

**Exploring the
“overflow tap” theory**

A. Heinemeyer et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Exploring the “overflow tap” theory: linking forest soil CO₂ fluxes and individual mycorrhizosphere components to photosynthesis

A. Heinemeyer¹, M. Wilkinson², R. Vargas³, J.-A. Subke⁴, E. Casella²,
J. I. L. Morison², and P. Ineson¹

¹Stockholm Environment Institute (SEI-York centre) and Centre for Terrestrial Carbon Dynamics (CTCD-York centre) at the Environment Department, University of York, York, YO10 5DD, UK

²Centre for Forestry & Climate Change, Forest Research, Alice Holt Lodge, Farnham, Surrey, GU10 4LH, UK

³Departamento de Biología de la Conservación, Centro de Investigación Científica y de Educación Superior de Ensenada (CICESE), Ensenada, BC, Mexico

⁴School of Natural Sciences, Biological and Environmental Sciences, University of Stirling, Stirling, FK9 4LA, Scotland, UK

Received: 9 March 2011 – Accepted: 11 March 2011 – Published: 23 March 2011

Correspondence to: A. Heinemeyer (andreas.heinemeyer@york.ac.uk)

Published by Copernicus Publications on behalf of the European Geosciences Union.

BGD

8, 3155–3201, 2011

Exploring the “overflow tap” theory

A. Heinemeyer et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Abstract

Quantifying soil organic carbon stocks and their dynamics accurately is crucial for better predictions of climate change feedbacks within the atmosphere-vegetation-soil system. However, the composition and environmental responses of the soil CO₂ efflux (R_s) are still debated and limited by field data. The objective of this study was to quantify the contribution of the various R_s components and to determine their temporal variability, environmental responses and dependence on gross primary productivity (GPP) using time series analysis. In a deciduous oak forest in SE England hourly replicated R_s fluxes over 4 years were obtained using automated soil CO₂ flux chambers and ecosystem CO₂ exchange using eddy covariance methodology. Mesh-bag and steel collar treatments prevented root or both roots and mycorrhizal hyphal in-growth, respectively, to allow separation of heterotrophic (R_h) and autotrophic (R_a) soil CO₂ fluxes and the R_a components, roots (R_r) and mycorrhizal hyphae (R_m).

Annual cumulative R_s values were very similar between years ($740 \pm 43 \text{ g C m}^{-2} \text{ yr}^{-1}$) with an average flux of $2.0 \pm 0.3 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, but R_s components varied. On average, annual R_r , R_m and R_h fluxes contributed 39, 18 and 43%, respectively, showing a large R_a contribution (57%) comprising considerable seasonal R_m contributions. 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 ($R^2 = 0.18$). However, R_a components showed strong apparent temperature responses around budburst and leaf fall but none during summer. Time series analysis revealed strong daily periodicities for R_s , whereas R_r was dominated by daily, R_m 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 the relationship with GPP was substantial 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, individual linkages to GPP stimulation of R_a components are required, in addition to individual temperature responses. The potential consequences

BGD

8, 3155–3201, 2011

Exploring the “overflow tap” theory

A. Heinemeyer et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



of these findings for understanding the limitations of long-term forest C sequestration are highlighted, as root-derived R_a stimulating R_m seems to function as a “C overflow tap”, possibly providing “fuel for priming” the turnover of soil organic carbon.

1 Introduction

5 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 $\sim 10\%$ 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 thus 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 the composition and environmental responses of soil CO_2 efflux (R_s) 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) is 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 and increased atmospheric CO_2 concentrations. In particular, how R_s and its biological components will respond to rising temperatures in situ is still uncertain (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 meaningful (Smith and Fang, 2010; Mahecha et al., 2010). Further, R_s shows

Exploring the “overflow tap” theory

A. Heinemeyer et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



time-lags behind gross primary productivity (GPP), apparently due to changes in C allocation patterns between shoots, roots and mycorrhizas (Mencuccini and Hölttä, 2010; Vargas et al., 2010b), a process still to be understood and included in models (Kuzyakov and Gavrichkova, 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 now a focus of research in order to better model forest C cycling (Hanson et al., 2000; Bond-Lamberty et al., 2004; Ekblad et al., 2005). There are three main scientific questions that justify this research: (i) How much of the measured R_s is predominantly heterotrophic R_h versus plant-derived R_a ? (ii) Do these components respond similarly to environmental change? (iii) How much of the “old” C is turned over as a result of new, recently fixed autotrophic C inputs (priming effect), potentially limiting long-term C-sequestration?

The desired separation of R_s components is challenging 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), which might respond more to plant C supply than to temperature (Heinemeyer et al., 2006). 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., 2010a). For example, although there can be 8000 m of ectomycorrhizal (ECM) hyphae per metre of root (Leake et al., 2004) few studies have measured the in situ R_m (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; Rygielwicz 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

BGD

8, 3155–3201, 2011

Exploring the “overflow tap” theory

A. Heinemeyer et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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 (cf. Heinemeyer et al., 2011).

The aims of this study were to: (i) obtain a long-term hourly dataset for above and below ground forest C-flux components; (ii) determine the contribution of R_h and R_a to R_s , including separation of R_a into R_r and R_m components; (iii) describe their individual responses to temperature and moisture; (iv) explore the temporal variation in R_s and its components and their synchrony with GPP.

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 year (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 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 about 5 and budburst occurred from March (understory) to May (trees). The average tree height was about 25 m with an age of 75–80 years. The soil is a surface water gleysol (England and Wales soil classification: Wickham series) with a shallow O-layer (~3 cm) and a total depth of 80 cm to the C horizon of the cretaceous clay, with a high water table. The $\text{pH}_{(\text{H}_2\text{O})}$ 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,

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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. R_s flux rates were calculated as the linear CO_2 increase (2 s readings) during chamber closure time (less than 2 min), discarding a 45 s mixing period. Soil surface collars (3.5 cm \times 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) attached to the collar rim. This provided an airtight collar seal with no disturbance to shallow root and hyphal networks (Heinemeyer et al., 2011), the seal was verified during routine maintenance checks. 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 \times 1 m) was fixed at 1 m height above each collar area. Hourly soil temperature profiles at 0, 2, 10 and 20 cm depths ($n = 3$) and soil moisture (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). The soil moisture probe was repositioned at monthly intervals. A similar hand-held moisture probe was periodically used to record soil moisture 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 tower measurements

Net ecosystem CO_2 exchange (NEE) was measured continuously with the eddy covariance (EC) methodology since 1999, after Moncrieff et al. (1997). Measurements

Exploring the “overflow tap” theory

A. Heinemeyer et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



and calculation procedures followed the “Euroflux” project, described by Aubinet et al. (2000). The equipment consisted of a sonic anemometer (Solent R2, Gill Instruments, Lyminster, UK) and a closed path CO₂ and H₂O infrared gas analyser (IRGA; LiCor 7500, Li-Cor Biosciences, Lincoln, Nebraska, USA). Sample air was drawn from the top of a 28 m high instrument mast tube (6 mm ID), through two in-line 1 µm PTFE Teflon filters (Gelman Acro 50, Pall Life Sciences, Ann Arbor, Michigan, USA) at a rate of 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 at a rate of 20 Hz using the Edisol software (<http://www.geos.ed.ac.uk/abs/research/micromet/edisol/>). 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 re-processed using the EdiRe software (www.geos.ed.ac.uk/abs/research/micromet). To calculate hourly, daily and annual NEE, missing data were substituted based on the standard gap-filling procedure (<http://www.bgc-jena.mpg.de/bgc-mdi/html/eddyproc/index.html>; Reichstein et al., 2005) employed by the CarboEurope project. 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 gross primary productivity (GPP) and total ecosystem respiration (R_{eco}). This uses night-time temperature regression models (Lloyd and Taylor, 1994) 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

BGD

8, 3155–3201, 2011

Exploring the “overflow tap” theory

A. Heinemeyer et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



occur completely within the woodland (within 350 m of the tower, 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

5 On 22 March 2007 12 soil collars were randomly installed within the enclosure around the eddy-covariance 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 random surface collars were left and under the other two collars was installed either a mesh-bag (diameter 25 cm × 45 cm deep with 42 μm pore size; Normesh Ltd.,
10 Oldham, UK) allowing in-growth by mycorrhizal hyphae but not roots, or a 1 μm mesh-bag to exclude both. However, the 1 μm mesh-bags were replaced in March 2008 by open-ended steel collars (same dimensions), as it was evident from the considerable hyphal in-growth that this mesh did not exclude hyphae. For mesh-bag insertion
15 soil was extracted with the steel collar in 5 cm horizons, and stored on trays for each horizon. Larger roots were removed and soil was then back-filled in horizon order to packing density. Consequently, measured CO₂ 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; steel collar). In March 2008 a fourth treatment was added, whereby
20 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 collars at a 30 cm diameter (S_{cut}). This enabled comparison with the S treatment but without the permanent barrier of a steel collar. All 12 or 16 collar locations were monitored with the automated gas sampling system (see above) at hourly intervals until December 2010. Following Heinemeyer et al. (2007), the contribution of individual R_s components was
25 calculated as:

$$1. R_r = \text{RMS}_{\text{resp}} - \text{MS}_{\text{resp}}$$

$$2. R_m = \text{MS}_{\text{resp}} - S_{\text{resp}}$$

Exploring the “overflow tap” theory

A. Heinemeyer et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



$$3. R_h = S_{\text{resp}}$$

$$4. R_a = R_m + R_r$$

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 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 NPP calculated as $GPP - (R_{\text{ab}} + R_a)$.

2.5 Temperature sensitivity

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

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; Grinstead et al., 2004) and more recently for R_s analyses (Vargas et al., 2010b). 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) was used because of its ability to produce a smooth picture in time-scale domain of non-stationary processes (e.g. R_s) and its suitability for

BGD

8, 3155–3201, 2011

Exploring the “overflow tap” theory

A. Heinemeyer et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Exploring the “overflow tap” theory

A. Heinemeyer et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



visual interpretation (Torrence and Compo, 1998). Wavelet analysis was applied on the temperature independent 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. 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. 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., 2010b).

Wavelet coherence analysis (WCA) was used to determine the temporal correlation between two hourly time series and to quantify the phase difference or time-lag between them at specific periods (e.g. 1-day, 8-day). 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 wavelet coherence analysis 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). As temperature is auto correlated with GPP and R_s (and its components) a conservative estimate of the influence of GPP on R_s and component fluxes was obtained by first removing the diel influence of soil temperature as described above for each day.

The phase relationships, which can be expressed in unit of time multiplied by the respective period, give 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 1-day periods was calculated from the wavelet coherence analysis to explore the potential fast control of recent photosynthesis on soil CO₂ 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 soil moisture 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 averages varied between 0.5 to $4.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 1) and showed a general association with the seasonal pattern of temperature, although there were marked changes in the apparent response rate during active canopy growth between budburst (spring) and leaf fall (autumn).

3.2 Separation of soil respiration components

The mesh collar insertion on 18 September 2007 and subsequent replacement with a steel collar (see Sect. 2.4) for root and mycorrhizal exclusion, respectively, resulted in a disturbance period lasting around six month (evidently higher CO_2 flux rates initially, then subsequent reduction; data not shown). The treatment CO_2 fluxes from the end of March 2008 onwards showed clear differences with daily CO_2 flux rates in the treatment order $\text{RMS} > \text{RM} > \text{S}$ (data not shown). Example results for the derived daily component fluxes in 2010 are shown in Fig. 2. Overall R_s showed large seasonal fluctuations which reflected different periods of high R_a and R_h activity. Generally R_h was

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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 larger increases coinciding with the emergence of ECM fruiting bodies around September to October (Fig. 2). However, in autumn daily R_m showed marked declines during periods of high or even increasing R_r . Fluxes from the S treatments compared well to those measured from repeatedly cut (S_{cut}) treatments (see Fig. 2 inset).

3.3 Environmental conditions and treatment effects on soil moisture

In general, the site temperature is relatively mild (1961–1990 mean annual air temperature = 9.4 °C), and monthly rainfall usually quite evenly distributed through the year (~65 mm/month), although near surface soil moisture can be less than 30% in summer (Tables 1, 2 and Fig. 3). The first three years (2007–2009) of measurement showed annual air temperatures 0.8–1.2 °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. 4b). Consequently, average annual near surface soil moisture was high in the first two (~50% v/v) and lower (~40%) in the last two years with summer values reaching ~20% (Fig. 3).

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 soil moisture 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 soil moisture towards the drier RMS treatments. Although during mid-summer differences were significant (mostly between RMS and S treatments), the mean soil moisture difference was less than 10%, 16% (Table 2) and 10% (Fig. 3) in 2008, 2009 and

BGD

8, 3155–3201, 2011

Exploring the “overflow tap” theory

A. Heinemeyer et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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. 3).

5 3.4 Interannual and seasonal forest and soil C flux components

The CO₂ flux components of the forest showed large interannual differences (Table 3) with the range of GPP = 40% of the 4 year mean, and for R_{eco} a range of 30%. Overall, net C gain (represented by a negative NEE) during the first two years was much higher than during the latter two (Table 3), both following a cold winter. GPP declined over the
10 four years and in 2010 was 65% smaller than in 2007. Annual above ground respiration (R_{ab} ; see Sect. 2.4) varied considerably and annual NPP (see Sect. 2.4) 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
15 C flux components (Fig. 4). In contrast, annual R_{s} (range of 9%) and the ratio $R_{\text{h}}/R_{\text{s}}$ changed little (~ 0.44) between the 3 years (Table 3).

The four-year time-courses of daily GPP and R_{s} components are shown in Fig. 4 together with the key environmental drivers of air and soil surface temperature, precipitation and soil moisture. As expected for a deciduous temperate forest, average monthly
20 GPP peaked in summer, with values ranging from 1.2 to 1.8 mol m⁻² d⁻¹ (Fig. 4) and monthly values of 400 g C m⁻² (Table 4). Larger variations in daily R_{s} in summer usually coincided with changes in GPP, particularly during summer (Fig. 4). Importantly, in 2009 and 2010 the oak canopy experienced major defoliation by moth caterpillars in the spring (mostly *Tortrix viridana*, but also *Operophtera brumata*, Pitman et al., 2010) and
25 in 2010 there was a -3°C air frost period after budburst in mid May as well as considerable oak mildew (*Erysiphe alphitoides*) outbreak throughout August and September, noticeably reducing forest C flux components during spring and autumn (Fig. 4), and causing very low seasonal (Table 3) and annual (Table 4) GPP totals.

Exploring the “overflow tap” theory

A. Heinemeyer et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



The monthly contribution of R_h to total R_s (Fig. 5b) decreased from a peak in winter (~ 0.55) to a low in summer (~ 0.35) due to increased R_a (Fig. 5a). However, the timing of the seasonal increase and the relative contribution of R_a components (R_r , R_m) varied between the 3 years (Fig. 5) due to varying R_m contributions in spring and autumn and R_r in summer and autumn. R_m increased early and substantially in 2008, remained low through 2009 and, although late, was high again in 2010. Generally, the annual average R_s , R_a and R_h values, were quite constant over the 3 years (Fig. 6), 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. 5) and a sharp decline in R_r contributions to R_s (Fig. 5b) in August 2010 during the dry summer period (Fig. 4b), which did not affect R_h or R_m . On average annual R_r , R_m and R_h fluxes contributed 39, 18 and 43%, respectively (Fig. 6, Table 3).

In order to relate the C flux component activities and responses to the environmental conditions and vegetation activity, the data were grouped into seasonal and developmental periods (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. 5b). 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 CO₂ fluxes

The daily and seasonal changes in the (apparent) response of R_s and its components to soil temperature (T) and moisture were investigated. Overall, daily R_s increased substantially with near-surface (2 cm) temperature ($R_s = 0.50e^{0.12T}$) and showed an apparent Q_{10} for daily fluxes of 3.4 ± 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

BGD

8, 3155–3201, 2011

Exploring the “overflow tap” theory

A. Heinemeyer et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



strong temperature response ($[0.23 e^{0.14T}; Q_{10} = 3.9 \pm 1.1, R^2 = 0.7]$) and $[0.27 e^{0.10T}; Q_{10} = 2.7 \pm 1.0, R^2 = 0.7]$, respectively), the individual R_a components R_r ($0.13 e^{0.14T}$) and R_m ($0.05 e^{0.14T}$) showed higher but less strong temperature responses over all three years ($Q_{10} = 4.1 \pm 1.1, R^2 = 0.4$ and $4.0 \pm 1.1, R^2 = 0.2$), respectively. The analysis for different developmental periods (Table 5) showed less range in Q_{10} values for R_h and a mean of approximately 2.7 ± 1.2 throughout but with a peak in 2010, but R_a and its components varied considerably. Whereas there was no significant relationship of R_a components with temperature in all summers ($Q_{10} < 1 \pm 1.5, R^2 \sim 0$), R_a showed very high apparent Q_{10} values in winter ($Q_{10} \approx 10 \pm 1.2$), particularly after the cold 2009/10 winter. There was also a strong (apparent) temperature response ($Q_{10} > 10$) of both R_a components before and during tree budburst in 2008 and 2009, although mostly with low confidence ($R^2 < 0.5$) and large SE.

Overall, an analysis of monthly R_s and its components during 2010 (with available treatment soil moistures) revealed only weak responses to soil moisture (Fig. 7). Total R_s and its components declined at moisture contents above 0.5 (v/v), but these monthly values occurred in winter and early spring, when there were also low temperatures (Fig. 4). Moreover, R_r and R_m showed a slight CO_2 flux decline with decreasing soil moisture 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. 8) is 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 years 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. 8a–d). In contrast, R_h showed a maximum periodicity at 1 year and R_m a seasonal (~ 150 days) periodicity (Fig. 8e, f). Synoptic events (~ 30 -days) strongly influenced R_{ab} and were also present with lower energy for R_h and R_m .

BGD

8, 3155–3201, 2011

Exploring the “overflow tap” theory

A. Heinemeyer et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



The subsequent wavelet coherence analysis (WCA) revealed linkages between canopy C uptake (GPP) and R_s and its components (Fig. 9). Firstly, seasonal differences were evident in the temporal correlation of R_s , R_r and R_m components to GPP (Fig. 9). Secondly, the analysis revealed a mostly 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. 9b). 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. 9c, Table 7). 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 with GPP at the same time period (i.e. red and dark areas in Fig. 10). The percentage totals of significant temporal correlations (red areas in Fig. 9) for several periods (summarized in Table 6), revealed an overall pattern of a mostly fast 1-day linkage between R_a components (i.e. R_r and R_m) and GPP and again a slower temporal response of >32 days mostly with R_m 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 R_s components and GPP (Table 6). Finally, the phase relationships of the temporal correlation between GPP and the soil CO₂ 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 in phase with R_s (11 ± 3 h), R_r (11 ± 5 h), R_m (11 ± 4 h) suggesting a strong and fast control on R_s (Fig. 10).

Exploring the “overflow tap” theory

A. Heinemeyer et al.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[I◀](#)[▶I](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

4 Discussion

4.1 Soil respiration component fluxes and the forest C budget

For the first time, multi-year hourly time series of forest CO₂ flux separation were provided, fully accounting for both R_a components, R_r and R_m . However, any separation technique requires assessing the issues of root or mycorrhizal exclusion and disturbance effects. Our data showed that, firstly, mycorrhizal hyphae penetrated a 1 μ m 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. Moreover, the root exclusion caused an increase in soil moisture in the MS and S treatment by about 15% (v/v) and mostly during summer (Table 2, Fig. 3) compared to the RMS treatment (see Ngao et al., 2007), which was minimized by rainfall exclusion (e.g. Fig. 3). 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. Overall, R_s showed little response to the range of soil moisture found here (Fig. 7), yet during the 2010 summer dry periods both R_r and R_m showed a tendency for lower rates (Fig. 7), similar to previously reported R_m response to moisture in a pine forest (Heinemeyer et al., 2007). While severed roots were removed in this study, another artifact 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. However, the fluxes measured at the S_{cut} treatment with this input were not higher than those from the S treatment (Fig. 2). Clearly, there is no perfect separation method as yet and more innovative solutions may be needed. These data thus provide a unique dataset to test process level understanding, model assumptions and development. In the following the focus is on a first analysis of the environmental and canopy linkages of the R_s flux and its components.

Importantly, the R_s flux (Fig. 1) revealed unique seasonal variability, particularly during the growing season and independently of temperature, which was investigated

BGD

8, 3155–3201, 2011

Exploring the “overflow tap” theory

A. Heinemeyer et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Exploring the “overflow tap” theory

A. Heinemeyer et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



further by flux component separation. The flux separation revealed high seasonal variation in the contributions of R_s components (Figs. 2 and 5). The R_h contribution of $\sim 40\%$ 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 R_a decreases because of collar insertion (Heinemeyer et al., 2011). Another yet manual R_s component sampling study on clay-rich soils (Moyano et al., 2008) showed similar R_r ($\sim 45\%$) but lower R_m ($\sim 5\%$), reflecting possible differences in seasonal dynamics between forests as well as a possible influence of mycorrhizas not being fully excluded by the $1\ \mu\text{m}$ mesh used or mesh-bag enclosed cut roots adding to decomposition fluxes (e.g. Sayer and Tanner, 2010).

The mean annual C budget (Table 3) of this temperate deciduous oak forest of ~ 1700 and $\sim 700\ \text{g C m}^{-2}\ \text{yr}^{-1}$ for GPP and NPP, respectively, is similar to other studies in the UK (Thomas et al., 2010), Europe (Hibbard et al., 2005) and globally (Melillo et al., 1993; Luysaert et al., 2007), and for ECM dominated forests (Vargas et al., 2010a). However, this is the first time that it is possible 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 CUE varied considerably (0.36–0.51), but 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 0.5–0.8 agreed with estimates for another temperate deciduous forest by Knohl et al. (2008). GPP varied considerably between years (Table 3; Fig. 4), and 2009 and 2010 had low CUE (~ 0.4) and large R_{eco}/GPP ratios (0.83), possibly due to the cold preceding winter, but particularly due to considerable leaf losses (caterpillar, mildew and frost damage) in 2010. Furthermore, the 2010 summer showed a more typical summer soil drying period which reduced NEE ($\sim 35\%$ 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 strong R_h response, and during the

(warmer) growing season this relationship disappeared (Table 5). Such effects have been reported for coniferous forests (Lagergren et al., 2008) but not for deciduous systems using a long-term R_s record with hourly resolution and separated components. Over the year, daily R_a and R_m variation was much less temperature dependent (39% and 20%, respectively) than R_s , although when particular seasons were analysed (Table 5), some very high apparent Q_{10} values were found for both R_a components during the budburst period. Yet these R_a relationships were only weak (i.e. high SE and low R^2) and the issues of using apparent Q_{10} values are acknowledged (Davidson et al., 2006; Subke and Bahn, 2010). Overall, 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 different from the proposed global average of 1.4 (Mahecha et al., 2010). However, these large seasonal changes suggest: (1) individual temperature responses for R_a and R_h components (Hartley et al., 2007a); (2) R_a dependence on substrate availability (Davidson et al., 2006; Hartley et al., 2007b) and responses to above ground phenology as proposed by Sampson et al. (2007); and (3) potential increased exudates increasing soil microbial r-strategists' Q_{10} values (Yuste et al., 2007). More importantly, R_m also showed high 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.

4.3 Mycorrhizal respiration as an autotrophic component and response to 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

BGD

8, 3155–3201, 2011

Exploring the “overflow tap” theory

A. Heinemeyer et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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 mycorrhizas (Heinemeyer et al., 2006), preferentially allocating C to R_{ab} and R_r . This supports the concept of a plant regulated process (Fitter et al., 1998). However, in 2010 when NPP was even more reduced compared to 2009 (Table 3) there was a pronounced R_r reduction but not in R_m (Fig. 5), which 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 C cost under stress (Vargas, 2009). Notably, structural C costs for mycorrhizal hyphae are much lower per length than for roots albeit with similar maintenance respiration (Fitter, 1991).

The presented annual estimate of R_a of 60% together with the strong linkage of R_a components to GPP (Fig. 9) supports the importance of considering the R_s plant soil continuum as proposed by Högborg and Read (2006). 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., 2007). Importantly, although both roots and mycorrhizas showed a fast link to GPP, R_m revealed longer correlation periods (Fig. 9, Table 6). Moreover, although R_m was driven by GPP at longer temporal scales (Fig. 9) this may not be a direct relationship, as it could be driven by 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 independent GPP (Fig. 8). Importantly, R_m and R_h showed strong seasonal and annual periodicities, respectively (Fig. 8), which were not temporally coupled with GPP (Fig. 9; Table 6), suggesting a number of C sources for R_m metabolism such as litter decomposition. Further, seasonal analysis 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. 10). 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 (Table 6). Both observations support the idea of a

BGD

8, 3155–3201, 2011

Exploring the “overflow tap” theory

A. Heinemeyer et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



tree regulated “C overflow tap” based on available GPP (Heinemeyer et al., 2007). Although such GPP linkages (Tang et al., 2005; Liu et al., 2006) and large time lags of R_s to GPP (Vargas et al., 2010b) have been reported previously, here they are evident for R_s and R_a components. Our understanding of the underlying processes is still limited and can only be hypothesized. However, periods of marked GPP and NPP reductions were observed in 2010 (Tables 3 and 4) through climatic (late spring frosts) and biological (caterpillar and mildew pests) events with subsequently reduced or delayed R_r and R_m , respectively, which supports a “tree regulated” C allocation from canopy to below ground.

4.4 Implications for modelling forest C dynamics and soil respiration

Although temperature was a major determinant of R_s 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 apparent Q_{10} 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 underlined the importance of C reserves available to both roots and mycorrhizas, both processes supported by isotopic studies (Mencuccini and Hölttä, 2010) and C allocation and turnover studies (e.g. Högberg et al., 2008). Thus C cycle models could be improved by treating the individual R_s components separately allowing 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). However, two central questions remain to be explored: which is in control of plant C allocation to R_r and R_m , plant or fungus and what are the periodicities (seasonal differences) and implications for decomposition and soil decomposition priming? Mycorrhizal mesh-bags and collar exclusion techniques offer a valuable opportunity to assess these research needs in combination with radiocarbon (^{14}C) or stable isotopes (^{13}C). Clearly, more in situ research under different environmental conditions (e.g. average years versus disturbance year, i.e. Vargas, 2009,

BGD

8, 3155–3201, 2011

Exploring the “overflow tap” theory

A. Heinemeyer et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



and variable NPP due to canopy pests, i.e. Schäfer et al., 2010) is needed. 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 considered (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 such as the MYCOFON model (Meier et al., 2010), lag periods of GPP allocation to R_s components (Kuzyakov and Gavrichkova, 2010) and the potential priming by mycorrhizal C of 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 elevated temperatures and carbon dioxide, altering SOC dynamics directly and indirectly through changes in plant productivity.

5 Conclusion

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

1. Large (57%) overall R_a contribution (R_r 39%, R_m 18%) to a relatively constant annual R_s with considerable interannual and seasonal variability in the R_a component contributions.
2. Strong overall apparent Q_{10} 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 fluxes but also longer term periodicities in R_a components suggesting an internal root and mycorrhizal C storage pool and C-access of R_m through SOM and litter decomposition.

BGD

8, 3155–3201, 2011

Exploring the “overflow tap” theory

A. Heinemeyer et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Exploring the “overflow tap” theory

A. Heinemeyer et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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

5. An overall separation of periods of either high R_r or R_m correlation to GPP indicating R_m was controlled by plant needs.

5 The time series analysis identified periodicities and linkages to GPP that underpin fundamental forest C cycle processes, which have wide reaching implications for the key question of whether forests will continue to sequester CO_2 or whether increased GPP will result in increased respiration (Heath et al., 2005). The presented results indicate that the mycorrhizal flux component might well contribute to a C sequestration limitation, functioning as a “C overflow tap” (Heinemeyer et al., 2007) and potentially as a “fuel for priming” the turnover of SOC. However, further research is required to address specifically the sources of C available to the fungus, i.e. from decomposition versus an internal root or mycorrhizal C pool.

10

15 *Acknowledgements.* This work was carried out within the UK Centre for Terrestrial Carbon Dynamics, funded by the National Environment Research Council (NERC) funded, grant F14/G6/105. The Li-Cor LI-8100 soil respiration equipment was purchased through NERC special equipment grant NE/C513550/1. Special thanks go to the Electronics Workshop, Biology Department at the University of York for building the customised, multiplexed system. Forest Research kindly provided site access and support through Edward Eaton for field site maintenance and Rona Pitman for litter additions.

20

References

- Atkin, O. K., Edwards, E. J., and Loveys, B. R.: Response of root respiration to changes in temperature and its relevance to global warming, *New Phytol.*, 147, 141–154, 2000.
- Aubinet, M. and Heinesch, B.: Estimation of the carbon sequestration by a heterogeneous forest: night flux corrections, heterogeneity of the site and inter-annual variability, *Glob. Change Biol.*, 8, 1053–1071, 2002.
- 25

Aubinet, M., Grelle, A., Ibrom, A., Rannik, Ü., Moncrieff, J., Foken, T., Kowalski, A. S., Martin, P. H., Berbigier, P., Bernhofer, C., Clement, R., Elbers, J., Granier, A., Grünwald, T., Morgenstern, K., Pilegaard, K., Rebmann, C., Snijders, W., Valentini, R., and Vesala, T.: Estimates of the annual net carbon and water exchange of forests: the EUROFLUX methodology, *Adv. Ecol. Res.*, 30, 113–175, 2000.

5 Baggs, E. M.: Partitioning the components of soil respiration: a research challenge, *Plant Soil*, 284, 1–5, 2006.

Bolin, B., Sukumar, R., Ciais, P., Cramer, W., Jarvis, P., Kheshgi, H., Nobre, C., Semenov, S., and Steffen, W.: Global Perspective, in: IPCC, Land Use, Land-Use Change, and Forestry. A Special Report of the IPCC, edited by: Watson, R. T., Noble, I. R., Bolin, B., Ravindranath, N. H., Verardo, D. J., and Dokken, D. J., pp. 23–51, Cambridge University Press, Cambridge, UK, 2000.

Bond-Lamberty, B. and Thomson, A.: A global database of soil respiration data, *Biogeosciences*, 7, 1915–1926, doi:10.5194/bg-7-1915-2010, 2010.

15 Bond-Lamberty, B., Wang, C. K., and Gower, S. T.: A global relationship between the heterotrophic and autotrophic components of soil respiration?, *Glob. Change Biol.*, 10, 1756–1766, 2004.

Coutry, P.-E., Buée, M., Diedhiou, A. G., Frey-Klett, P., Le Tacon, F., Rineau, F., Turpault, M.-P., Uroz, S., and Garbaye, J.: The role of ectomycorrhizal communities in forest ecosystem processes: New perspectives and emerging concepts, *Soil Biol. Biochem.*, 42, 679–698, 2010.

20 Cox, P. M., Betts, R. A., Jones, C. D., Spall, S. A., and Totterdell, I. J.: Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model, *Nature*, 408, 184–187, 2000.

25 Daubechies, I.: The wavelet transform, time-frequency localization and signal analysis, *IEEE T. Inform. Theory*, 36, 961–1005, 1990.

Davidson, E. A., Janssens, I. A., and Luo, Y.: On the variability of respiration in terrestrial ecosystems moving beyond Q_{10} , *Glob. Change Biol.*, 12, 154–164, 2006.

30 Ekblad, A., Boström, B., Holm, A., and Comstedt, D.: Forest soil respiration rate and delta C-13 is regulated by recent above ground weather conditions, *Oecologia*, 143, 136–142, 2005.

Fenn, K., Malhi, Y., and Morecroft, M.: Soil CO₂ efflux in a temperate deciduous forest: Environmental drivers and component contributions, *Soil Biol. Biochem.*, 42, 1685–1693, 2010.

Fitter, A. H.: Costs and benefits of mycorrhizas: Implications for functioning under natural

BGD

8, 3155–3201, 2011

Exploring the “overflow tap” theory

A. Heinemeyer et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Exploring the “overflow tap” theory

A. Heinemeyer et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



conditions, *Experientia*, 47, 350–355, 1991.

Fitter, A. H., Graves, J. D., Watkins, N. K., Robinson, D., and Scrimgeour, C.: Carbon transfer between plants and its control in networks of arbuscular mycorrhizas, *Funct. Ecol.*, 12, 406–412, 1998.

5 Fitter, A. H., Heinemeyer, A., Husband, R., Olsen, E., Ridgway, K. P., and Staddon, P. L.: System responses to environmental change: the mycorrhizal component, *Can. J. Bot.*, 82, 1–7, 2004.

Fontaine, S., Henault, C., Aamor, A., Bdioui, N., Bloor, J. M. G., Maire, V., Mary, B., Revallot, S., and Maron, P. A.: Fungi mediate long term sequestration of carbon and nitrogen in soil through their priming effect, *Soil Biol. Biochem.*, 43, 86–96, 2011.

10 Govindan, R. B., Raethjen, J., Kopper, F., Claussen, J. C., and Deuschl, G.: Estimation of time delay by coherence analysis, *Physica A.*, 350, 277–295, 2005.

Grace, J. and Rayment, M.: Respiration in the balance, *Nature*, 404, 819–820, 2000.

Grinsted, A., Moore, J. C., and Jevrejeva, S.: Application of the cross wavelet transform and wavelet coherence to geophysical time series, *Nonlin. Processes Geophys.*, 11, 561–566, doi:10.5194/npg-11-561-2004, 2004.

Hanson, P. J., Edwards, N. T., Garten, C. T., and Andrews, J. A.: Separating root and soil microbial contributions to soil respiration from total soil respiration: a review of methods and observations, *Biogeochemistry*, 48, 115–146, 2000.

20 Hartley, I. P., Heinemeyer, A., Evans, S. P., and Ineson, P.: The effect of soil warming on bulk soil versus rhizosphere respiration, *Glob. Change Biol.*, 13, 2654–2667, 2007a.

Hartley, I. P., Heinemeyer, A., and Ineson, P.: Effects of three years of soil warming and shading on the rate of soil respiration: substrate availability and not thermal acclimation mediates observed response, *Glob. Change Biol.*, 13, 1761–1770, 2007b.

25 Heath, J., Ayres, E., Possel, M., Bardgett, R. D., Black, H. I. J., Grant, H., Ineson, P., and Kerstiens, G.: Rising atmospheric CO₂ reduces sequestration of root-derived soil carbon, *Science*, 309, 1711–1713, 2005.

Heinemeyer, A., Ineson, P., Ostle, N., and Fitter, A. H.: Respiration of the external mycelium in the arbuscular mycorrhizal symbiosis shows strong dependence on recent photosynthates and acclimation to temperature, *New Phytol.*, 171, 159–170, 2006.

30 Heinemeyer, A., Hartley, I. P., Evans, S. P., Carreira de la Fuente, J. A., and Ineson, P.: Forest soil CO₂ flux: uncovering the contribution and environmental responses of ectomycorrhizas, *Glob. Change Biol.*, 13, 1786–1797, 2007.

Exploring the “overflow tap” theory

A. Heinemeyer et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



- Heinemeyer, A., Di Bene, C., Lloyd, A. R., Tortorella, D., Baxter, R., Huntley, B., Gelsomino A., and Ineson, P.: Soil respiration: implications of the plant-soil continuum and respiration chamber collar-insertion depth on measurement and modelling of soil CO₂ efflux rates in three ecosystems, *Eur. J. Soil Sci.*, 62, 82–94, 2011.
- 5 Hibbard, K. A., Law, B. E., Reichstein, M., and Sulzman, J.: An analysis of soil respiration across Northern Hemisphere temperate ecosystems, *Biogeochemistry*, 73, 29–70, 2005.
- Högberg, P. and Read, D. J.: Towards a more plant physiological perspective on soil ecology, *TRENDS in Ecol. Evol.*, 21, 548–554, 2006.
- Högberg, P., Högberg, M. N., Göttlicher, S. G., Betson, N. R., Keel, S. G., Metcalfe, D. B.,
10 Campbell, C., Schindlbacher, A., Hurry, V., Lundmark, T., Linder, S., and Näsholm, T.: High temporal resolution tracing of photosynthate carbon from the tree canopy to forest soil microorganisms, *New Phytol.*, 177, 220–228, 2008.
- Kirschbaum, M. U. F.: Will changes in soil organic matter act as a positive or negative feedback on global warming?, *Biogeochemistry*, 48, 21–51, 2000.
- 15 Kirschbaum, M. U. F.: The temperature dependence of organic-matter decomposition – still a topic of debate, *Soil Biol. Biochem.*, 38, 2510–2518, 2006.
- Knohl, A., Søe, A. R. B., Kutsch, W. L., Göckede, M., and Buchmann N.: Representative estimates of soil and ecosystem respiration in an old beech forest, *Plant Soil*, 302, 189–202, 2008.
- 20 Kormann, R. and Meixner, F. X.: An analytical footprint model for non-neutral stratification, *Bound.-Lay. Meteorol.*, 99, 207–224, 2001.
- Kutsch, W., Bahn, M., and Heinemeyer, A.: Soil carbon relations – an overview, in: *Soil Carbon Dynamics: An Integrated Methodology*, edited by: Kutsch, W., Bahn, M., and Heinemeyer, A., Cambridge University Press, ISBN: ISBN-13: 9780521865616, 2009.
- 25 Kuzyakov, Y.: Response: Object- versus method-oriented terminology, *Soil Biol. Biochem.*, 38, 2999–3000, 2006a.
- Kuzyakov, Y.: Sources of CO₂ efflux from soil and review of partitioning methods, *Soil Biol. Biochem.*, 38, 425–448, 2006b.
- Kuzyakov, Y. and Gavrishkova, O.: Time lag between photosynthesis and carbon dioxide efflux from soil: a review of mechanisms and controls, *Glob. Change Biol.*, 16, 3386–3406, 2010.
- 30 Lagergren, F., Lindroth, A., Dellwik, E., Ibrom, A., Lankreijer, H., Launiainen, S., Mölder, M., Kolari, P., Pilegaard, K., and Vesala, T.: Biophysical controls on CO₂ fluxes of three Northern forests based on long-term eddy covariance data, *Tellus B*, 60, 143–152, 2008.

- Lasslop, G., Reichstein, M., Papale, D., Richardson, A. D., Arneeth, A., Barr, A., Stoy, P., and Wohlfahrt, G.: Separation of net ecosystem exchange into assimilation and respiration using a light response curve approach: critical issues and global evaluation, *Glob. Change Biol.*, 16, 187–208, 2010.
- 5 Leake, J., Johnson, D., Donnelly, D., Muckle, G., Boddy, L., and Read, D.: Networks of power and influence: the role of mycorrhizal mycelium in controlling plant communities and agroecosystem functioning, *Can. J. Bot.*, 82, 1016–1045, 2004.
- Leuning, R. and Moncrieff, J.: Eddy-covariance CO₂ flux measurements using open- and closed-path CO₂ analysers: corrections for analysers water vapour sensitivity and dampening of fluctuations in air sampling tubes, *Bound-Lay. Meteorol.*, 53, 63–76, 1990.
- 10 Lindahl, B. D., Ihrmark, K., Boberg, J., Trumbore, S. E., Högberg, P., Stenlid, J., and Finlay, R. D.: Spatial separation of litter decomposition and mycorrhizal nitrogen uptake in a boreal forest, *New Phytol.*, 173, 611–620, 2007.
- Liu, Q., Edwards, N. T., Post, W. M., Gu, L., Ledford, J., and Lenhart, S.: Temperature-independent diel variation in soil respiration observed from a temperate deciduous forest, *Glob. Change Biol.*, 12, 1–10, 2006.
- 15 Luysaert, S., Inglima, I., Jung, M., Richardson, A. D., Reichstein, M., Papale, D., Paio, S. L., Schulze, E.-D., Wingate, L., Matteucci, G., Aragao, L., Aubinet, M., Beer, C., Bernhofer, C., Black, K. G., Bonal, D., Bonnefond, J.-M., Chambers, J., Ciais, P., Cook, B., Davis, K. J., Dolman, A. J., Gielen, B., Goulden, M., Grace, J., Granier, A., Grelle, A., Griffis, T., Grunwald, T., Guidolotti, G., Hanson, P. J., Harding, R., Hollinger, D. Y., Hutyra, L. R., Kolari, P., Kruijt, B., Kutsch, W., Lagergren, F., Laurila, T., Law, B. E., Maire, G. L., Lindroth, A., Loustau, D., Malhi, Y., Mateus, J., Migliavacca, M., Misson, L., Montagnani, L., Moncrieff, J., Moors, E., Munger, J. W., Nikinmaa, E., Ollinger, S. V., Pita, G., Rebmann, C., Rouspard, O., Saigusa, N., Sanz, M. J., Seufert, G., Sierra, C., Smith, M.-L., Tang, J., Valentini, R., Vesala, T., and Janssens, I. A.: CO₂ balance of boreal, temperate, and tropical forests derived from a global database, *Glob. Change Biol.*, 13, 2509–2537, 2007.
- 20 Mahecha, M. D., Reichstein, M., Carvalhais, N., Lasslop, G., Lange, H., Seneviratne, S. I., Vargas, R., Ammann, C., Arain, M. A., and Cescatti, A.: Global Convergence in the temperature sensitivity of respiration at ecosystem level, *Science*, 329, 838–840, 2010.
- Massman, W. J.: The attenuation of concentration fluctuations in turbulent flow through a tube, *J. Geophys. Res.*, 96D, 15269–15273, 1991.
- 25 Melillo, J. M., McGuire, A. D., Kicklighter, D. W., Moore III, B., Corosmarty, C. J., and Schloss,

BGD

8, 3155–3201, 2011

**Exploring the
“overflow tap” theory**

A. Heinemeyer et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Exploring the “overflow tap” theory

A. Heinemeyer et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



A. L.: Global climate change and terrestrial net primary productivity, *Nature*, 363, 234–240, 1993.

Mencuccini, M. and Hölttä, T.: The significance of phloem transport for the speed with which canopy photosynthesis and belowground respiration are linked, *New Phytol.*, 185, 189–203, 2010.

Moncrieff, J. B., Massheder, J. M., Verhoef, A., Elbers, J., Heutsunkveld, B. H., Scott, S., de Bruin, H., Kabat, P. Soegaard, H., and Jarvis, P. G.: A system to measure surface fluxes of energy, momentum and carbon dioxide, *J. Hydrology*, 188–189, 589–611, 1997.

Moyano, F. E., Kutsch, W. L., and Rebmann, C.: Soil respiration in relation to photosynthetic activity in broad-leaf and needle-leaf forest stands, *Agr. Forest Meteorol.*, 148, 135–143, 2008.

Ngao, J., Longdoz, B., Granier, A., and Epron, D.: Estimation of autotrophic and heterotrophic components of soil respiration by trenching is sensitive to corrections for root decomposition and changes in soil water content, *Plant Soil*, 301, 99–110, 2007.

Pitman, R. M., Vanguelova, E. I., and Benham, S. E.: The effects of phytophagous insects in water and soil nutrient concentrations and fluxes through forest stands of the Level II monitoring network in the UK, *Sci. Tot. Environ.*, 409, 169–181, 2010.

Raich, J. W. and Potter, C. S.: Global patterns of carbon dioxide emissions from soils, *Global Biogeochem. Cycles*, 9, 23–36, 1995.

Reichstein, M., Falge, E., Baldocchi, D., Papale, D., Valentini, R., Aubinet, M., Berbigier, P., Bernhofer, C., Buchmann, N., Gilmanov, T., Granier, A., Grünwald, T., Havránková, K., Janous, D., Knohl, A., Laurela, T., Lohila, A., Loustau, D., Matteucci, G., Meyers, T., Miglietta, F., Ourcival, J.-M., Rambal, S., Rotenberg, E., Sanz, M., Seufert, G., Vaccari, F., Vesala, T., and Yakir, D.: On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm, *Glob. Change Biol.*, 11, 1–16, 2005.

Rygielwicz, P. T. and Andersen, C. P.: Mycorrhizae alter quality and quantity of carbon allocated below ground, *Nature*, 369, 58–60, 1994.

Sampson, D. A., Janssens, I. A., Yuste, J. C., and Ceulemans, R.: Basal rates of soil respiration are correlated with photosynthesis in a mixed temperate forest, *Glob. Change Biol.*, 13, 2008–2017, 2007.

Sayer, E. J. and Tanner, E. V. J.: A new approach to trenching experiments for measuring root-rhizosphere respiration in a lowland tropical forest, *Soil Biol. Biochem.*, 42, 347–352, 2010.

- Schäfer, K. V. R., Clark, K. L., Skowronski, N., and Hamerlynck, E. P.: Impact of insect defoliation on forest carbon balance as assessed with a canopy assimilation model, *Glob. Change Biol.*, 16, 546–560, 2010.
- Schimel, D. S., Braswell, B. H., Holland, E. A., Mckeown, R., Ojima, D. S., Painter, T. H., Parton, W. J., and Townsend, A. R.: Climatic, edaphic, and biotic controls over storage and turnover of carbon in soils, *Glob. Biogeochem. Cycles*, 8, 279–293, 1994.
- Schlesinger, W. H. and Andrews, J. A.: Soil respiration and the global carbon cycle, *Biogeochemistry*, 48, 7–20, 2000.
- Smith, P. and Fang, C.: A warm response by soils, *Nature*, 464, 499–500, 2010.
- Söderström, B. and Read, D. J.: Respiratory activity of intact and excised ectomycorrhizal mycelial systems growing in unsterilized soil, *Soil Biol. Biochem.*, 19, 231–236, 1987.
- Subke, J.-A. and Bahn, M.: On the ‘Temperature Sensitivity’ of soil respiration: Can we use the immeasurable to predict the unknown?, *Soil Biol. Biochem.*, 42, 1653–1656, 2010.
- Subke, J.-A., Inglima, I., and Cotrufo, F.: Trends and methodological impacts in soil CO₂ efflux partitioning: A metaanalytical review, *Glob. Change Biol.*, 12, 1–23, 2006.
- Sulzman, E. W., Brant, J. B., Bowden, R. D., and Lajtha, K.: Contribution of aboveground litter, belowground litter, and rhizosphere respiration to total soil CO₂ efflux in an old growth coniferous forest, *Biogeochemistry*, 73, 231–256, 2005.
- Talbot, J. M., Allison, S. D., and Treseder, K. K.: Decomposers in disguise: mycorrhizal fungi as regulators of soil C dynamics in ecosystems under global change, *Functional Ecology*, 22, 955–963, 2008.
- Tang, J., Baldocchi, D., and Xu, L.: Tree photosynthesis modulates soil respiration on a diurnal time scale, *Glob. Change Biol.*, 11, 1298–1304, 2005.
- Tarnocai, C., Canadell, J. G., Schuur, E. A. G., Kuhry, P., Mazhitova, G., and Zimov, S.: Soil organic carbon pools in the northern circumpolar permafrost region, *Glob. Biogeochem. Cycles*, 23, GB2023, doi:10.1029/2008gb003327, 2009.
- Thomas, M. V., Malhi, Y., Fenn, K. M., Fisher, J. B., Morecroft, M. D., Lloyd, C. R., Taylor, M. E., and McNeil, D. D.: Carbon dioxide fluxes over an ancient broadleaved deciduous woodland in southern England, *Biogeosciences Discuss.*, 7, 3765–3814, doi:10.5194/bgd-7-3765-2010, 2010.
- Torrence, C. and Compo, G. P.: A practical guide to wavelet analysis, *B. Am. Meteorol. Soc.*, 79, 61–78, 1998.
- Vargas, R.: On the fate of old stored carbon after large-infrequent disturbances in plants, *Plant*

BGD

8, 3155–3201, 2011

Exploring the “overflow tap” theory

A. Heinemeyer et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Sig. Beh., 4(7), 617–619, 2009.

Vargas, R., Baldocchi, D. D., Querejeta, J. I., Curtis, P. S., Hasselquist, N. J., Janssens, I. A., Allen, M. F., and Montagnani, L.: Ecosystem CO₂ fluxes of arbuscular and ectomycorrhizal dominated vegetation types are differentially influenced by precipitation and temperature, *New Phytol.*, 185, 226–236, 2010a.

Vargas, R., Detto, M., Baldocchi, D. D., and Allen, M. F.: Multiscale analysis of temporal variability of soil CO₂ production as influenced by weather and vegetation, *Glob. Change Biol.*, 16, 1589–1605, 2010b.

Yuste, J. C., Baldocchi, D. D., Gershenson, A., Goldstein, A., Misson, L., and Wong, S.: Microbial soil respiration and its dependency on carbon inputs, soil temperature and moisture, *Glob. Change Biol.*, 13, 1–18, 2007.

BGD

8, 3155–3201, 2011

**Exploring the
“overflow tap” theory**

A. Heinemeyer et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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 CO₂ flux chambers (T_{chamb}) together with soil moisture (SM) at 6 cm in the mineral layer, and precipitation sums (Precip). The 30-year long-term averages are provided for comparison; n.a. indicates data not available.

	T_{air}	T_{chamb}	Precip	SM
Month	(°C)	(°C)	(mm)	(%)
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-year (1961–1990)	9.4	n.a.	780	n.a.

**Exploring the
“overflow tap” theory**

A. Heinemeyer et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Table 2. Soil moisture (%) measured in each of 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 \pm s.d.; significant differences between treatments are indicated by different letters, based on a one-way ANOVA (n.s. = non 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	\pm 0.01	B	0.43	\pm 0.03		0.51	\pm 0.02	C	
MS	0.41	\pm 0.05	B	0.48	\pm 0.05		0.59	\pm 0.08	AB	
S	0.50	\pm 0.01	A	0.50	\pm 0.01		0.62	\pm 0.02	A	
S_{cut}	0.42	\pm 0.05	B	0.47	\pm 0.03		0.60	\pm 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	\pm 0.02	C	0.50	\pm 0.04	B	0.37	\pm 0.05	B	0.45	\pm 0.11	
MS	0.57	\pm 0.05	C	0.57	\pm 0.05	A	0.54	\pm 0.06	A	0.58	\pm 0.10	
S	0.63	\pm 0.01	A	0.62	\pm 0.02	A	0.60	\pm 0.02	A	0.63	\pm 0.02	
S_{cut}	0.61	\pm 0.01	AB	0.59	\pm 0.04	A	0.58	\pm 0.03	A	0.53	\pm 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	\pm 0.00	B	0.58	\pm 0.01	B	0.57	\pm 0.02	B	0.55	\pm 0.02	B	0.46	\pm 0.02	B
MS	0.61	\pm 0.05	AB	0.61	\pm 0.05	AB	0.61	\pm 0.03	AB	0.59	\pm 0.02	A	0.53	\pm 0.01	A
S	0.65	\pm 0.03	A	0.65	\pm 0.04	A	0.63	\pm 0.01	A	0.61	\pm 0.02	A	0.56	\pm 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	\pm 0.03	B	0.26	\pm 0.02	C	0.24	\pm 0.02	B	0.26	\pm 0.03	B	0.32	\pm 0.04	B
MS	0.46	\pm 0.01	A	0.34	\pm 0.02	B	0.29	\pm 0.01	A	0.33	\pm 0.01	A	0.37	\pm 0.02	AB
S	0.46	\pm 0.01	A	0.38	\pm 0.01	A	0.32	\pm 0.01	A	0.34	\pm 0.01	A	0.39	\pm 0.01	A

Title Page

Abstract Introduction

Conclusions References

Tables Figures

◀ ▶

◀ ▶

Back Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Exploring the
“overflow tap” theory

A. Heinemeyer et al.

Table 4. Monthly ecosystem C fluxes for gross primary productivity (GPP) and soil respiration fluxes (in $\text{g C m}^{-2} \text{month}^{-1}$) 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), soil moisture (SM) and the corresponding C flux ratios. Soil respiration (R_s) component fluxes included replacements of missing values due to late start of monitoring by temperature regression (shown in grey; n.a. denotes no data available). Phenological periods (for 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.

	Period	Phenology	T_{air} °C	Precip mm	SM %	GPP g C m^{-2}	R_s/R_{eco} ratio	R_s g C m^{-2}	R_r g C m^{-2}	R_m g C m^{-2}	R_a g C m^{-2}	R_h g C m^{-2}
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

Title Page

Abstract Introduction

Conclusions References

Tables Figures

◀ ▶

◀ ▶

Back Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Table 5. Seasonal and annual average apparent Q_{10} values (with \pm SE and R^2 in grey) for 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 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 and abbreviations given 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	

Title Page

Abstract Introduction

Conclusions References

Tables Figures

◀ ▶

◀ ▶

Back Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Exploring the “overflow tap” theory

A. Heinemeyer et al.

Title Page

Abstract Introduction

Conclusions References

Tables Figures

◀ ▶

◀ ▶

Back Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Table 6. Percentage of days with significant temporal correlations between gross primary production (GPP) and total soil respiration rate (R_s) and its components root (R_r) and mycorrhizal (R_m) respiration at the Straits Enclosure, Alice Holt forest from 2007 to 2010. Correlations calculated at multiple periods (1- to 128-days) for each year and over the entire experiment. See Table 3 for abbreviations; n.a. denotes no data available.

Period		Percent of significant days			Period		Percent of significant day		
(days)	Years	GPP- R_s	GPP- R_r	GPP- R_m	(days)	Years	GPP- R_s	GPP- R_r	GPP- R_m
1	2007	10.9	n.a.	n.a.	16	2007	0.0	n.a.	n.a.
	2008	13.4	10.3	13.2		2008	0.0	0.0	0.0
	2009	9.2	9.5	9.0		2009	0.1	1.8	0.8
	2010	9.6	7.8	8.9		2010	0.7	1.4	0.0
	Total	43.0	27.6	31.1		Total	0.9	3.3	0.8
2	2007	1.6	n.a.	n.a.	32	2007	0.9	n.a.	n.a.
	2008	2.5	3.0	0.1		2008	8.8	4.1	3.8
	2009	1.5	2.1	2.9		2009	1.6	6.4	15.0
	2010	1.9	0.7	2.8		2010	0.0	0.0	0.0
	Total	7.4	5.7	5.7		Total	11.3	10.5	18.8
4	2007	0.9	n.a.	n.a.	64	2007	0.0	n.a.	n.a.
	2008	2.1	0.9	2.3		2008	0.0	0.0	0.0
	2009	1.3	2.6	2.0		2009	0.0	11.1	18.0
	2010	1.5	1.0	0.5		2010	0.0	0.0	0.0
	Total	5.8	4.5	4.8		Total	0.0	11.1	18.0
8	2007	1.4	n.a.	n.a.	128	2007	8.3	n.a.	n.a.
	2008	1.9	1.7	1.4		2008	11.5	0.0	0.0
	2009	3.0	2.1	3.8		2009	0.0	0.0	0.0
	2010	0.7	0.2	3.0		2010	0.0	0.0	4.9
	Total	7.1	4.0	8.2		Total	19.8	0.0	4.9



Exploring the
“overflow tap” theory

A. Heinemeyer et al.

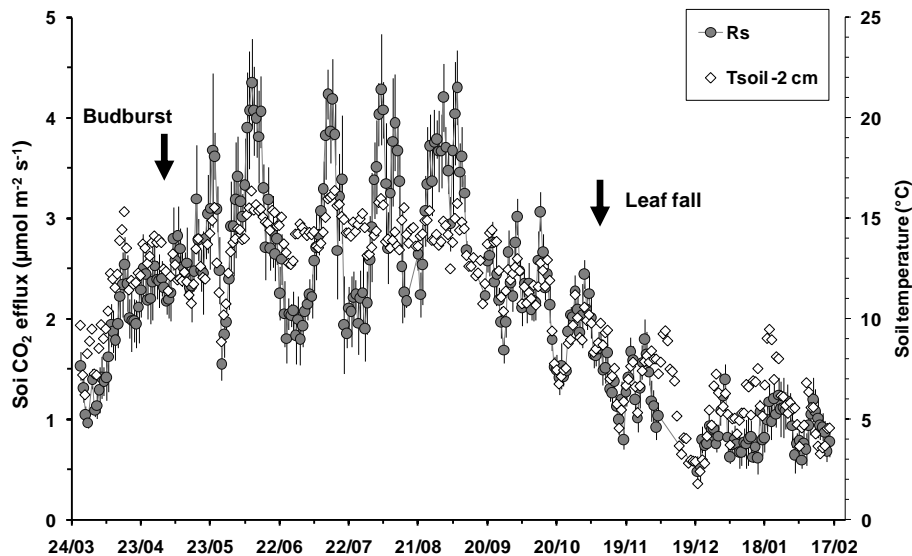


Fig. 1. Mean daily CO_2 efflux from soil respiration (R_s) measured from surface collars and soil temperature (T_{soil}) at 2 cm depth at the Straits Enclosure, Alice Holt forest from 24 March 2007 to 17 February 2008. Bars indicate \pm s.d. ($n = 12$ until 18 September and thereafter $n = 4$), and arrows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

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Exploring the
“overflow tap” theory

A. Heinemeyer et al.

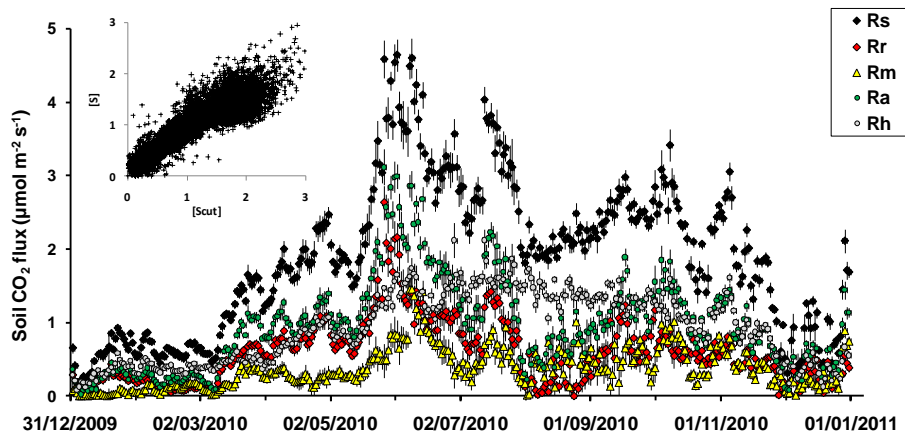


Fig. 2. Mean (\pm SE) daily soil CO₂ flux for total soil respiration (R_s) and its components (i.e. root (R_r), mycorrhizal (R_m) and heterotrophic (R_h) flux) at the Straits Enclosure, Alice Holt forest as derived from hourly flux measurements during 2010 from the different treatment plots ($n = 4$). 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.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



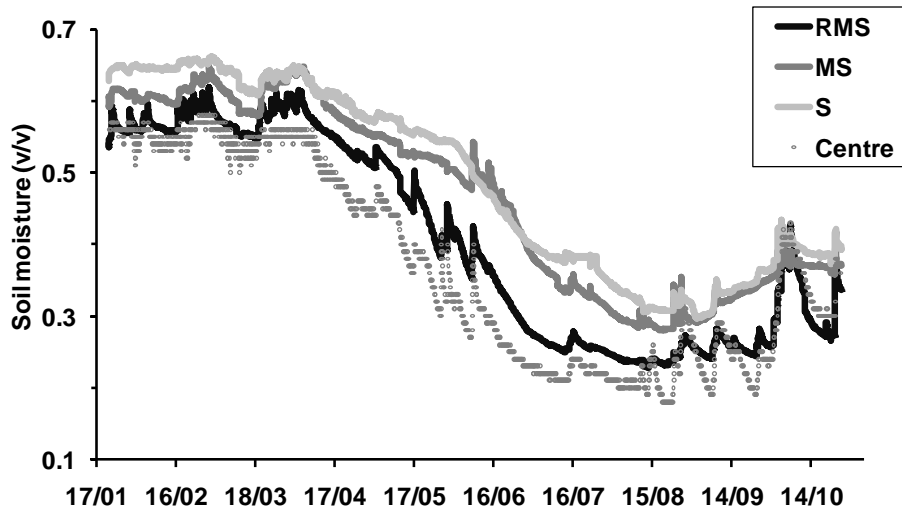


Fig. 3. Seasonal changes of soil moisture (v/v) at the Straits Enclosure, Alice Holt forest in 2010 measured hourly at 6 cm depth for three replicated ($n = 4$) soil collar treatments (surface collar, RMS), mycorrhizal 41 μ m mesh bag (MS) and steel collar (S) and in the undisturbed central area (Centre). The average SE was ~ 0.02 (v/v) for all treatments (not shown for clarity).

**Exploring the
“overflow tap” theory**

A. Heinemeyer et al.

Title Page

Abstract Introduction

Conclusions References

Tables Figures

◀ ▶

◀ ▶

Back Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Exploring the
“overflow tap” theory

A. Heinemeyer et al.

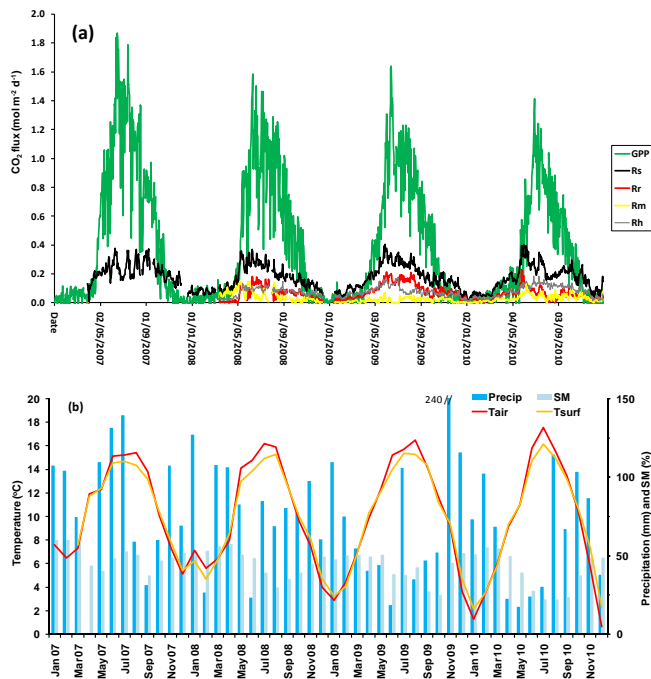


Fig. 4. (a) Mean daily ecosystem CO₂ flux components (mol m⁻² d⁻¹) at the Straits Enclosure, Alice Holt forest from 2007 to 2010, comprising gross primary productivity (GPP) and total soil respiration (R_s), and contributions from roots (R_r), mycorrhizal hyphae (R_m) and heterotrophic soil respiration (R_h). (b) Monthly average air temperature (T_{air}), soil surface temperature (T_{surf}), precipitation sum (Precip) and soil moisture (SM) during the same period.

Exploring the
“overflow tap” theory

A. Heinemeyer et al.

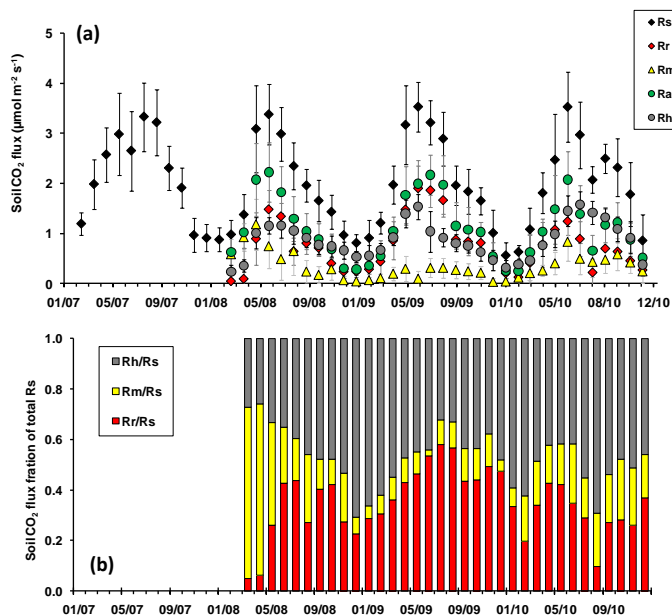


Fig. 5. (a) Monthly mean CO₂ efflux from soil respiration (R_s), and contributions from roots (R_r), mycorrhizal hyphae (R_m), autotrophic ($R_a = R_r + R_m$) and heterotrophic soil fluxes (R_h) at the Straits Enclosure, Alice Holt forest from 2007 to 2010. Separated flux components were only available from March 2008. Shown are averages \pm s.d. ($n = 4$). (b) Monthly CO₂ flux component fractions (e.g. R_h/R_s).

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



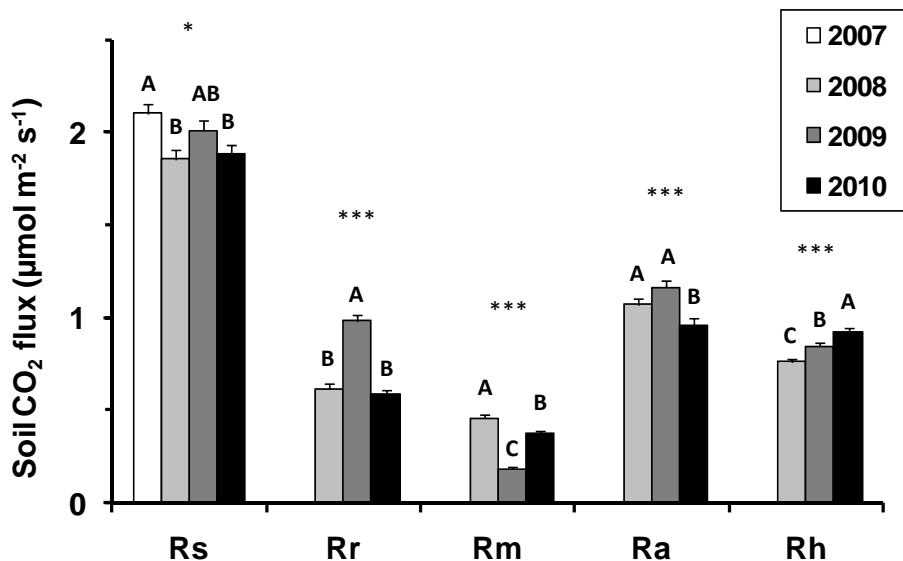


Fig. 6. Annual average rates of soil respiration (R_s), and contributions from roots (R_r), mycorrhizal hyphae (R_m), autotrophic ($R_a = R_r + R_m$) and heterotrophic soil fluxes (R_h) at the Straits Enclosure, Alice Holt forest from 2007 (for components only from 2008) to 2010. Shown are averages \pm SE ($n = 4$). Statistically significant differences between years for each component are indicated with different letters, calculated from Tukey’s B post-hoc test, with overall ANOVA P-values shown (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$).

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



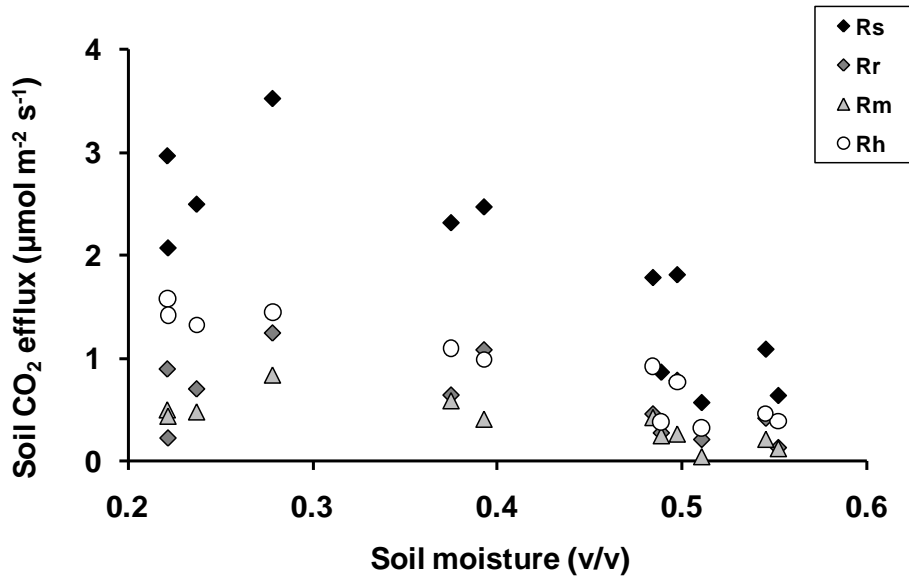


Fig. 7. Monthly average total soil respiration (R_s) and its components, i.e. root (R_r), mycorrhizal hyphae (R_m) and heterotrophic (R_h) respiration at the Straits Enclosure, Alice Holt forest during 2010, against the mean volumetric soil moisture (v/v) measured at 6 cm mineral soil depth in the individual treatments.

Exploring the
“overflow tap” theory

A. Heinemeyer et al.

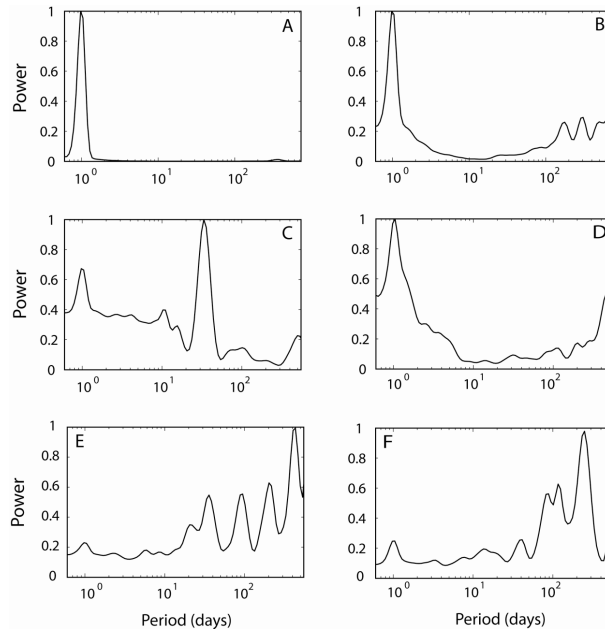


Fig. 8. Global wavelet power spectrum of individual (temperature independent) hourly CO_2 fluxes of GPP (**A**), R_s (**B**), R_{ab} (**C**), R_r (**D**), R_h (**E**), and R_m (**F**) at the Straits Enclosure, Alice Holt forest from 2007 to 2010. Note that the Nyquist theorem states that only half the length of the time series can be interpreted correctly, thus only 1.5 years are shown.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



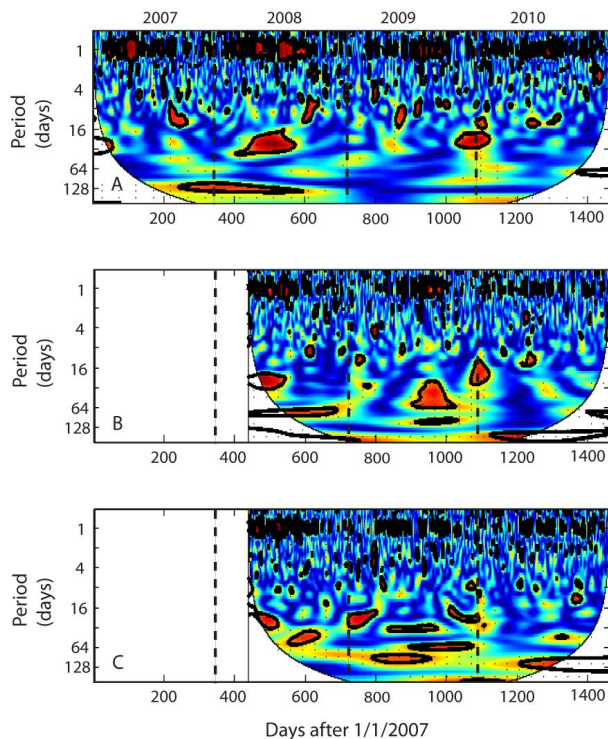


Fig. 9. Wavelet coherence analysis (WCA) output showing temporal correlation over four years (2007–2010) between GPP and the temperature independent soil CO₂ efflux, R_s (**A**) and its components, R_r (**B**) and R_m (**C**) at the Straits Enclosure, Alice Holt forest. The shades for power values are 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.

**Exploring the
“overflow tap” theory**

A. Heinemeyer et al.

Title Page	
Abstract	Introduction
Conclusions	References
Tables	Figures
◀	▶
◀	▶
Back	Close
Full Screen / Esc	
Printer-friendly Version	
Interactive Discussion	



Exploring the
“overflow tap” theory

A. Heinemeyer et al.

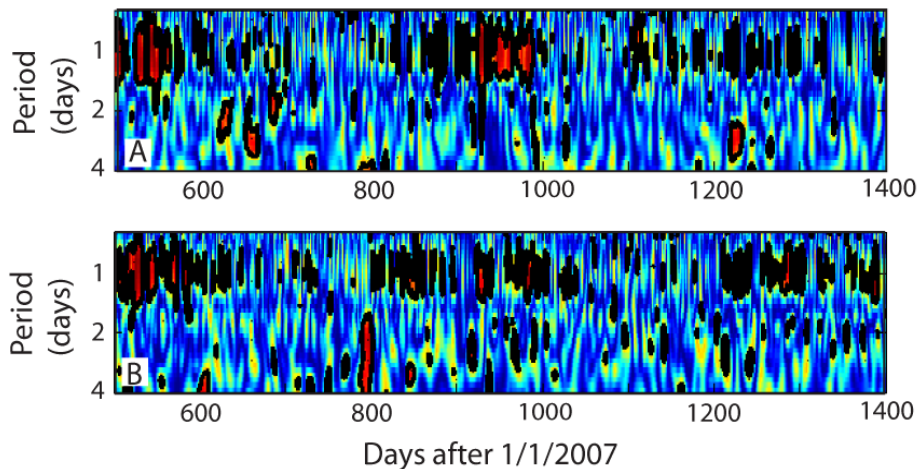


Fig. 10. Wavelet coherence analysis (WCA) output showing temporal correlation between GPP and the temperature independent soil CO₂ efflux, R_s and its components: R_r (**A**) and R_m (**B**) for the enlarged 1-day to 4-day periods as in Fig. 9.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[I◀](#)[▶I](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)