0.46	±	0.01	A	0.34	±	0.02	B	0.29	±	0.01	A	0.33	±	0.01	A	0.37	±	0.02	AB
S	0.46	±	0.01	A	0.38	±	0.01	A	0.32	±	0.01	A	0.34	±	0.01	A	0.39	±	0.01	A

but also *Operophtera brumata*, Pitman et al., 2010) and in 2010 there was a −3 °C air frost period after budburst in mid May as well as a substantial oak mildew (*Erysiphe alphitoides*) outbreak throughout August and September, noticeably reducing forest C flux components during spring and autumn (Fig. 3b), and causing very low annual (Table 3) and seasonal (Table 4) GPP totals.

The monthly relative contribution of R_h to total R_s (Fig. 4b) decreased from a peak in winter (∼0.65) to a low in summer (∼0.35) due to increased R_a (Fig. 4a). However, the timing of the seasonal increase and the relative contribution of R_a components (R_r, R_m) varied between the 3 yr (Fig. 4) due to varying R_m contributions in spring and autumn and R_r in summer and autumn. Generally, the annual average R_s, R_a and R_h values were quite constant over the 3 yr (Fig. 5), but the components of R_a varied, and in 2009 R_r was significantly higher and R_m lower (Table 3). The monthly respiration time course also revealed this difference (Fig. 4) and a sharp decline in R_r contributions to R_s (Fig. 4b) in August 2010 during the dry summer period (Fig. 3b, c), although R_h and R_m were much less affected. On average annual R_r, R_m and R_h fluxes contributed 38, 18 and 44 %, respectively (Fig. 5, Table 3).

In order to relate the component CO_2 fluxes and any correlations to environmental conditions and vegetation activity, the data were grouped into seasonal and developmental episodes (Table 4). This revealed that the seasonal increase in R_a generally occurred *before* budburst of the trees, mostly due to R_r but in 2008 also R_m, and was reflected in a pronounced reduction of the heterotrophic contribution to R_s (R_h/R_s ratio; Fig. 4b). Moreover, in 2010 monthly R_a was about 25 % lower in late spring and summer than in previous years (Table 4), corresponding to a 66 % reduction in GPP coinciding with caterpillar and frost damage.

3.5 Environmental responses of autotrophic and heterotrophic soil CO_2 fluxes

Daily R_s increased substantially with near-surface (−2 cm) temperature ($R_s = 0.50e^{0.12T}$) and showed an average apparent Q_{10} for daily fluxes of $\sim 3.2 \pm 1.0$ ($R^2 = 0.8$; Table 5). Relationships between R_s components and deeper soil temperatures were also examined, and showed similar although weaker relationships. Although both daily R_a and R_h rates also showed a strong apparent temperature response (0.23 $e^{0.14T}$; $Q_{10} = 3.9 \pm 1.1$, $R^2 = 0.7$ and 0.27 $e^{0.10T}$; $Q_{10} = 2.7 \pm 1.1$, $R^2 = 0.6$, respectively), the individual R_a components R_r (0.13 $e^{0.14T}$) and R_m (0.05 $e^{0.14T}$) showed no meaningful temperature responses over all three years ($Q_{10} = 4.1 \pm 1.1$, $R^2 = 0.4$ and 4.0 ± 1.1, $R^2 = 0.2$), respectively. The analysis for different developmental periods (Table 5) showed a narrow range in apparent Q_{10} values for

Table 3. Annual ecosystem C flux sums at the Straits Enclosure, Alice Holt forest, (in $g\,C\,m^{-2}$; calculated from daily values) and C flux ratios for 2007 to 2010. NEE is net ecosystem CO_2 exchange with uptake shown as negative values, GPP is gross primary productivity, R_{eco} is ecosystem respiration, NPP is net primary productivity, and CUE is carbon use efficiency = NPP/GPP. Total soil respiration, R_s, included replacing missing values due to late start of monitoring or system failure by values from a temperature regression (shown in italics for yearly sums; n.a. denotes no data available). Separation of R_s components only occurred from 2008: autotrophic (R_a, sum of root, R_r and mycorrhizal hyphal respiration, R_m) and heterotrophic (R_h) respiration. The annual NPP was calculated as GPP $-$ ($R_{ab} + R_a$), where R_{ab} is above ground respiration (i.e. $R_{eco} - R_s$); * denotes that averages for soil flux components and respective ratios only reflect 2008–2010 data.

Year	NEE	GPP	CUE	R_{eco}	R_{eco}/GPP	NPP	R_{ab}	R_s	R_h/R_s	R_s/R_{eco}	R_r	R_m	R_a	R_h
2007	−518	2044	n.a.	1501	0.73	n.a.	n.a.	*791*	n.a.	*0.53*	n.a.	n.a.	n.a.	n.a.
2008	−621	1751	0.51	1130	0.65	893	450	697	0.42	0.62	233	173	407	290
2009	−300	1716	0.36	1416	0.83	616	658	760	0.42	0.54	371	69	441	320
2010	−228	1345	0.42	1117	0.83	559	422	713	0.49	0.64	222	142	364	350
Average	−417	1714	0.43*	1291	0.76	690*	498*	723*	0.44*	0.60*	276*	128*	404*	320*
s.d.	184	286	0.08	197	0.09	179	138	33	0.04	0.05	83	53	39	30

Table 4. Monthly ecosystem C fluxes for gross primary productivity (GPP) and soil respiration fluxes (in $g\,C\,m^{-2}\,month^{-1}$) averaged over particular phenological periods at the Straits Enclosure, Alice Holt forest from 2007 to 2010 together with air temperature (T_{air}), precipitation sums (Precip), volumetric soil moisture content (SMC; v/v) and the corresponding C flux ratios. Soil respiration (R_s) component fluxes included replacements of missing values due to late start of monitoring or system failure by temperature regression (shown in italics; n.a. denotes no data available). Phenological periods (for the tree canopy) correspond to: **Inactive**: December–March; **pre budburst**: April; **budburst**: May; **active**: June–August; **senescence**: September–October; **leaf fall**: November. See Table 3 for explanation of additional abbreviations.

			T_{air}	Precip	SMC	GPP	R_s/R_{eco}	R_s	R_r	R_m	R_a	R_h
	Period	Phenology	°C	mm	%	$g\,C\,m^{-2}\,month^{-1}$	ratio	$g\,C\,m^{-2}\,month^{-1}$	$g\,C\,m^{-2}\,month^{-1}$	$g\,C\,m^{-2}\,month^{-1}$	$g\,C\,m^{-2}\,month^{-1}$	$g\,C\,m^{-2}\,month^{-1}$
2007	Winter	Inactive	7.1	95	60	13	*0.73*	*38*	n.a.	n.a.	n.a.	n.a.
	Spring	Pre budburst	11.9	1	44	78	0.52	60	n.a.	n.a.	n.a.	n.a.
	Spring	Budburst	12.3	110	41	290	0.48	83	n.a.	n.a.	n.a.	n.a.
	Summer	Active	15.2	110	51	429	0.39	94	n.a.	n.a.	n.a.	n.a.
	Autumn	Senescence	12.0	46	42	167	0.84	83	n.a.	n.a.	n.a.	n.a.
	Autumn	Leaf fall	7.3	107	49	15	1.06	54	n.a.	n.a.	n.a.	n.a.
2008	Winter	Inactive	6.1	83	54	12	0.62	30	*8*	*7*	*15*	*15*
	Spring	Pre budburst	8.0	106	57	36	0.57	43	3	29	32	11
	Spring	Budburst	14.1	83	51	218	0.72	99	29	38	67	33
	Summer	Active	15.6	59	39	364	0.68	93	37	20	56	36
	Autumn	Senescence	11.2	79	37	165	0.56	57	24	7	31	27
	Autumn	Leaf fall	7.5	97	45	18	0.60	45	13	9	21	23
2009	Winter	Inactive	4.6	75	50	11	0.57	29	9	2	12	17
	Spring	Pre budburst	9.9	40	49	72	0.42	61	27	6	33	29
	Spring	Budburst	12.2	44	50	210	0.55	102	47	9	57	45
	Summer	Active	15.8	53	40	360	0.50	102	57	8	65	37
	Autumn	Senescence	12.9	49	26	142	0.68	60	27	8	35	25
	Autumn	Leaf fall	9.2	241	45	28	0.62	51	25	7	32	19
2010	Winter	Inactive	3.6	90	53	11	0.52	26	10	3	13	13
	Spring	Pre budburst	9.2	22	50	36	0.67	56	24	8	32	24
	Spring	Budburst	11.0	17	39	83	0.82	79	35	13	48	32
	Summer	Active	16.3	56	24	296	0.56	90	25	19	43	47
	Autumn	Senescence	12.0	85	31	143	0.75	76	21	17	38	38
	Autumn	Leaf fall	5.7	87	48	17	0.87	56	14	13	27	28

Table 5. Seasonal and annual average apparent Q_{10} values (with ±SE and R^2) derived from daily total soil respiration, R_s, and its component fluxes over particular phenological periods at the Straits Enclosure, Alice Holt forest from 2007 to 2010. Q_{10} values calculated from the slopes of linear (best fit) regressions of $\log_{10}$ transformed CO_2 fluxes (after Atkin et al., 2000), against either the soil temperature at 2 cm soil depth for R_s and R_h or soil surface temperature for R_a, R_r and R_m. Phenological periods (for tree canopy) are defined in Table 4. Abbreviations defined in Table 3; blank entries are due to no data.

	Period	Phenology	R_s		SE	R^2	R_r		SE	R^2	R_m		SE	R^2	R_a		SE	R^2	R_h		SE	R^2
2007	Winter	Inactive																				
	Spring	Pre budburst	3.3	±	1.1	0.9																
	Spring	Budburst	3.4	±	1.2	0.7																
	Summer	Active	3.6	±	1.3	0.2																
	Autumn	Senescence	2.9	±	1.0	0.9																
	Autumn	Leaf fall	2.8	±	1.2	0.6																
	2007		**2.8**	±	**1.0**	**0.7**																
2008	Winter	Inactive	1.9	±	1.1	0.3	0.4	±	4.6	0.0	2.2	±	1.4	0.3	2.1	±	1.4	0.2	4.7	±	1.5	0.5
	Spring	Pre budburst	2.9	±	1.1	0.8	2.6	±	2.0	0.1	2.5	±	1.2	0.6	2.5	±	1.1	0.7	3.9	±	1.1	0.9
	Spring	Budburst	3.4	±	1.2	0.6	38.2	±	2.9	0.3	4.7	±	1.8	0.2	4.2	±	1.2	0.5	2.0	±	1.4	0.1
	Summer	Active	0.7	±	1.2	0.0	0.2	±	1.8	0.1	0.8	±	2.2	0.0	0.4	±	1.4	0.1	1.5	±	1.2	0.1
	Autumn	Senescence	2.2	±	1.1	0.7	2.4	±	1.1	0.5	7.1	±	1.9	0.2	2.7	±	1.1	0.5	1.7	±	1.1	0.4
	Autumn	Leaf fall	2.7	±	1.2	0.5	5.1	±	1.4	0.4	22.2	±	1.8	0.5	9.0	±	1.4	0.6	1.0	±	1.4	0.0
	2008		**3.3**	±	**1.0**	**0.8**	**9.2**	±	**1.2**	**0.4**	**2.8**	±	**1.2**	**0.1**	**3.7**	±	**1.1**	**0.7**	**2.9**	±	**1.1**	**0.5**
2009	Winter	Inactive	1.9	±	1.1	0.8	7.5	±	1.1	0.7	2.8	±	2.0	0.0	7.3	±	1.1	0.7	3.1	±	1.1	0.5
	Spring	Pre budburst	2.9	±	1.1	0.8	4.9	±	1.2	0.7	22.8	±	7.8	0.1	5.5	±	1.2	0.7	2.3	±	1.2	0.5
	Spring	Budburst	3.4	±	1.3	0.1	7.8	±	1.3	0.7	139.4	±	9.8	0.1	9.2	±	1.4	0.6	3.9	±	1.2	0.6
	Summer	Active	0.7	±	1.1	0.4	0.6	±	1.2	0.1	0.0	±	4.5	0.1	0.7	±	1.2	0.1	0.9	±	1.3	0.0
	Autumn	Senescence	2.2	±	1.1	0.6	2.2	±	1.2	0.2	3.4	±	1.6	0.1	2.4	±	1.3	0.2	1.1	±	1.1	0.0
	Autumn	Leaf fall	2.7	±	1.1	0.8	1.5	±	1.2	0.1	44.5	±	3.9	0.2	2.2	±	1.2	0.5	2.8	±	1.4	0.2
	2009		**3.3**	±	**1.0**	**0.8**	**4.6**	±	**1.0**	**0.8**	**4.4**	±	**1.2**	**0.2**	**4.5**	±	**1.0**	**0.8**	**2.2**	±	**1.0**	**0.5**
2010	Winter	Inactive	7.4	±	1.1	0.8	12.6	±	1.3	0.5	13.5	±	1.5	0.3	14.0	±	1.2	0.7	3.6	±	1.1	0.6
	Spring	Pre budburst	4.0	±	1.1	0.9	4.2	±	1.1	0.8	0.7	±	1.5	0.1	2.7	±	1.1	0.8	6.8	±	1.2	0.8
	Spring	Budburst	4.1	±	1.2	0.8	4.7	±	1.2	0.7	4.2	±	1.2	0.7	4.6	±	1.2	0.7	2.8	±	1.1	0.8
	Summer	Active	0.7	±	1.3	0.0	0.9	±	2.8	0.0	0.1	±	1.9	0.1	0.4	±	1.7	0.0	1.9	±	1.1	0.3
	Autumn	Senescence	1.9	±	1.1	0.6	1.4	±	1.2	0.2	1.9	±	1.3	0.1	1.7	±	1.1	0.2	2.1	±	1.0	0.8
	Autumn	Leaf fall	4.9	±	1.2	0.6	4.4	±	1.3	0.4	4.8	±	1.3	0.4	4.0	±	1.2	0.5	5.2	±	1.1	0.8
	2010		**3.5**	±	**1.0**	**0.8**	**2.8**	±	**1.1**	**0.3**	**4.2**	±	**1.1**	**0.5**	**3.3**	±	**1.1**	**0.6**	**3.3**	±	**1.0**	**0.9**

R_h and a mean of approximately 2.7 ± 1.1 throughout but with a peak in 2010. R_a and its components, by contrast, varied considerably. Whereas there was no significant relationship of R_a components with temperature in all summers ($Q_{10} < 1 \pm 1.5$, $R^2 \sim 0.1$), R_a showed exceptionally high apparent Q_{10} values in winter ($Q_{10} \sim 7.8 \pm 1.3$, $R^2 \sim 0.5$), particularly after the cold 2009/10 winter.

An analysis of monthly R_s and its components during 2010 (with available treatment soil moistures) revealed only weak responses to soil moisture (Fig. 6). Total R_s and its components declined at SMC above 0.5 (v/v), but these monthly values occurred in winter and early spring, when there were also low temperatures (Fig. 3a). R_r and R_m showed a slight CO_2 flux decline with decreasing SMC below 0.3 (v/v).

3.6 Temporal variation and temporal relationships of CO_2 fluxes

To simplify the results of the wavelet analysis, the wavelet global power spectrum (Fig. 7) was used to summarize the power contained in the spectral signature of each time series (note that the Nyquist theorem states that only half the length of the time series can be interpreted correctly, i.e. only 1.5 yr for all component fluxes). This analysis revealed strong periodicity at the 1-day time scale across the three growing seasons (2008–2010) for GPP, R_s, R_{ab} and R_r (Fig. 7a–d). In contrast, R_h showed a maximum periodicity at 1 yr and R_m a seasonal (∼150 days) periodicity (Fig. 7e, f). Larger synoptic scale meteorological events (∼30-days) strongly influenced R_{ab} and were also present with lower energy for R_h and R_m.

The subsequent WCA revealed linkages between canopy C uptake (GPP) and R_s and its components (Fig. 8). Firstly, seasonal differences were evident in the temporal correlation of the temperature de-trended R_s, R_r and R_m components

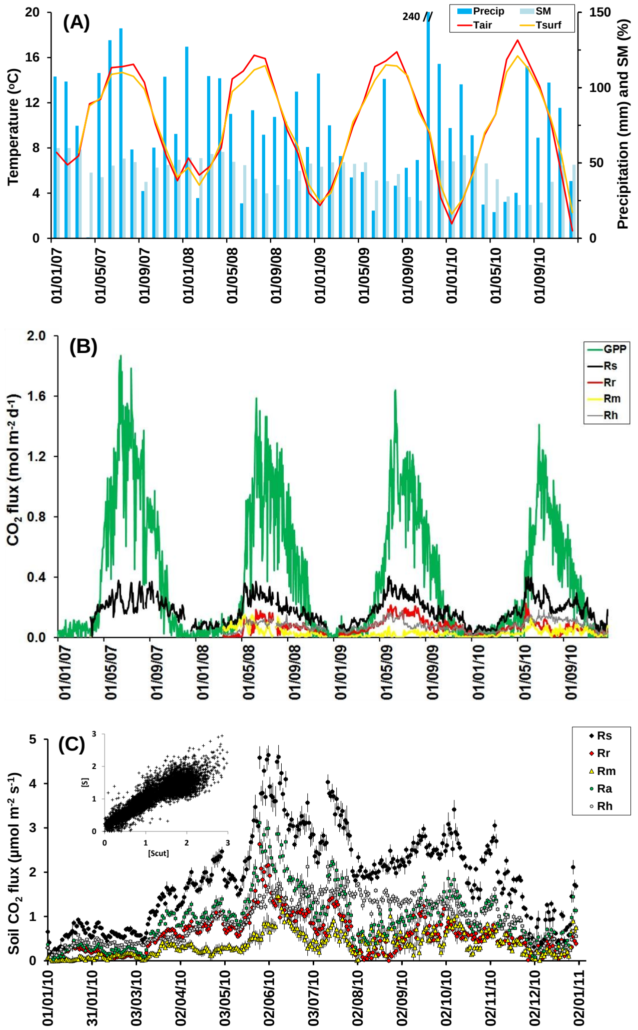

Fig. 3. (A) Monthly average air temperature (Tair), soil surface temperature (Tsurf), precipitation sum (Precip) and soil volumetric moisture content (SM) at the Straits Enclosure, Alice Holt forest from 2007 to 2010. **(B)** Mean daily ecosystem CO_2 flux components (mol CO_2 m^{-2} d^{-1}) during the same period, comprising gross primary productivity (GPP) and total soil respiration (R_s), and contributions from roots (R_r), mycorrhizal hyphae (R_m) and heterotrophic soil respiration (R_h). **(C)** Mean (± SE) daily soil CO_2 flux for total respiration (R_s) and its components (i.e. root (R_r), mycorrhizal (R_m) and heterotrophic (R_h) flux) derived from hourly flux measurements during 2010 from the different treatment plots ($n = 4$). R_a is the sum of R_r and R_m. The inset shows the mean hourly fluxes of steel collar (S) versus repeatedly cut (S_{cut}) treatments.

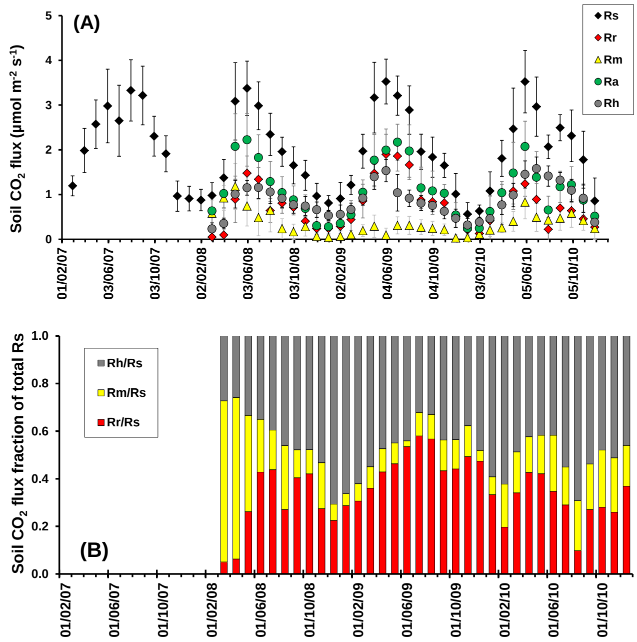

Fig. 4. (A) Monthly mean CO_2 efflux from soil respiration (R_s), and contributions from roots (R_r), mycorrhizal hyphae (R_m), autotrophic ($R_a = R_r + R_m$) and heterotrophic soil fluxes (R_h) at the Straits Enclosure, Alice Holt forest from 2007 to 2010. Separated flux components only available from March 2008. Averages ±s.d. ($n = 4$). **(B)** Monthly CO_2 flux component fractions (e.g. R_h/R_s).

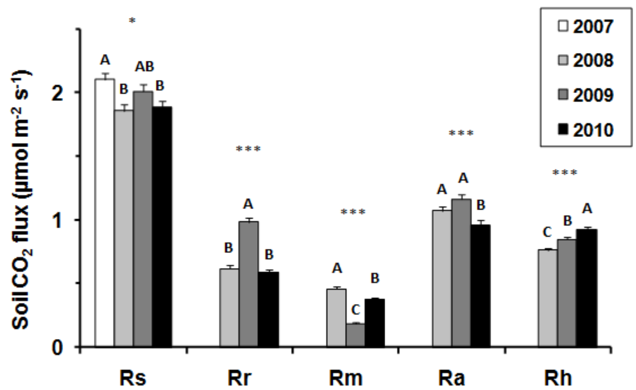

Fig. 5. Annual average rates of soil respiration (R_s), and contributions from roots (R_r), mycorrhizal hyphae (R_m), autotrophic (R_a = $R_r + R_m$) and heterotrophic soil fluxes (R_h) at the Straits Enclosure, Alice Holt forest from 2007 to 2010. Averages ± SE ($n = 4$). Statistically significant differences between years for each component are indicated with different letters, calculated from Tukey's post-hoc test, with overall ANOVA P-values shown ($*P < 0.05$; $**P < 0.01$; $***P < 0.001$).

to GPP (Fig. 8). Secondly, the analysis revealed a predominately fast linkage between total R_s and GPP, mostly at the 1-day period but also at around 8 and 32 days, which was also evident in the correlation of R_r with GPP (Fig. 8b). Thirdly, R_m also showed evidence of a fast temporal linkage with GPP, but showed a much more pronounced temporal correlation than R_r linkages at 8 to >32 days across the growing seasons (Fig. 8c, Supplement Table 1). The results show that although R_m was also influenced at the 1-day time-scale by GPP, it appeared that this temporal correlation was mostly evident when R_r had no or a less strong temporal correlation

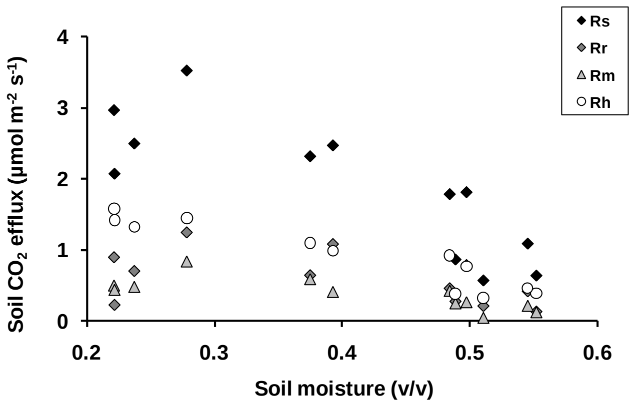

Fig. 6. Monthly average soil respiration (R_s) and its components, i.e. root (R_r), mycorrhizal hyphae (R_m) and heterotrophic (R_h) respiration at the Straits Enclosure, Alice Holt forest during 2010, against the mean volumetric soil moisture content (v/v) measured at 6 cm mineral soil depth in the individual treatments.

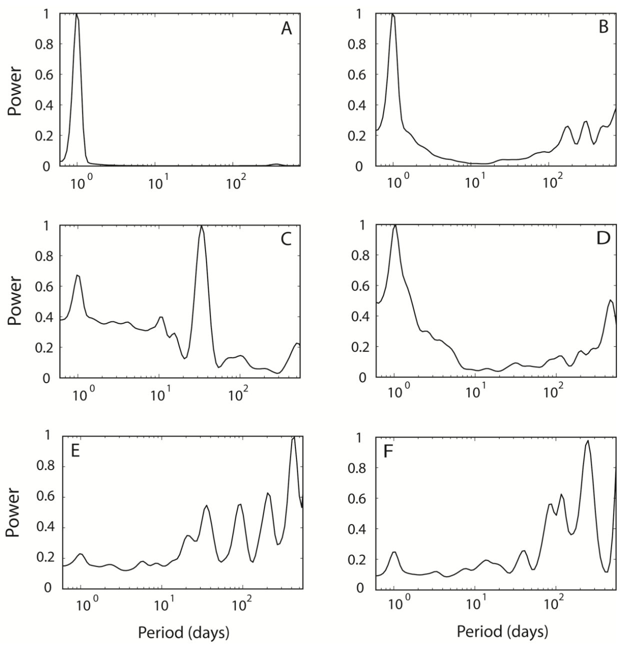

Fig. 7. Global wavelet power spectrum of individual (temperature independent) hourly CO_2 fluxes of GPP **(A)**, R_s **(B)**, R_{ab} **(C)**, R_r **(D)**, R_h **(E)**, and R_m **(F)** at the Straits Enclosure, Alice Holt forest from 2007 to 2010. Note that the Nyquist theorem states that only half the length of the time series can be interpreted correctly, thus only 1.5 yr are shown.

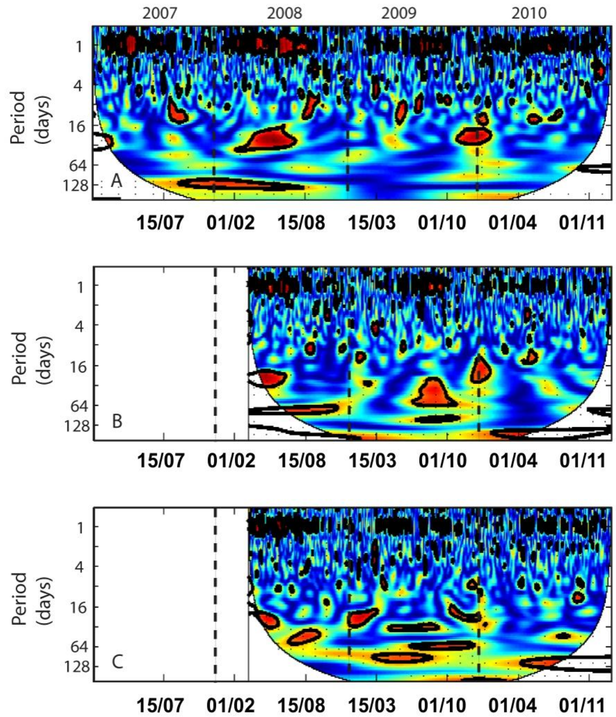

Fig. 8. Wavelet coherence analysis (WCA) output showing temporal correlation over four years (2007–2010) between GPP and the temperature independent soil CO_2 efflux, R_s **(A)** and its components, R_r **(B)** and R_m **(C)** at the Straits Enclosure, Alice Holt forest. The shades for power values are from blue (low values) to red (high values), thick black contour lines represent the 5 % significance level; the thin black lines indicate the cone of influence that delimits the region not influenced by edge effects. Dashed lines separate the four years. See previous figures for abbreviations.

with GPP at the same time period (i.e. red and dark areas in Fig. 9). The percentage of days with significant temporal correlations (red areas in Fig. 8) for several periods (1 to 128 days) revealed an overall (2007–2010) pattern of a mostly fast 1-day linkage between GPP and R_a components, R_r (28 %) and R_m(31 %), and a longer temporal response of $>$32 days mostly with R_m (19 %) but with considerable differences between years. Importantly, in 2010, the year of lowest GPP and NPP (Table 3), there was a substantial reduction in the temporal correlation between both R_a components and GPP for all periods (Supplement Table 1). Finally, the phase relationships of the temporal correlation between GPP and the soil CO_2 flux components for the 1-day period were used to estimate the synchrony of these fluxes (see Sect. 2.6). Calculating the phase relationship or synchrony for the 1-day period showed that GPP was mainly out of phase (i.e. R_s (11 ± 3 h), R_r (11 ± 5 h), R_m (11 ± 4 h) showed time-lags from GPP) suggesting a strong control of antecedent GPP on R_s.

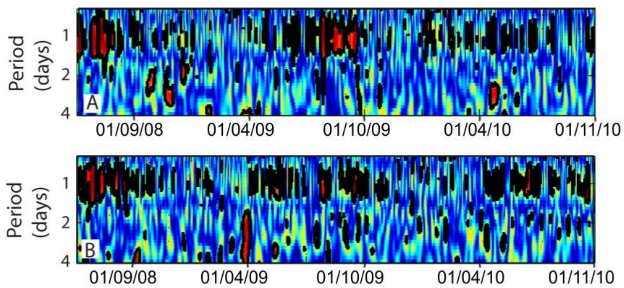

Fig. 9. Wavelet coherence analysis (WCA) output showing temporal correlation between GPP and the temperature independent soil CO_2 efflux components: R_r **(A)** and R_m **(B)** for the enlarged 1-day to 4-day periods as in Fig. 8. See previous figures for abbreviations.

4 Discussion

4.1 Soil respiration component fluxes and the forest C budget

We have provided multi-year hourly time series of forest CO_2 flux separation, fully accounting for both R_a components, R_r and R_m. Importantly, the R_s flux (Fig. 1) revealed seasonal variability, and showed clear temperature dependence during winter but less so during the growing season. The separation of R_s into its components revealed high seasonal variation in their contributions (Figs. 3 and 4). The annual R_h contribution of ∼44 % was at the lower end of the range reported by Subke et al. (2006), which included a wide range of partitioning methods. However, many of those forest studies potentially suffered from R_a decreases because of collar insertion (Heinemeyer et al., 2011). Another R_s component sampling study on clay-rich soils (Moyano et al., 2008) showed similar R_r (∼45 %) but lower R_m (∼5 %), possibly reflecting differences in seasonal dynamics between forests and methods.

The mean annual C budget (Table 3) of this temperate deciduous oak forest of ∼1700 and ∼700 $g\,C\,m^{-2}\,yr^{-1}$ for GPP and NPP, respectively, is similar to other studies in the UK (Thomas et al., 2011), Europe (Hibbard et al., 2005) and globally (Melillo et al., 1993; Luyssaert et al., 2007), and for ECM dominated forests (Vargas et al., 2010b). However, our data set enabled us to fully account for the R_a component of R_s (i.e. the respiration by roots and mycorrhizas) to derive forest NPP based on in situ hourly CO_2 flux data. Interestingly, the annual CUE varied considerably (0.36–0.51), although within the range observed by DeLucia et al. (2007), as did the individual components of R_{eco}. The annual R_s/R_{eco} of between 0.5–0.6 agreed with estimates for another temperate deciduous forest by Knohl et al. (2008). GPP varied considerably between years (Table 3; Fig. 3), and 2009 and 2010 had low CUE (∼0.4) and large R_{eco}/GPP ratios (0.83), possibly attributable to the preceding cold winter, and considerable leaf losses (caterpillar, mildew and frost damage) in 2010. Furthermore, 2010 showed a more typical summer soil drying period with reduced NEE (∼60 % lower than 2008).

4.2 Environmental responses of the individual soil respiration flux components

Although temperature near the soil surface explained most of the annual variability in daily R_s fluxes ($R^2 = 0.8$), this reflected mostly the temporal correlation between summer temperature and plant activity and consequently higher R_a fluxes (Subke and Bahn, 2010; Phillips et al., 2011). Seasonally, R_s showed a tight coupling to temperature during winter (Fig. 1) due to the dominance of R_h in this period, but during the (warmer) growing season this relationship disappeared (Table 5) . Such effects have been reported for coniferous forests (Lagergren et al., 2008, Gaumont-Guay et al., 2008) but not for deciduous systems. Over the year, daily R_a and R_m variation was much less temperature dependent (39 % and 20 %, respectively) than R_s. Overall, apparent Q_{10} values were most robust (i.e. high R^2) in winter and showed considerable seasonal changes and were not always (particularly R_h) significantly (i.e. considering the SE and R^2) different from the proposed global average of 1.4 (Mahecha et al., 2010). However, these large seasonal changes (despite the absolute values) and low robustness (i.e. high SE and low R^2) of the apparent temperature sensitivity confirms: (1) individual temperature responses for R_a and $R_h$components (Hartley et al., 2007a); (2) R_a dependence on seasonal substrate availability (Davidson et al., 2006; Hartley et al., 2007b); and (3) responses to above ground phenology as proposed by Sampson et al. (2007). More importantly, R_m also showed high apparent Q_{10} values in autumn (Table 5), coinciding with ECM fruiting body appearance and increased CO_2 flux contributions in 2008 and 2010. Such seasonal R_m activity has previously been observed by Heinemeyer et al. (2007) for a coniferous forest and likely reflects substrate availability rather than a temperature response.

Overall, R_s showed little response to the range of SMCs found here (Fig. 6), yet during the 2010 summer dry periods both R_r and R_m showed a tendency for lower rates (Fig. 6), similar to the previously reported R_m response to moisture in a pine forest (Heinemeyer et al., 2007).

4.3 Mycorrhizal respiration as an autotrophic component and regulation of C supply

The decision whether R_m is included in R_a or R_h is inherently difficult (Baggs, 2006; Kuzyakov, 2006a) as ECM are multifunctional, able to access C sources from both GPP and litter decomposition (Lindahl et al., 2007). It is thus essential to understand in situ mycorrhizal C-dynamics and their dependency on GPP and to quantify their different environmental responses (Fitter et al., 2004). In 2009, a year of high rates of R_{eco} and R_{ab} and particularly low CUE there was high R_r but very low R_m (Table 3). The plants seem to have reduced the C allocation to the mycorrhizal partners under C-limitation (i.e. reduced NPP), as shown for arbuscular mycorrhizal systems (Heinemeyer et al., 2006), preferentially allocating C to R_{ab} and R_r. This further supports the concept of a plant regulated mycorrhizal C allocation (Fitter et al., 1998) and an "overflow tap" regulation under surplus C. However, this did not occur in 2010 when NPP was even more reduced than in 2009 (Table 3), when there was a pronounced reduction of R_r but not of R_m (Fig. 4). This could reflect either mycorrhizal access to stored C and/or C sources from decomposition or a plant C allocation strategy towards ECM enabling higher nutrient acquisition for less structural C cost under NPP limitations (Vargas, 2009). Notably, this happened after a cold winter which may have caused damage to fine roots and mycorrhizal hyphae through soil freezing. As structural C costs for mycorrhizal hyphae are much lower per length than for roots albeit with similar maintenance respiration (Fitter, 1991), the plants may have preferentially allocated C to regrow mycorrhizal hyphae to benefit from more efficient nutrient uptake for less C costs. Moreover, although R_m was correlated with GPP at longer temporal scales (Fig. 8) this is unlikely a direct relationship, and most likely reflects access to stored C either in the plant or the fungus that is later used to support R_m as there was no strong seasonal periodicity evident in the temperature de-trended GPP (Fig. 7). In fact, both R_m and R_h showed strong seasonal and annual periodicities, respectively (Fig. 7), which were not temporally coupled with GPP (Fig. 8), suggesting other C sources for metabolism such as from litter decomposition. Further, seasonal analysis at shorter temporal scales indicated differences in the linkage of GPP to either R_r or R_m; although both components showed a strong 1-day GPP influence, when the link to R_r was strong there was less correlation with R_m (Fig. 9). Furthermore, there were temporal correlations evident between R_m and GPP at periods of 2–8 days and at >64-day periods but much less so for R_r (Fig. 8, Supplement Table 1). Although such GPP linkages (Tang et al., 2005; Liu et al., 2006) and long time lags between R_s and GPP have been reported previously (Vargas et al., 2010a), here they are evident for R_s and both R_a components. Moreover, periods of marked GPP and NPP reductions were observed in 2010 (Tables 3 and 4) through weather (late spring frosts) and biological (caterpillar herbivory and mildew disease) events with subsequently reduced or delayed R_r and R_m, respectively. All these observations support the concept of a tree regulated C "overflow tap" based on available GPP (Heinemeyer et al., 2007) by showing that antecedent GPP influences individual R_a components differently. However, we acknowledge that the "overflow tap" functioning is likely to be complex as available C as well as C costs for root versus fungal mycelia growth and nutrient status will have an influence. For example, although low nutrient status forests can be expected to generally allocate more available C to the mycorrhizal fungus (i.e. nutrient demand driven allocation), this might also occur in nutrient rich forests after damage to the fine root system (i.e. C cost driven allocation).

4.4 Implications for modelling forest C dynamics and soil respiration

Although R_s was significantly correlated with temperature this was not the case for R_a components during the period when the tree canopy was photosynthetically active (Table 5). Overall, these findings confirm that the use of an apparent Q_{10} in ecosystem models is a questionable concept (Davidson et al., 2006), because of the strong seasonal GPP influence on R_a components, independent of temperature. The time series analysis revealed a mostly rapid C connection within a few days from canopy to R_s components as has been reported in studies with manual measurements (Moyano et al., 2008). Importantly, both roots and mycorrhizas showed a fast link to GPP (i.e. at the 1-day period), but R_m also revealed much longer (weekly to monthly) periods with strong temporal correlation (Fig. 8). The time series analysis also underlined the importance of potential C reserves available to both roots and mycorrhizas, which are supported by isotopic studies (Mencuccini and Hölttä, 2010) and C allocation and turnover studies (e.g. Högberg et al., 2008). The results highlight that the time series analysis can reconcile the observations from flux measurements and isotope experiments (e.g. Subke et al., 2009; Mencuccini and Hölttä, 2010; Wingate et al., 2010) to link canopy and soil processes (Vargas et al., 2011). Both the large estimated R_a values found here (56 % of R_s) and the strong linkage of both R_a components to GPP (Figs. 8, 9) emphasise that these different soil CO_2 flux components need to be considered independently with their biotic and abiotic drivers. They also support the importance of considering the R_s plant-soil-continuum as proposed by Högberg and Read (2006). Thus C cycle models could be improved by treating the individual R_s components separately and should also allow for internal plant and fungal C storage pools and mobilization. Moreover, the observed interannual variation in canopy and soil CO_2 fluxes indicates that better model representation of growing conditions and phenology is required (Lagergren et al., 2008).

Two central questions remain to be explored further: (1) which is in control of plant C allocation to R_r and R_m: plant or fungus?, and (2) what are the implications for soil decomposition? Clearly, more in situ research is needed under different environmental conditions (e.g. average years versus disturbance year, Vargas, 2009, or variable NPP due to insect defoliation, Schäfer et al., 2010) and using isotopic research. Furthermore, the high frequency data revealed that the short-term, temperature-independent R_a component linked to GPP may lead to uncertain temperature-based night-time R_{eco} corrections in EC flux calculations (Aubinet et al., 2002; Reichstein et al., 2005) so that correlations of GPP and R_{eco} may need to be reconsidered (Lasslop et al., 2010).

The results here may allow the parameterization of more realistic soil C turnover models that include decomposition and plant-derived R_s fluxes (e.g. MYCOFON, Meier et al., 2010) and lag periods of GPP allocation to R_s components

(Kuzyakov and Gavrichkova, 2010). Such flux component separation could also be deployed to investigate the potential priming effect of mycorrhizal C (i.e. exudates) on SOM decomposition (Talbot et al., 2008; Fontaine et al., 2011). Model incorporation of these mechanisms will be fundamental in assessing the stability of future SOC stocks due to climate change altering SOC dynamics directly and indirectly through changes in plant productivity (Heath et al., 2005).

4.5 Limitations and future research considerations and applications

We have assumed that the temporal dynamics of soil chamber CO_2 fluxes and soil moisture measurements in one small area are representative of those in the whole eddy covariance flux footprint, and that there are no larger-scale spatial variations in the temporal dynamics and relative magnitudes of CO_2 flux contributions. However, the chamber CO_2 fluxes may not represent R_s across the whole eddy covariance flux footprint, and ideally we would have sampled R_s across the footprint area; but due to technical and practical limitations it was not possible to have multiple high time-resolution systems at multiple sites. As others have done recently (e.g. Thomas et al., 2011), we equated eddy covariance CO_2 flux estimates with NEE, as we could not estimate canopy CO_2 storage reliably, which may have led to errors in estimates of NEE at short time scales, particularly at dawn and dusk conditions, although the errors will be smaller for the hourly and daily averaging periods used here.

Overall, we acknowledge some limitations of using mesh or collar exclusions. However, R_s from deep collars did show good agreement with fluxes from the repeatedly cut treatments and measured R_s proportions (contributions of R_a versus R_h and R_S versus R_{eco}) agreed well with those in the literature. Although these comparisons give confidence, we cannot ignore the possible errors and emphasise that improved measurement techniques should be developed. Any physical separation technique requires assessing the issues of root or mycorrhizal exclusion and disturbance effects. Our data showed that, firstly, mycorrhizal hyphae penetrated a 1 µm nylon mesh and as such the S treatment needs to consider either finer meshes or solid boundaries and, secondly, the exclusion treatments caused a disturbance effect lasting about six months. While severed roots were removed in this study (limiting increased decomposition), another artefact which would apply to most root exclusion methods such as trenching is that excluding roots and ECM from the MS and S treatments prevents the litter additions they normally contribute, and thus may cause an underestimation of normal heterotrophic respiration. Moreover, the root exclusion caused an increase in SMC in the MS and S treatment by about 15 % (v/v) and mostly during summer (Table 2, Fig. 2) compared to the RMS treatment (see Ngao et al., 2007), which was minimized by rainfall exclusion (e.g. Fig. 2). An alternative approach would have been to add water to the RMS treatments, but this would have made the RMS treatment unrepresentative of the rest of the forest, hindering comparison to NEE derived fluxes.

Our apparent seasonal temperature response analysis (Table 5) has obvious problems and limitations (Davidson et al., 2006; Subke and Bahn, 2010), and was intended to provide an overview in relation to previous literature, and background information for the temperature de-trending for the time series analysis. We acknowledge that different approaches such as time frequency decomposition would give a more confident approach; we particularly looked only at seasonal responses in order to exclude the influence of any diel hysteresis effects (Phillips et al., 2011). However, we intend to examine our data further in a future temperature-focused analysis, particularly considering diel hysteresis (Phillips et al., 2011), seasonality (Subke and Bahn, 2010) and scale dependence (Mahecha et al., 2010) as well as a detailed eddy covariance footprint analysis.

The temperature de-trending approach for the WCA used the depth of maximum temperature correlation with total R_s. Although this is arbitrary, it was the most appropriate temperature depth available to de-trend diurnal CO_2 flux variations and remove potential auto-correlations with other variables. We recognize that this approach could be improved, specifically considering where the production of CO_2 is done in the soil at different depths rather than using overall R_s (see Subke and Bahn, 2010). However, the goal of the current manuscript was to understand the partitioning of the total R_s flux and the temporal dynamics and correlations of its flux components.

5 Conclusions

The research on exploring environmental controls on R_s fluxes and linkages to canopy CO_2 uptake revealed:

1. Large (56 %) overall R_a contribution (R_r 38 %, R_m 18 %) to a relatively constant annual R_s with considerable interannual and seasonal variability in the R_a components.

2. Strong overall apparent temperature responses of R_s except during summer, and the latter was due to negligible temperature responses by R_a components.

3. An overall short-term periodicity in canopy and soil CO_2 fluxes but also longer term periodicities in R_a components suggesting an internal root and mycorrhizal C storage pool and additional C supply of R_m through soil organic matter and litter decomposition.

4. Significant temporal correlation of R_s to GPP through the R_a components mainly at a 1-day period indicating fast C allocation to R_s in this forest.

5. An overall separation of periods when either high R_r or R_m are temporally correlated with GPP indicating that R_m was probably controlled by plant C allocation.

The time series analysis identified periodicities and linkages to GPP which have implications for the key question for climate change research of whether forests will continue to sequester CO_2 or whether increased GPP will result in increased respiration (Heath et al., 2005). The results support previous work suggesting that the mycorrhizal flux component may contribute to a C sequestration limitation, functioning as a C "overflow tap" (Heinemeyer et al., 2007) and potentially priming the turnover of SOC. However, further research is required on, the processes regulating this "overflow tap" and the sources of C available to the fungus which should help explain the observed interannual variation in soil flux component contributions and their correlations with GPP.

Supplementary material related to this article is available online at: http://www.biogeosciences.net/9/79/2012/ bg-9-79-2012-supplement.pdf.

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